Part 3

Communities and Ecosystems

Introduction

In nature, areas of land and volumes of water contain assemblages of different species, in different proportions and doing different things. These communities of organisms have properties that are the sum of the properties of the individual denizens plus their interactions. The interactions are what make the community more than the sum of its parts. Just as it is a reasonable aim for a physiologist to study the behavior of different sorts of cells and tissues and then attempt to use a knowledge of their interactions to explain the behavior of a whole organism, so ecologists may use their knowledge of interactions between organisms in an attempt to explain the behavior and structure of a whole community. Community ecology, then, is the study of patterns in the structure and behavior of multispecies assemblages. Ecosystem ecology, on the other hand, is concerned with the structure and behavior of the same systems but with a focus on the flux of energy and matter.

We consider first the nature of the community. Community ecologists are interested in how groupings of species are distributed, and the ways these groupings can be influenced by both abiotic and biotic environmental factors. In Chapter 16 we start by explaining how the structure of communities can be measured and described, before focusing on patterns in community structure in space, in time and finally in a more complex, but more realistic spatiotemporal setting.

Communities, like all biological entities, require matter for their construction and energy for their activities. We examine the ways in which arrays of feeders and their food bind the inhabitants of a community into a web of interacting elements, through which energy (Chapter 17) and matter (Chapter 18) are moved. This ecosystem approach involves primary producers, decomposers and detritivores, a pool of dead organic matter, herbivores, carnivores and parasites *plus* the physicochemical environment that provides living conditions and acts both as a source and a sink for energy and matter. In Chapter 17, we deal with large-scale patterns in primary productivity before turning to the factors that limit productivity, and its fate, in terrestrial and aquatic settings. In Chapter 18, we consider the ways in which the biota accumulates, transforms and moves matter between the various components of the ecosystem.

In Chapter 19 we return to some key population interactions dealt with earlier in the book, and consider the ways that competition, predation and parasitism can shape communities. Then in Chapter 20 we recognize that the influence of a particular species often ramifies beyond a particular competitor, prey or host population, through the whole food web. The study of food webs lies at the interface of community and ecosystem ecology and we focus both on the population dynamics of interacting species in the community and on the consequences for ecosystem processes such as productivity and nutrient flux.

In Chapter 21 we attempt an overall synthesis of the factors, both abiotic and biotic, that determine species richness. Why the number of species varies from place to place, and from time to time, are interesting questions in their own right as well as being questions of practical importance. We will see that a full understanding of patterns in species richness has to draw on an understanding of all the ecological topics dealt with in earlier chapters of the book.

Finally, in the last of our trilogy of chapters dealing with the application of ecological theory, we consider in Chapter 22 the application of theory related to succession, food web ecology, ecosystem functioning and biodiversity. We conclude by recognizing that the application of ecological theory never proceeds in isolation – the sustainable use of natural resources requires that we also incorporate economic and sociopolitical perspectives.

To pursue an analogy we introduced earlier, the study of ecology at the community/ecosystem level is a little like making a study of watches and clocks. A collection can be made and the contents of each timepiece classified. We can recognize characteristics that they have in common in the way they are constructed and patterns in the way they behave. But to understand how they work, they must be taken to pieces, studied and put back together again. We will have understood the nature of natural communities when we *know* how to recreate those that we have, often inadvertently, taken to pieces.

Chapter 16

The Nature of the Community: Patterns in Space and Time

16.1 Introduction

Physiological and behavioral ecologists are concerned primarily with individual *organisms*. Coexisting individuals of a single species possess characteristics – such as density, sex ratio, age-class structure, rates of natality and immigration, mortality and emigration – that are unique to *populations*. We explain the behavior of a population in terms of the behavior of the individuals that comprise it. In their turn, activities at the population level have consequences for the next level up – that of the *community*. The community is an assemblage of species populations that occur together in space and time. Community ecology seeks to understand the manner in which groupings of species are distributed in nature, and the ways these groupings can be influenced by their abiotic environment (Part 1 of this textbook) and by interactions among species populations (Part 2). One challenge for community ecologists is to discern and explain patterns arising from this multitude of influences.

the search for rules of community assembly

In very general terms, the species that assemble to make up a community are determined by: (i) dispersal constraints; (ii) environmental constraints; and (iii) internal dynamics (Figure 16.1) (Belyea & Lancaster, 1999). Ecologists search for rules of community assembly, and we discuss these in this chapter and a number of others (particularly Chapters 19–21).

communities have collective properties . . .

. . . and emergent properties not possessed by the individual populations that comprise them

A community is composed of individuals and populations, and we can identify and study straightforward *collective* properties, such as species diversity and community biomass. However, we have already seen that organisms of the same and different species interact with each other in processes of mutualism, parasitism, predation and competition. The nature of the community is obviously more than just the sum of its constituent species. There are *emergent* properties that appear when the community is the focus of attention, as there are in other cases where we are concerned with the behavior of complex mixtures. A cake has emergent properties of texture and flavor that are not apparent simply from a survey of the ingredients. In the case of ecological communities, the limits to similarity of competing species (see Chapter 19) and the stability of the food web in the face of disturbance (see Chapter 20) are examples of emergent properties.

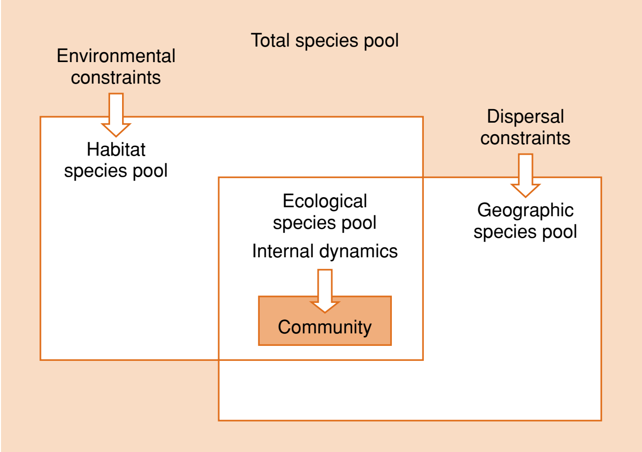


Figure 16.1 The relationships among five types of species pools: the total pool of species in a region, the geographic pool (species able to arrive at a site), the habitat pool (species able to persist under the abiotic conditions of the site), the ecological pool (the overlapping set of species that can both arrive and persist) and the community (the pool that remains in the face of biotic interactions). (Adapted from Belyea & Lancaster, 1999; Booth & Swanton, 2002.)

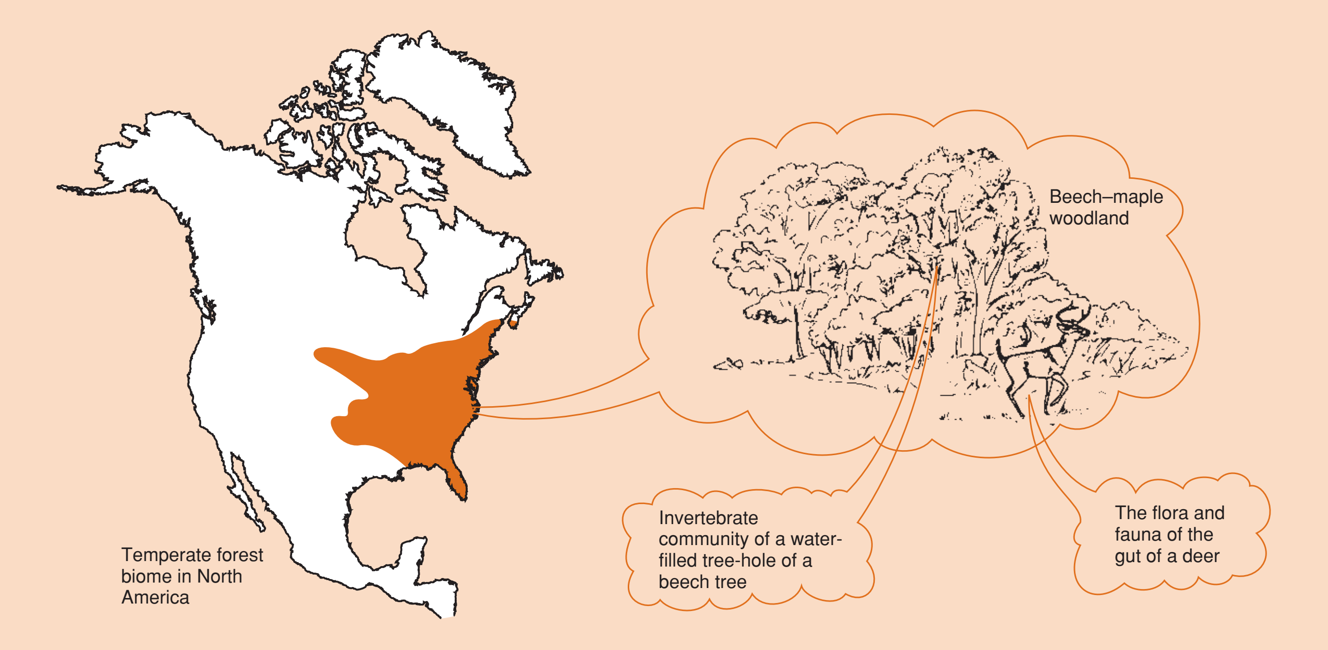


Figure 16.2 We can identify a hierarchy of habitats, nesting one into the other: a temperate forest biome in North America; a beech–maple woodland in New Jersey; a water-filled tree hole; or a mammalian gut. The ecologist may choose to study the community that exists on any of these scales.

Science at the community level poses daunting problems because the database may be enormous and complex. A first step is usually to search for patterns in the community's collective and emergent properties. Patterns are repeated consistencies, such as the repeated grouping of similar growth forms in different places, or repeated trends in species richness along different environmental gradients. Recognition of patterns leads, in turn, to the forming of hypotheses about the causes of these patterns. The hypotheses may then be tested by making further observations or by doing experiments.

A community can be defined at any scale within a hierarchy of habitats. At one extreme, broad patterns in the distribution of community types can be recognized on a global scale. The temperate forest biome is one example; its range in North America is shown in Figure 16.2. At this scale, ecologists usually recognize climate as the overwhelming factor that determines the limits of vegetation types. At a finer scale, the temperate forest biome in parts of New Jersey is represented by communities of two species of tree in particular, beech and maple, together with a very large number of other, less conspicuous species of plants, animals and microorganisms. Study of the community may be focused at this scale. On an even finer habitat scale, the characteristic invertebrate community that inhabits water-filled holes in beech trees may be studied, or the flora and fauna in the gut of a deer in the forest. Amongst these various scales of community study, no one is more legitimate than another. The scale appropriate for investigation depends on the sorts of questions that are being asked.

communities can be recognized at a variety of levels – all equally legitimate

Community ecologists sometimes consider all of the organisms existing together in one area, although it is rarely possible to do this without a large team of taxonomists. Others restrict their attention within the community to a single taxonomic group (e.g. birds, insects or trees), or a group with a particular activity (e.g. herbivores or detritivores).

The rest of this chapter is in six sections. We start by explaining how the structure of communities can be measured and described (Section 16.2). Then we focus on patterns in community structure: in space (Section 16.3), in time (Sections 16.4–16.6) and finally in a combined spatiotemporal setting (Section 16.7).

16.2 Description of community composition

species richness: the number of species present in a community

One way to characterize a community is simply to count or list the species that are present. This sounds a straightforward procedure that enables us to describe and compare communities by their species 'richness' (i.e. the number of species present). In practice, though, it is often surprisingly difficult, partly because

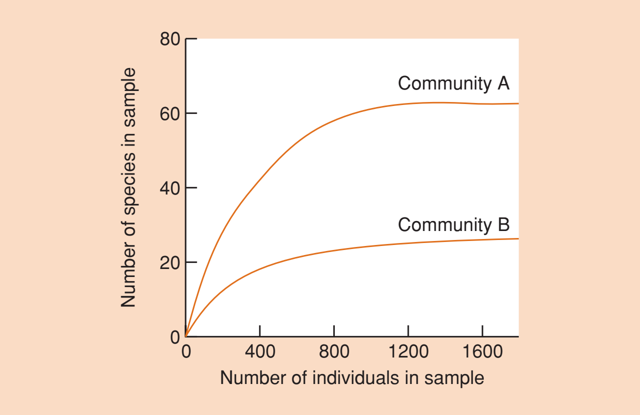


Figure 16.3 The relationship between species richness and the number of individual organisms from two contrasting hypothetical communities. Community A has a total species richness considerably in excess of community B.

of taxonomic problems, but also because only a subsample of the organisms in an area can usually be counted. The number of species recorded then depends on the number of samples that have been taken, or on the volume of the habitat that has been explored. The most common species are likely to be represented in the first few samples, and as more samples are taken, rarer species will be added to the list. At what point does one cease to take further samples? Ideally, the investigator should continue to sample until the number of species reaches a plateau (Figure 16.3). At the very least, the species richnesses of different communities should be compared on the basis of the same sample sizes (in terms of area of habitat explored, time devoted to sampling or, best of all, number of individuals or modules included in the samples). The analysis of species richness in contrasting situations figures prominently in Chapter 21.

16.2.1 Diversity indices

diversity incorporates richness, commonness and rarity

An important aspect of community structure is completely ignored, though, when the composition of the community is described simply in terms of the number of species present. It misses the information that some species are rare and others common. Consider a community of 10 species with equal numbers in each, and a second community, again consisting of 10 species, but with more than 50% of the individuals belonging to the most common species and less than 5% in each of the other nine. Each community has the same species richness, but the first, with a more 'equitable' distribution of abundances, is clearly more *diverse* than the second. Richness and equitablity combine to determine community diversity.

Knowing the numbers of individuals present in each species may not provide a full answer either. If the community is closely defined (e.g. the warbler community of a woodland), counts of the number of individuals in each species may suffice for many purposes. However, if we are interested in all the animals in the woodland, then their enormous disparity in size means that simple counts would be very misleading. There are also problems if we try to count plants (and other modular organisms). Do we count the number of shoots, leaves, stems, ramets or genets? One way round this problem is to describe the community in terms of the biomass per species per unit area.

Simpson's diversity index

The simplest measure of the character of a community that takes into account both the abundance (or biomass) patterns and the species richness, is Simpson's diversity index. This is calculated by determining, for each species, the proportion of individuals or biomass that it contributes to the total in the sample, i.e. the proportion is P_i for the ith species:

$$\text{Simpson's index, } D = \frac{1}{\sum_{i=1}^{S} P_i^2}, \qquad (16.1)$$

where S is the total number of species in the community (i.e. the richness). As required, for a given richness, D increases with equitability, and for a given equitability, D increases with richness.

'equitability' or 'evenness'

Equitability can itself be quantified (between 0 and 1) by expressing Simpson's index, D, as a proportion of the maximum possible value D would assume if individuals were completely evenly distributed amongst the species. In fact, $D_{\max} = S$. Thus:

$$\text{equitability, } E = \frac{D}{D_{\max}} = \frac{1}{\sum_{i=1}^{S} P_i^2} \times \frac{1}{S}. \qquad (16.2)$$

Shannon's diversity index

Another index that is frequently used and has essentially similar properties is the Shannon diversity index, H. This again depends on an array of P_i values. Thus:

$$\text{diversity, } H = -\sum_{i=1}^{S} P_i \ln P_i \qquad (16.3)$$

and:

$$\text{equitability, } J = \frac{H}{H_{\max}} = \frac{-\sum_{i=1}^{S} P_i \ln P_i}{\ln S}. \qquad (16.4)$$

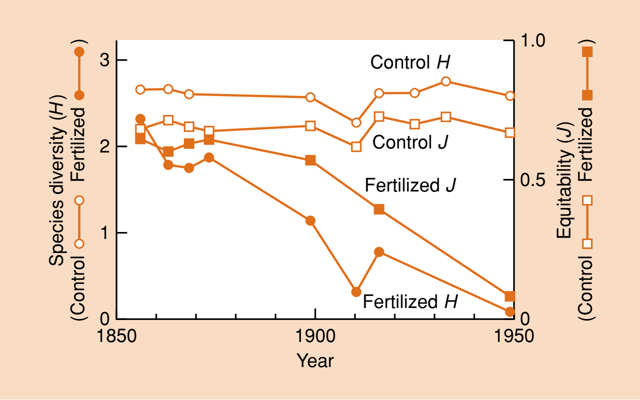


Figure 16.4 Species diversity (H) and equitability (J) of a control plot and a fertilized plot in the Rothamsteard 'Parkgrass' experiment. (After Tilman, 1982.)

An example of an analysis of diversity is provided by a uniquely long-term study that has been running since 1856 in an area of grassland at Rothamsted in England. Experimental plots have received a fertilizer treatment once every year, whilst control plots have not. Figure 16.4 shows how species diversity (H) and equitability (J) of the grass species changed between 1856 and 1949. Whilst the unfertilized area has remained essentially unchanged, the fertilized area has shown a progressive decline in diversity and equitability. One possible explanation may be that high nutrient availability leads to high rates of population growth and a greater chance of the most productive species coming to dominate and, perhaps, competitively exclude others.

16.2.2 Rank–abundance diagrams

Of course, attempts to describe a complex community structure by one single attribute, such as richness, diversity or equitability, can be criticized because so much valuable information is lost. A more complete picture of the distribution of species abundances in a community makes use of the full array of P_i values by plotting P_i against rank. Thus, the P_i for the most abundant species is plotted first, then the next most common, and so on until the array is completed by the rarest species of all. A rank–abundance diagram can be drawn for the number of individuals, or for the area of ground covered by different sessile species, or for the biomass contributed to a community by the various species.

rank–abundance models may be based on statistical or biological arguments

A range of the many equations that have been fitted to rank–abundance diagrams is shown in Figure 16.5. Two of these are statistical in origin (the log series and log-normal) with no foundation in any assumptions about how the species may interact with one another. The others take some account of the relationships between the conditions, resources and species-abundance patterns (niche-orientated models) and are more likely to help us understand the mechanisms underlying community organization (Tokeshi, 1993). We illustrate the diversity of approaches by describing the basis of four of Tokeshi's niche-orientated models (see Tokeshi, 1993, for a complete treatment). The *dominance–preemption model*, which produces the least equitable species distribution, has successive species preempting a dominant portion (50% or more) of the remaining niche space; the first, most dominant species takes more than 50% of the total niche space, the next more than 50% of what remains, and so on. A somewhat more equitable distribution is represented by the *random fraction model*, in which successive species invade and take over an arbitrary portion of the niche space of any species previously present. In this case, irrespective of their dominance status, all species are subjected to niche division with equal probability. The *MacArthur fraction model*, on the other hand, assumes that species with larger niches are more likely to be invaded by new species; this results in a more equitable distribution than the random fraction model. Finally, the *dominance–decay model* is the inverse of the dominance–preemption model, in that the largest niche in an existing assemblage is always subject to a subsequent (random) division. Thus, in this model the next invading species is supposed to colonize the niche space of the species currently most abundant, yielding the most equitable species abundances of all the models.

community indices are abstractions that may be useful when making comparisons

Rank–abundance diagrams, like indices of richness, diversity and equitability, should be viewed as abstractions of the highly complex structure of communities that may be useful when making comparisons. In principle, the idea is that finding the best fitting model should give us clues as to underlying processes, and perhaps as to how these vary from sample to sample. Progress so far, however, has been limited, both because of problems of interpretation and the practical difficulty of testing for the best fit between model and data (Tokeshi, 1993). However, some studies have successfully focused attention on a change in dominance/evenness relationships in relation to environmental change. Figure 16.5c shows how, assuming a geometric series can be appropriately applied, dominance steadily increased, whilst species richness decreased, during the Rothamsted long-term grassland experiment described above. Figure 16.5d shows how invertebrate species richness and equitability were both greater on an architecturally complex stream plant *Ranunculus yezoensis*, which provides more potential niches, than on a structurally simple plant *Sparganium emersum*. The rank–abundance diagrams of both are closer to the random fraction model than the MacArthur fraction model. Finally, Figure 16.5e shows how attached bacterial assemblages (biofilms), during colonization of

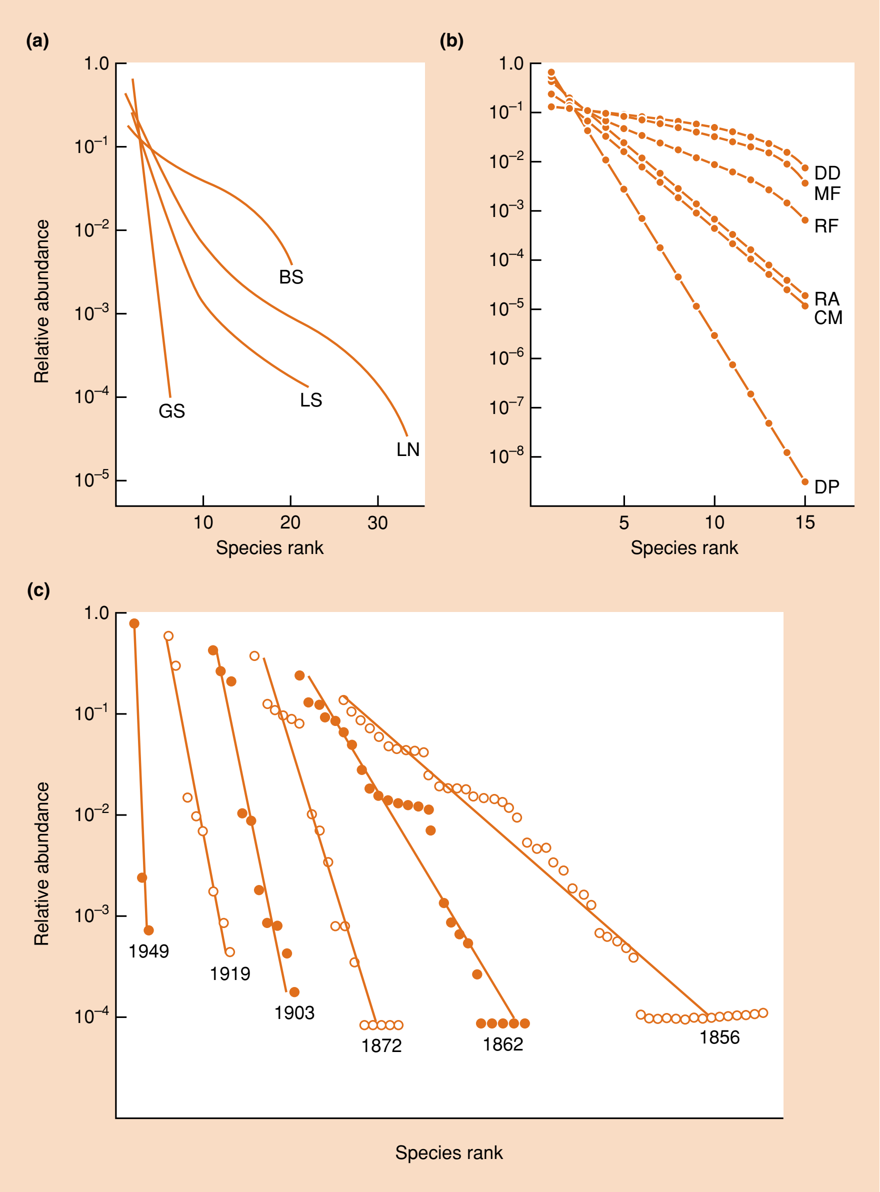


Figure 16.5 (a, b) Rank–abundance patterns of various models. Two are statistically orientated (LS and LN), whilst the rest can be described as niche orientated. (a) BS, broken stick; GS, geometric series; LN, log-normal; LS, log series. (b) CM, composite; DD, dominance decay; DP, dominance preemption; MF, MacArthur fraction; RA, random assortment; RF, random fraction. (c) Change in the relative abundance pattern (geometric series fitted) of plant species in an experimental grassland subjected to continuous fertilizer from 1856 to 1949. ((a–c) after Tokeshi, 1993.)

glass slides in a lake, change from a log-normal to a geometric pattern as the biofilm ages.

the energetics approach: an alternative to taxonomic description

Taxonomic composition and species diversity are just two of many possible ways of describing a community. Another alternative (not necessarily better but quite different) is to describe communities and ecosystems in terms of their standing crop and the rate of production of biomass by plants, and its use and conversion by heterotrophic microorganisms and animals. Studies that are orientated in this way may begin by describing the food web, and then define the biomasses at each trophic level and the flow of energy and matter from the physical environment through the living organisms and back to the physical environment. Such an approach can allow patterns to be detected amongst communities and ecosystems that may have no taxonomic features in common. This approach will be discussed in Chapters 17 and 18.

Much recent research effort has been devoted to understanding the link between species richness and ecosystem functioning (productivity, decomposition and nutrient dynamics). Understanding the role of species richness in ecosystem processes has particular significance for how humans respond to biodiversity loss. We discuss this important topic in Section 21.7.

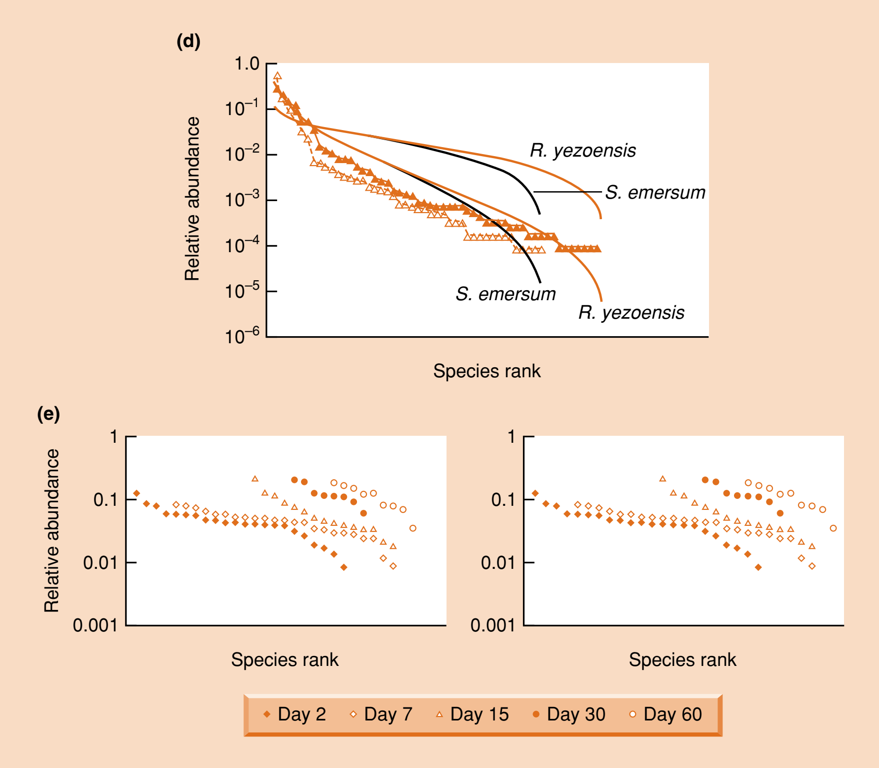


Figure 16.5 (*cont'd*) (d) Comparison of rank–abundance patterns for invertebrate species living on a structurally complex stream plant *Ranunculus yezoensis* (▲) and a simple plant *Sparganium emersum* (△); fitted lines represent the MacArthur fraction model (——, the upper one for *R. yezoensis* and the lower one for *S. emersum*) and the random fraction model (——, the upper one for *R. yezoensis* and the lower one for *S. emersum*). (After Taniguchi *et al*., 2003.) (e) Rank–abundance patterns (based on a biomass index) for bacterial assemblages in lake biofilms of different ages (symbols from left to right represent days 2, 7, 15, 30, 60). (After Jackson *et al*., 2001.)

16.3 Community patterns in space

16.3.1 Gradient analysis

Figure 16.6 shows a variety of ways of describing the distribution of vegetation used in a classic study in the Great Smoky Mountains (Tennessee), USA, where tree species give the vegetation its main character. Figure 16.6a shows the characteristic associations of the dominant trees on the mountainside, drawn as if the communities had sharp boundaries. The mountainside itself provides a range of conditions for plant growth, and two of these, altitude and moisture, may be particularly important in determining the distribution of the various tree species. Figure 16.6b shows the dominant associations graphed in terms of these two environmental dimensions. Finally, Figure 16.6c shows the abundance of each individual tree species (expressed as a percentage of all tree stems present) plotted against the single gradient of moisture.

species distributions along gradients end not with a bang but with a whimper

Figure 16.6a is a subjective analysis that acknowledges that the vegetation of particular areas differs in a characteristic way from that of other areas. It could be taken to imply that the various communities are sharply delimited. Figure 16.6b gives the same impression. Note that both Figure 16.6a and b are based on descriptions of the *vegetation*. However, Figure 16.6c sharpens the focus by concentrating on the pattern of distribution of the individual *species*. It is then immediately obvious that there is considerable overlap in their abundance – there are no sharp boundaries. The various tree species are now revealed as being strung out along the gradient with the tails of their distributions overlapping. The results of this 'gradient analysis' show that the limits of the distributions of each species 'end not with a bang but with a whimper'. Many other gradient studies have produced similar results.

Perhaps the major criticism of gradient analysis as a way of detecting pattern in communities is that the choice of the gradient is almost always subjective. The investigator searches for some feature of the environment that appears to matter to the organisms and then organizes the data about the species concerned along a gradient of that factor. It is not necessarily the most appropriate factor to have chosen. The fact that the species from a community can be arranged in a sequence along a gradient of some environmental factor does not prove that this factor is the most important one. It may only imply that the factor chosen is more or less loosely correlated with whatever really matters in the lives of the species involved. Gradient analysis is only a small step on the way to the objective description of communities.

choice of gradient is almost always subjective

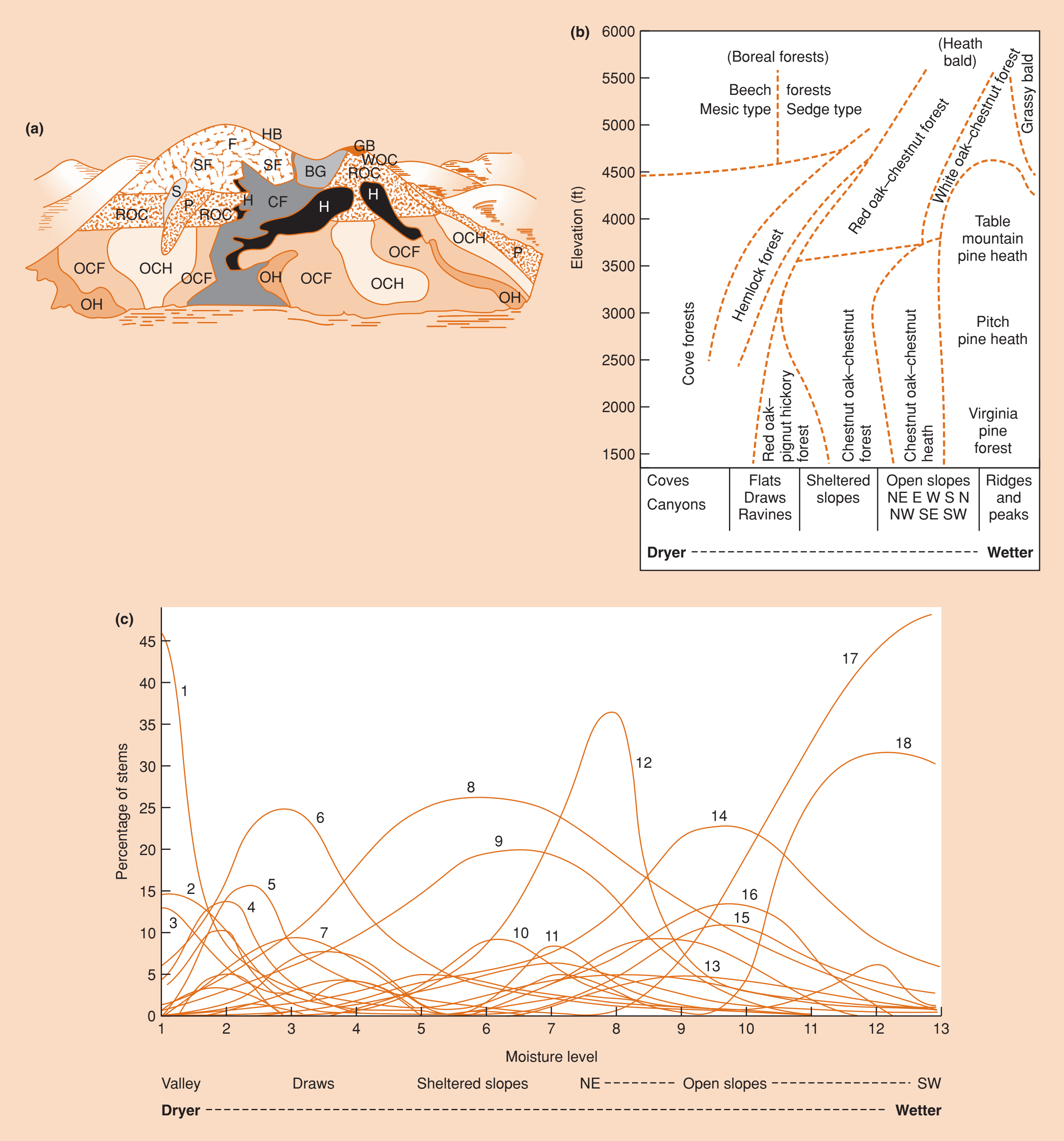
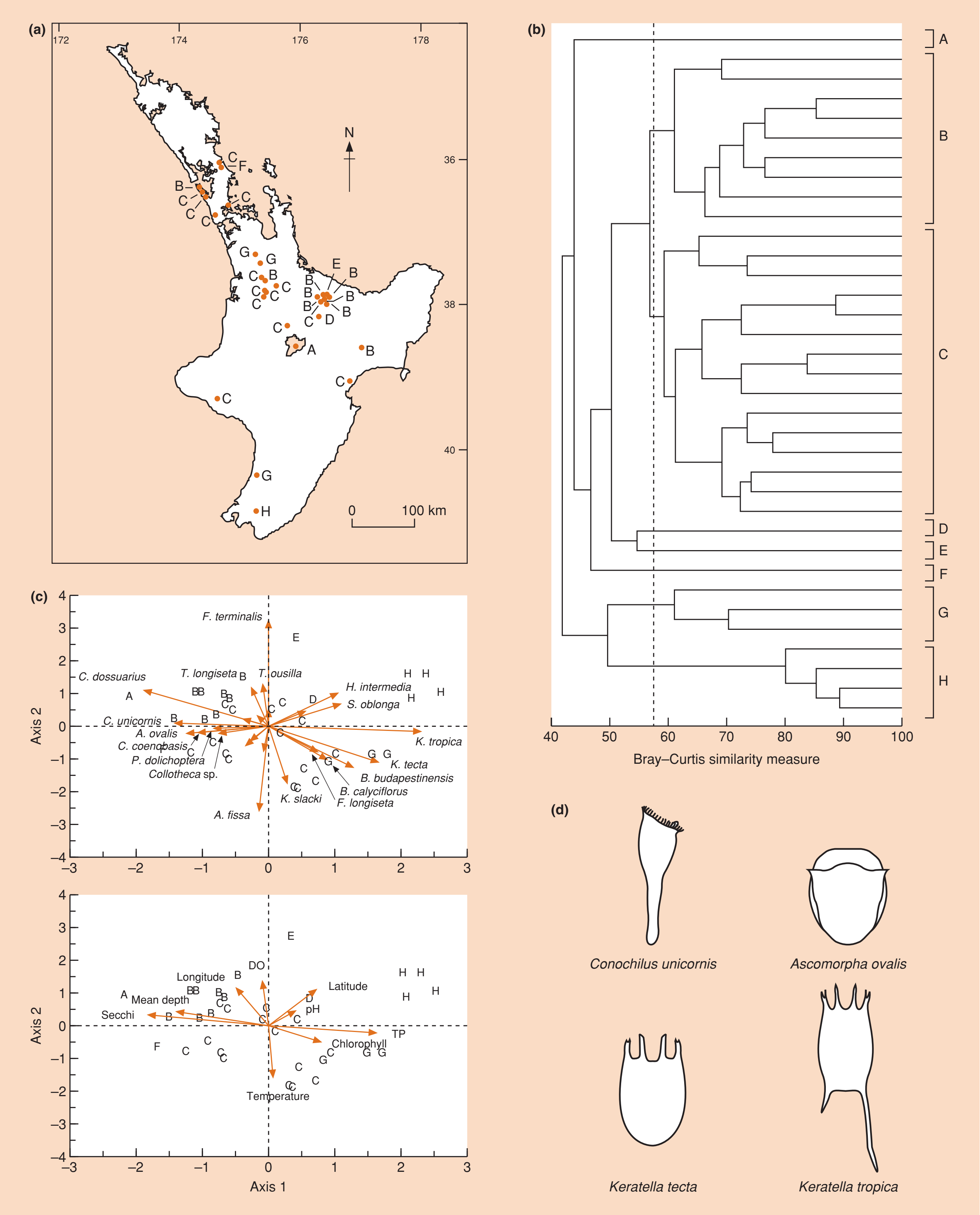


Figure 16.6 Three contrasting descriptions of distributions of the characteristic dominant tree species of the Great Smoky Mountains, Tennessee. (a) Topographic distribution of vegetation types on an idealized west-facing mountain and valley. (b) Idealized graphic arrangement of vegetation types according to elevation and aspect. (c) Distributions of individual tree populations (percentage of stems present) along the moisture gradient. Vegetation types: BG, beech gap; CF, cove forest; F, Fraser fir forest; GB, grassy bald; H, hemlock forest; HB, heath bald; OCF, chestnut oak–chestnut forest; OCH, chestnut oak–chestnut heath; OH, oak–hickory; P, pine forest and heath; ROC, red oak–chestnut forest; S, spruce forest; SF, spruce–fir forest; WOC, white oak–chestnut forest. Major species: 1, *Halesia monticola*; 2, *Aesculus octandra*; 3, *Tilia heterophylla*; 4, *Betula alleghaniensis*; 5, *Liriodendron tulipifera*; 6, *Tsuga canadensis*; 7, *B. lenta*; 8, *Acer rubrum*; 9, *Cornus florida*; 10, *Carya alba*; 11, *Hamamelis virginiana*; 12, *Quercus montana*; 13, *Q. alba*; 14, *Oxydendrum arboreum*; 15, *Pinus strobus*; 16, *Q. coccinea*; 17, *P. virginiana*; 18, *P. rigida*. (After Whittaker, 1956.)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(c)
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Axis 2
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C. dossuarius
T. longiseta
T. pusilla
H. intermedia
S. oblonga
C. unicornis
A. ovalis
C. coenobasis
P. dolichoptera
Collotheca sp.
K. tropica
K. tecta
B. budapestinensis
B. calyciflorus
F. longiseta
K. slacki
A. fissa
Longitude
DO
Latitude
Mean depth
Secchi
pH
TP
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Temperature
(d)
Conochilus unicornis
Ascomorpha ovalis
Keratella tecta
Keratella tropica

16.3.2 Classification and ordination of communities

Formal statistical techniques have been defined to take the subjectivity out of community description. These techniques allow the data from community studies to sort themselves, without the investigator putting in any preconceived ideas about which species tend to be associated with each other or which environmental variables correlate most strongly with the species distributions. One such technique is classification.

classification involves grouping similar communities together in clusters

Classification begins with the assumption that communities consist of relatively discrete entities. It produces groups of related communities by a process conceptually similar to taxonomic classification. In taxonomy, similar individuals are grouped together in species, similar species in genera, and so on. In community classification, communities with similar species compositions are grouped together in subsets, and similar subsets may be further combined if desired (see Ter Braak & Prentice, 1988, for details of the procedure).

The rotifer communities of a number of lakes in the North Island of New Zealand (Figure 16.7a) were subjected to a classification technique called cluster analysis (Duggan *et al.*, 2002). Eight clusters or classes were identified (Figure 16.7b), each based solely on the arrays of species present and their abundances. The spatial distribution of each class of rotifer community in the New Zealand lakes is shown in Figure 16.7a. Note that there is little consistent spatial relationship; communities in each class are dotted about the island. This illustrates one of the strengths of classification. Classification methods show the structure within a series of communities without the necessity of picking out some supposedly relevant environmental variable in advance, a procedure that is necessary for gradient analysis.

in ordination, communities are displayed on a graph so that those most similar in composition are closest together

Ordination is a mathematical treatment that allows communities to be organized on a graph so that those that are most similar in both species composition and relative abundance will appear closest together, whilst communities that differ greatly in the relative importance of a similar set of species, or that possess quite different species, appear far apart. Figure 16.7c shows the application of an ordination technique called canonical correspondence analysis (CCA) to the rotifer communities (Ter Braak & Smilauer 1998). CCA also allows the community patterns to be examined in terms of environmental variables. Obviously, the success of the method now depends on having sampled an appropriate variety of environmental variables. This is a major snag in the procedure – we may not have measured the qualities in the environment that are most relevant. The relationships between rotifer community composition and a variety of physicochemical factors are shown in Figure 16.7c. The link between classification and ordination can be gauged by noting that communities falling into classes A–H, derived from classification, are also fairly distinctly separated on the CCA ordination graph.

subsequently, it is necessary to ask what varies along the axes of the graph

Community classes A and B tend to be associated with high water transparency ('Secchi depth'), whereas those in classes G and H are associated with high total phosphorus and chlorophyll concentrations; the other lake classes take up intermediate positions. Lakes that have been subject to a greater level of runoff of agricultural fertilizers or input of sewage are described as eutrophic. These tend to have high phosphorus concentrations, leading to higher chlorophyll levels and lower transparency (a greater abundance of phytoplankton cells). Evidently, the rotifer communities are strongly influenced by the level of eutrophication to which the lakes are subject. Species of rotifer that are characteristic of particularly eutrophic conditions, such as *Keratella tecta* and *K. tropica* (Figure 16.7d), were strongly represented in classes G and H, while those associated with more pristine conditions, such as *Conochilus unicornis* and *Ascomorpha ovalis*, were common in classes A and B.

The level of eutrophication, however, is not the only significant factor in explaining rotifer community composition. Class C communities, for example, while characteristic of intermediate phosphorus concentrations, can be differentiated along axis 2 according to dissolved oxygen concentration and lake temperature (themselves negatively related because oxygen solubility declines with increasing temperature).

ordination can generate hypotheses for subsequent testing

What do these results tell us? First, and most specifically, the correlations with environmental factors, revealed by the analysis, give us some specific hypotheses to test about the relationship between community composition and underlying environmental factors. (Remember that correlation does not necessarily imply

Figure 16.7 (*opposite*) (a) Thirty-one lakes in the North Island of New Zealand where rotifer communities (78 species in total) were sampled and described. (b) Results of cluster analysis (classification) on species composition data from the 31 lakes (based on the Bray–Curtis similarity measure); lake communities that are most similar cluster together and eight clusters are identified (A–H). (c) Results of canonical correspondence analysis (ordination). The positions in ordination space are shown for lake sites (shown as letters A–H corresponding to their classification), individual rotifer species (orange arrows in top panel) and environmental factors (orange arrows in lower panel). (d) Silhouettes of four of the rotifer species. (After Duggan *et al.*, 2002.)

causation. For example, dissolved oxygen and community composition may vary together because of a common response to another environmental factor. A direct causal link can only be proved by controlled experimentation.)

A second, more general point is relevant to the discussion of the nature of the community. The results emphasize that under a particular set of environmental conditions, a predictable association of species is likely to occur. It shows that community ecologists have more than just a totally arbitrary and ill-defined set of species to study.

16.3.3 Problems of boundaries in community ecology

are communities discrete entities with sharp boundaries?

There may be communities that are separated by clear, sharp boundaries, where groups of species lie adjacent to, but do not intergrade into, each other. If they exist, they are exceptional. The meeting of terrestrial and aquatic environments might appear to be a sharp boundary but its ecological unreality is emphasized by the otters or frogs that regularly cross it and the many aquatic insects that spend their larval lives in the water but their adult lives as winged stages on land or in the air. On land, quite sharp boundaries occur between the vegetation types on acidic and basic rocks where outcrops meet, or where serpentine (a term applied to a mineral rich in magnesium silicate) and nonserpentine rocks are juxtaposed. However, even in such situations, minerals are leached across the boundaries, which become increasingly blurred. The safest statement we can make about community boundaries is probably that they do not exist, but that some communities are much more sharply defined than others. The ecologist is usually better employed looking at the ways in which communities grade into each other, than in searching for sharp cartographic boundaries.

the community: not so much a superorganism . . .

In the first quarter of the 20th century there was considerable debate about the nature of the community. Clements (1916) conceived of the community as a sort of *superorganism* whose member species were tightly bound together both now and in their common evolutionary history. Thus, individuals, populations and communities bore a relationship to each other resembling that between cells, tissues and organisms.

In contrast, the *individualistic* concept devised by Gleason (1926) and others saw the relationship of coexisting species as simply the results of similarities in their requirements and tolerances (and partly the result of chance). Taking this view, community boundaries need not be sharp, and associations of species would be much less predictable than one would expect from the superorganism concept.

The current view is close to the individualistic concept. Results of direct gradient analysis, ordination and classification all indicate that a given location, by virtue mainly of its physical characteristics, possesses a reasonably predictable association of species. However, a given species that occurs in one predictable association is also quite likely to occur with another group of species under different conditions elsewhere.

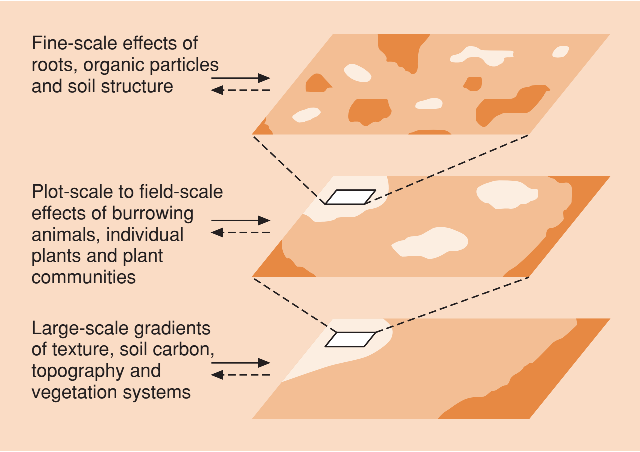


Figure 16.8 Determinants of spatial heterogeneity of communities of soil organisms including bacteria, fungi, nematodes, mites and collembolans. (After Ettema & Wardle, 2002.)

A further point needs to be born in mind when considering the question of environmental patchiness and boundaries. Spatial heterogeneity in the distribution of communities can be viewed within a series of nested scales. Figure 16.8, for example, shows patterns in spatial heterogeneity in communities of soil organisms operating at scales from hectares to square millimeters (Ettema & Wardle, 2002). At the largest scale, these reflect patterns in environmental factors related to topography and the distribution of different plant communities. But at the other extreme, fine-scale patterns may be present as a result of the location of individual plant roots or local soil structure. The boundaries of patterns at these various scale are also likely to be blurred.

. . . more a level of organization

Whether or not communities have more or less clear boundaries is an important question, but it is not the fundamental consideration. Community ecology is the study of the *community level of organization* rather than of a spatially and temporally definable unit. It is concerned with the structure and activities of the multispecies assemblage, usually at one point in space and time. It is not necessary to have discrete boundaries between communities to study community ecology.

16.4 Community patterns in time

Just as the relative importance of species varies in space, so their patterns of abundance may change with time. In either case, a species will occur only where and when: (i) it is capable of reaching a location; (ii) appropriate conditions and resources exist there; and (iii) competitors, predators and parasites do not preclude it. A temporal sequence in the appearance and disappearance of species therefore seems to require that conditions, resources and/or the influence of enemies themselves vary with time.

For many organisms, and particularly short-lived ones, their relative importance in the community changes with time of year as the individuals act out their life cycles against a background of seasonal change. Sometimes community composition shifts because of externally driven physical change, such as the build up of silt in a coastal salt marsh leading to its replacement by forest. In other cases, temporal patterns are simply a reflection of changes in key resources, as in the sequence of heterotrophic organisms associated with fecal deposits or dead bodies as they decompose (see Figure 11.2). The explanation for such temporal patterns is relatively straightforward and will not concern us here. Nor will we dwell on the variations in abundance of species in a community from year to year as individual populations respond to a multitude of factors that influence their reproduction and survival (dealt with in Chapters 5, 6 and 8–14).

Our focus will be on patterns of community change that follow a disturbance, defined as a relatively discrete event that removes organisms (Townsend & Hildrew, 1994) or otherwise disrupts the community by influencing the availability of space or food resources, or by changing the physical environment (Pickett & White, 1985). Such disturbances are common in all kinds of community. In forests, they may be caused by high winds, lightning, earthquakes, elephants, lumberjacks or simply by the death of a tree through disease or old age. Agents of disturbance in grassland include frost, burrowing animals and the teeth, feet, dung or dead bodies of grazers. On rocky shores or coral reefs, disturbances may result from severe wave action during hurricanes, tidal waves, battering by logs or moored boats or the fins of careless scuba divers.

16.4.1 Founder-controlled and dominance-controlled communities

founder control: many species are equivalent in their ability to colonize

In response to disturbances, we can postulate two fundamentally different kinds of community response according to the type of competitive relationships exhibited by the component species – founder controlled and dominance controlled (Yodzis, 1986). *Founder-controlled* communities will occur if a large number of species are approximately equivalent in their ability to colonize an opening left by a disturbance, are equally well fitted to the abiotic environment and can hold the location until they die. In this case, the result of the disturbance is essentially a lottery. The winner is the species that happens to reach and establish itself in the disturbed location first. The dynamics of founder-controlled communities are discussed in Section 16.7.4.

dominance control: some potential colonizers are competitively dominant

Dominance-controlled communities are those where some species are competitively superior to others so that an initial colonizer of an opening left by a disturbance cannot necessarily maintain its presence there. In these cases, disturbances lead to reasonably predictable sequences of species because different species have different strategies for exploiting resources – early species are good colonizers and fast growers, whereas later species can tolerate lower resource levels and grow to maturity in the presence of early species, eventually outcompeting them. These situations are more commonly known by the term *ecological succession*, defined as the *nonseasonal, directional and continuous pattern of colonization and extinction on a site by species populations*.

16.4.2 Primary and secondary successions

primary succession: an exposed landform uninfluenced by a previous community

Our focus is on successional patterns that occur on newly exposed landforms. If the exposed landform has not previously been influenced by a community, the sequence of species is referred to as a primary succession. Lava flows and pumice plains caused by volcanic eruptions (see Section 16.4.3), craters caused by the impact of meteors (Cockell & Lee, 2002), substrate exposed by the retreat of a glacier (Crocker & Major, 1955) and freshly formed sand dunes (see Section 16.4.4) are examples. In cases where the vegetation of an area has been partially or completely removed, but where well-developed soil and seeds and spores remain, the subsequent sequence of species is termed a secondary succession. The loss of trees locally as a result of disease, high winds, fire or felling may lead to secondary successions, as can cultivation followed by the abandonment of farmland (so-called old field successions – see Section 16.4.5).

secondary succession: vestiges of a previous community are still present

Successions on newly exposed landforms typically take several hundreds of years to run their course. However, a precisely analagous process occurs amongst the animals and algae on recently denuded rock walls in the marine subtidal zone, and this succession takes only a decade or so (Hill *et al.*, 2002). The research life of an ecologist is sufficient to encompass a subtidal succession but not that following glacial retreat. Fortunately, however, information can sometimes be gained over the longer timescale. Often, successional stages in time are represented by community gradients in space. The use of historic maps, carbon dating or other techniques may enable the age of a community since exposure of the landform to be estimated. A series of communities currently in existence, but corresponding to different lengths of time since the onset of succession, can be inferred to reflect succession. However, whether or not different communities that are spread out in space really do represent various stages of succession must be judged with caution. We must remember, for example, that in northern temperate areas the vegetation we see may still be undergoing recolonization and responding to climatic change following the last ice age (see Chapter 1).

16.4.3 Primary succession on volcanic lava

facilitation: early successional species on volcanic lava pave the way for later ones

A primary succession on basaltic volcanic flows on Miyake-jima Island, Japan, was inferred from a known chronosequence (16, 37, 125 and >800 years old) (Figure 16.9a). In the 16-year-old flow, soil was very sparse and lacking in nitrogen; vegetation was absent except for a few small alder trees (*Alnus sieboldiana*). In the older plots, 113 taxa were recorded, including ferns, herbaceous perennials, lianas and trees. Of most significance in this primary succession were: (i) the successful colonization of the bare lava by the nitrogen-fixing alder; (ii) the facilitation (through improved nitrogen availability) of mid-successional *Prunus speciosa* and the late successional evergreen tree *Machilus thunbergii*; (iii) the formation of a mixed forest and the shading out of *Alnus* and *Prunus*; and (iv) finally, the replacement of *Machilus* by the longer lived *Castanopsis sieboldii* (Figure 16.9b).

16.4.4 Primary succession on coastal sand dunes

importance of seed availability rather than facilitation in sand dune succession

An extensive chronosequence of dune-capped beach ridges has been undertaken on the coast of Lake Michigan in the USA. Thirteen ridges of known

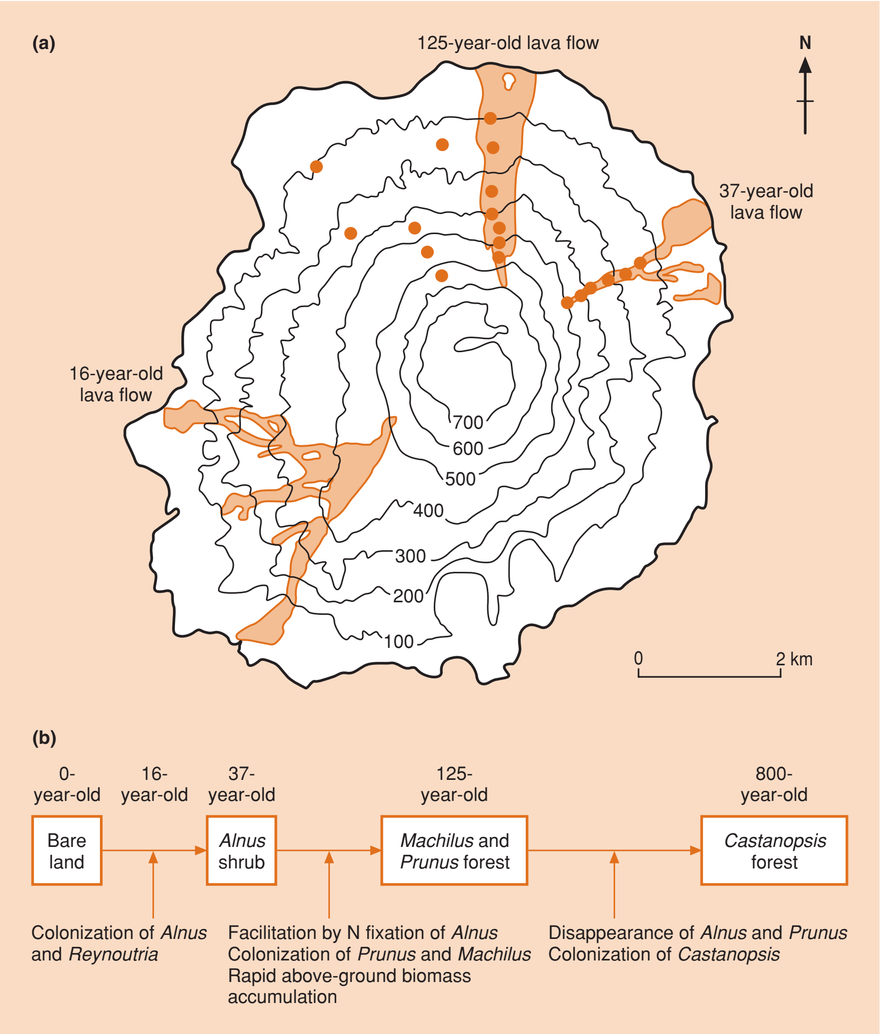


Figure 16.9 (a) Vegetation was described on 16-, 37- and 125-year-old lava flows on Miyake-jima Island, Japan. Analysis of the 16-year-old flow was nonquantitative (no sample sites shown). Sample sites on the other flows are shown as solid circles. Sites outside the three flows are at least 800 years old. (b) The main features of the primary succession in relation to lava age. (After Kamijo *et al.*, 2002.)

age (30–440 years old) show a clear pattern of primary succession to forest (Lichter, 2000). The dune grass *Ammophila breviligulata* dominates the youngest, still mobile dune ridge, but shrubby *Prunus pumila* and *Salix* spp. are also present. Within 100 years, these are replaced by evergreen shrubs such as *Juniperus communis* and by prairie bunch grass *Schizachrium scoparium*. Conifers such as *Pinus* spp., *Larix laricina*, *Picea strobus* and *Thuja occidentalis* begin colonizing the dune ridges after 150 years, and a mixed forest of *Pinus strobus* and *P. resinosa* develops between 225 and 400 years. Deciduous trees such as the oak *Quercus rubra* and the maple *Acer rubrum* do not become important components of the forest until 440 years.

It used to be thought that early successional dune species facilitated the later species by adding organic matter to the soil and increasing the availability of soil moisture and nitrogen (as in the volcanic primary succession). However, experimental seed addition and seedling transplant experiments have shown that later species are capable of germinating in young dunes (Figure 16.10a). While the more developed soil of older dunes may improve the performance of late successional species, their successful colonization of young dunes is mainly constrained by limited seed dispersal, together with seed predation by rodents (Figure 16.10b). *Ammophila* generally colonizes young, active dunes through horizontal vegetative growth. *Schizachrium*, one of the

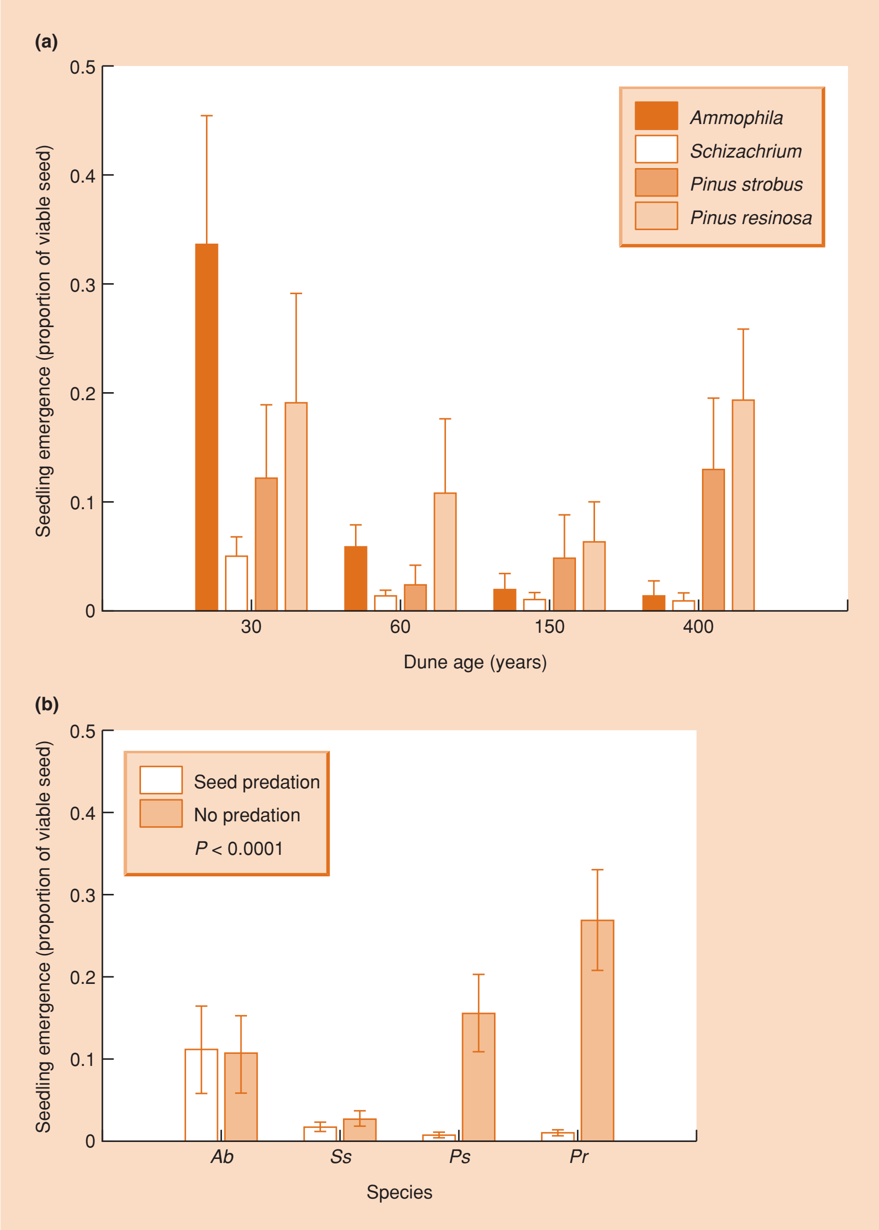


Figure 16.10 (a) Seedling emergence (means + SE) from added seeds of species typical of different successional stages on dunes of four ages. (b) Seedling emergence of the four species (*Ab*, *Ammophila breviligulata*, *Ss*, *Schizachrium scoparium*, *Ps*, *Pinus strobus*, *Pr*, *Pinus resinosa*) in the presence and absence of rodent predators of seeds (After Lichter, 2000.)

dominants of open dunes before forest development, has rates of germination and seedling establishment that are no better than *Pinus*, but its seeds are not preyed upon. Also, *Schizachrium* has the advantage of quickly reaching maturity and can continue to provide seeds at a high rate. These early species are eventually competitively excluded as trees establish and grow. Lichter (2000) considers that dune succession is better described in terms of the transient dynamics of colonization and competitive displacement, rather than the result of facilitation by early species (improving soil conditions) followed by competitive displacement.

16.4.5 Secondary successions in abandoned fields

abandoned old fields: succession to forest in North America . . .

Successions on old fields have been studied particularly along the eastern part of the USA where many farms were abandoned by farmers who moved west after the frontier was opened up in the 19th century (Tilman, 1987, 1988). Most of the precolonial mixed conifer–hardwood forest had been destroyed, but regeneration was swift. In many places, a series of sites that were abandoned for different, recorded periods of time are available for study. The typical sequence of dominant vegetation is: annual weeds, herbaceous perennials, shrubs, early successional trees and late successional trees.

. . . but to grassland in China

Old-field succession has also been studied in the productive Loess Plateau in China, which for millennia has been affected by human activities so that few areas of natural vegetation remain. The Chinese government has launched some conservation projects focused on the recovery of damaged ecosystems. A big question mark is whether the climax vegetation of the Plateau will prove to be grassland steppe or forest. Wang (2002) studied the vegetation at four plots abandoned by farmers for known periods of time (3, 26, 46 and 149 years). He was able to age some of his plots in an unusual manner. Graveyards in China are sacred and human activities are prohibited in their vicinity – gravestone records indicated how long ago the older areas had been taken out of agricultural production. Of a total of 40 plant species identified, several were considered dominant at the four successional stages (in terms of relative abundance and relative ground cover). In the first stage (recently abandoned farmland) *Artemesia scoparia* and *Seraria viridis* were most characteristic, at 26 years *Lespedeza davurica* and *S. viridis* dominated, at 46 years *Stipa bungeana*, *Bothriochloa ischaemun*, *A. gmelinii* and *L. davurica* were most important, while at 149 years *B. ischaemun* and *A. gmelinii* were dominant (Figure 16.11). The early successional species were annuals and biennials with high seed production. By 26 years, the perennial herb *L. davurica*, with its ability to spread laterally by vegetative means and a well-developed root system, had replaced *A. scoparia*.

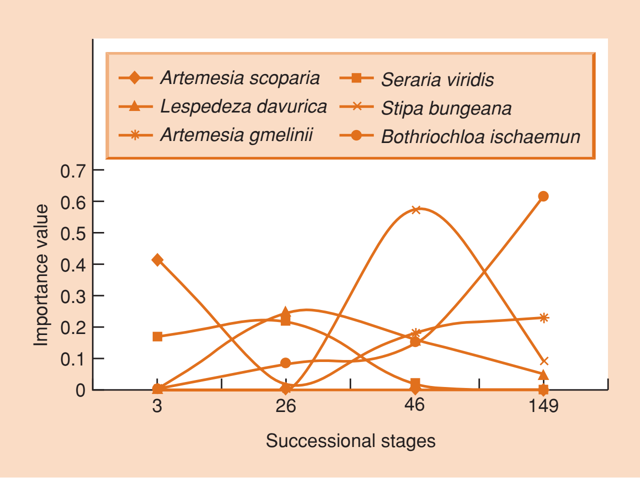


Figure 16.11 Variation in the relative importance of six species during an old-field succession on the Loess Plateau in China. (After Wang, 2002.)

The 46-year-old plot was characterized by the highest species richness and diverse life history strategies, dominated by perennial lifestyles. The dominance of *B. ischaemun* at 149 years was related to its perennial nature, ability to spread clonally and high competitive ability. As in Tilman's (1987, 1988) North American studies, soil nitrogen content increased during the succession and may have facilitated some species in the succession. Wang concludes that the grass *B. ischaemun* is the characteristic climax species in this Loess Plateau habitat, and thus the vegetation seems likely to succeed to steppe grassland rather than forest.

16.5 Species replacement probabilities during successions

forest succession can be represented as a tree-by-tree replacement model . . .

A model of succession developed by Horn (1981) sheds some light on the successional process. Horn recognized that in a hypothetical forest community it would be possible to predict changes in tree species composition given two things. First, one would need to know for each tree species the probability that, within a particular time interval, an individual would be replaced by another of the same species or of a different species. Second, an initial species composition would have to be assumed.

Horn considered that the proportional representation of various species of saplings established beneath an adult tree reflected the probability of an individual tree's replacement by each of those species. Using this information, he estimated the probability, after 50 years, that a site now occupied by a given species will be taken over by another species or will still be occupied by

Table 16.1 A 50-year tree-by-tree transition matrix from Horn (1981). The table shows the probability of replacement of one individual by another of the same or different species 50 years hence.

	Occupant 50 years hence			
Present occupant	*Grey birch*	*Blackgum*	*Red maple*	*Beech*
Grey birch	0.05	0.36	0.50	0.09
Blackgum	0.01	0.57	0.25	0.17
Red maple	0.0	0.14	0.55	0.31
Beech	0.0	0.01	0.03	0.96

Table 16.2 The predicted percentage composition of a forest consisting initially of 100% grey birch. (After Horn, 1981.)

	Age of forest (years)						
Species	*0*	*50*	*100*	*150*	*200*	*∞*	*Data from old forest*
Grey birch	100	5	1	0	0	0	0
Blackgum	0	36	29	23	18	5	3
Red maple	0	50	39	30	24	9	4
Beech	0	9	31	47	58	86	93

the same species (Table 16.1). Thus, for example, there is a 5% chance that a location now occupied by grey birch will still support grey birch in 50 years' time, whereas there is a 36% chance that blackgum will take over, a 50% chance for red maple and 9% for beech.

Beginning with an observed distribution of the canopy species in a stand in New Jersey in the USA known to be 25 years old, Horn modeled the changes in species composition over several centuries. The process is illustrated in simplified form in Table 16.2 (which deals with only four species out of those present). The progress of this hypothetical succession allows several predictions to be made. Red maple should dominate quickly, whilst grey birch disappears. Beech should slowly increase to predominate later, with blackgum and red maple persisting at low abundance. All these predictions are borne out by what happens in the real succession (final column).

. . . that predicts a stable species composition and the time taken to reach it

The most interesting feature of Horn's so-called Markov chain model is that, given enough time, it converges on a stationary, stable composition that is independent of the initial composition of the forest. The outcome is inevitable (it depends only on the matrix of replacement probabilities) and will be achieved whether the starting point is 100% grey birch or 100% beech, 50% blackgum and 50% red maple, or any other combination (as long as adjacent areas provide a source of seeds of species not initially present). Korotkov *et al.* (2001) have used a similar Markov modeling approach to predict the time it should take to reach the climax state from any other stage in old-field successions culminating in mixed conifer–broadleaf forest in central Russia. From field abandonment to climax is predicted to take 480–540 years, whereas a mid-successional stage of birch forest with spruce undergrowth should take 320–370 years to reach the climax.

Since Markov models seem to be capable of generating quite accurate predictions, they may prove to be a useful tool in formulating plans for forest management. However, the models are simplistic and the assumption that transition probabilities remain constant in space and over time and are not affected by historic factors, such as initial biotic conditions and the order of arrival of species, are likely to be wrong in many cases (Facelli & Pickett, 1990). Hill *et al.* (2002) addressed the question of spatiotemporal variation in species replacement probabilities in a subtidal community succession including sponges, sea anenomes, polychaetes and encrusting algae. In this case, the predicted successions and endpoints were similar whether replacement probabilities were averaged or were subject to realistic spatial or temporal variation. And the outcomes of all three models were very similar to the observed community structure (Figure 16.12).

16.6 Biological mechanisms underlying successions

an ideal theory of succession should predict *and* explain

Despite the advantages of simple Markov models, a theory of succession should ideally not only predict but also explain. To do this, we need to consider the *biological* basis for the replacement values in the model, and here we have to turn to alternative approaches.

16.6.1 Competition–colonization trade-off and successional niche mechanisms

a trade-off between colonization and competitive ability?

Rees *et al.* (2001) drew together a diversity of experimental, comparative and theoretical approaches to produce some generalizations about vegetation dynamics. Early successional plants have a series of correlated traits, including high fecundity, effective dispersal, rapid growth when resources are abundant, and poor growth and survival when resources are scarce. Late successional species usually have the opposite traits, including an ability to grow, survive and compete when resources are scarce. In the absence of disturbance, late successional species eventually outcompete early species, because they reduce resources beneath the levels required by the early successional species. Early species persist for two reasons: (i) because their dispersal ability and high fecundity permits them to colonize and establish in recently disturbed sites before late successional species can arrive; or (ii) because rapid growth under resource-rich conditions allows them to temporarily outcompete late successional species even if they arrive at the same time. Rees and his colleagues refer to the first mechanism as a *competition–colonization trade-off* and the second as the *successional niche* (early conditions suit early species because of their niche requirements). The competition–colonization trade-off is strengthened by a further physiological inevitability. Huge differences in per capita seed production among plant species are inversely correlated to equally large variations in seed size; plants producing tiny seeds tend to produce many more of them than plants producing large seeds (see Section 4.8.5). Thus, Rees *et al.* (2001) point out that small-seeded species are good colonists (many propagules) but poor competitors (small seed food reserves), and vice versa for large-seeded species.

16.6.2 Facilitation

the importance of facilitation – but not always

Cases of competition–colonization trade-offs and/or successional niche relations are prominent in virtually every succession that has been described, including all those in the previous section. In addition, we have seen cases where early species may change the abiotic environment in ways (e.g. increased soil nitrogen) that make it easier for later species to establish and thrive. Thus, *facilitation* has to be added to the list of phenomena underlying some successions. We cannot say how common this state of affairs is. However, the converse is by no means uncommon; thus, many plant species alter the environment in a way that makes it more, rather than less, suitable for themselves (Wilson & Agnew, 1992). Thus, for example, woody vegetation can trap water from fog or ameliorate frosts, improving the conditions for growth of the species concerned, whilst grassy swards can intercept surface flowing water and grow better in the moister soil that is created.

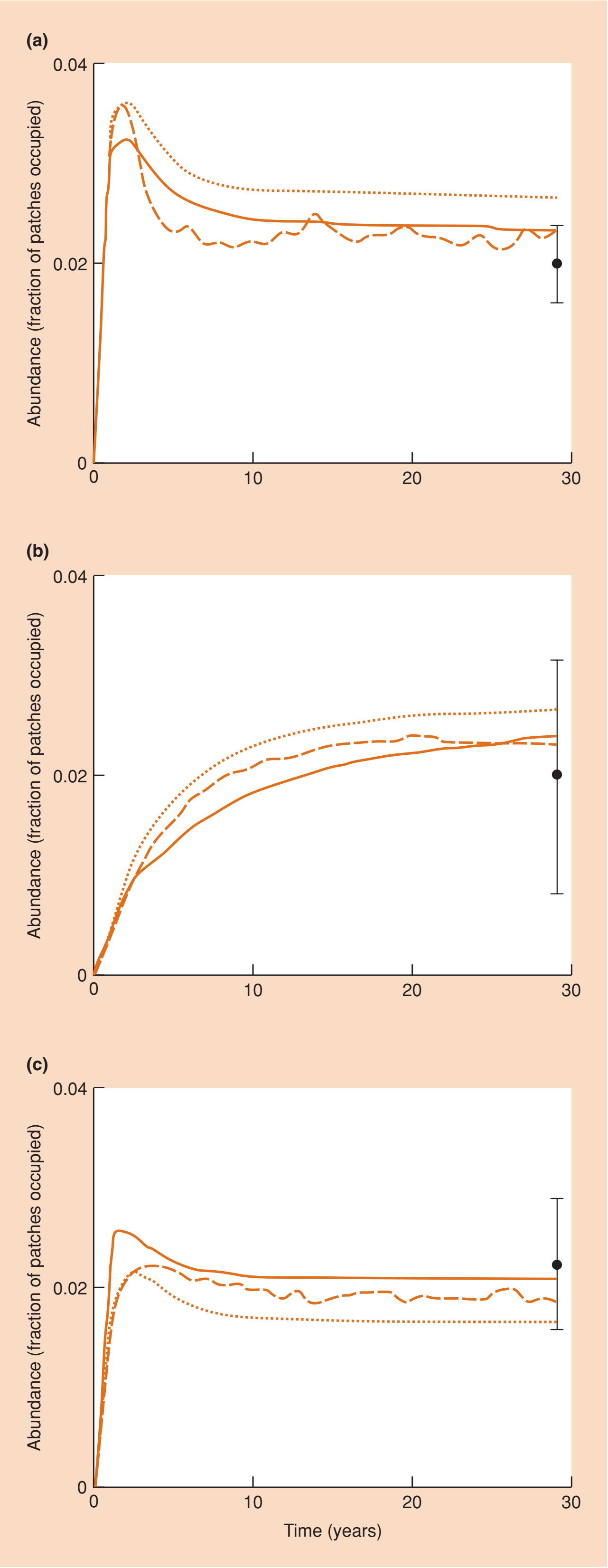


Figure 16.12 (*left*) Simulated recovery dynamics (Markov chain models) of three of the species that make up a subtidal community starting from 100% bare rock for spatially varying, time varying or homogeneous replacement probabilities: (a) the bryozoan *Crisia eburnea*, (b) the sea anenome *Metridium senile* and (c) encrusting coralline algae. The points at the end of each plot (±95% confidence intervals) are the observed abundances at a site in the Gulf of Maine, USA. (After Hill *et al.*, 2002.)

16.6.3 Interactions with enemies

an important role for seed predation?

Rees *et al.* (2001) point out that it follows from the competition–colonization trade-off that recruitment of competitively dominant plants should be determined largely by the rate of arrival of their seeds. This means that herbivores that reduce seed production are more likely to reduce the density of dominant competitors than of subordinates. Recall that this is just what happened in the sand-dune study described in Section 16.4.4. In a similar vein, Carson and Root (1999) showed that by removing insect predators of seeds, the meadow goldenrod (*Solidago altissima*), which normally appears about 5 years into an old-field succession, became dominant after only 3 years. This happened because release from seed predation allowed it to outcompete earlier colonists more quickly.

Thus, apart from competition–colonization trade-off, successional niche and facilitation, we have to add a fourth mechanism – interactions with enemies – if we are to fully understand plant successions. Experimental approaches, such as that employed to understand the role of seed predators, have also shown that the nature of soil food webs (Gange & Brown, 2002), the presence and disturbance of litter (Ganade & Brown, 2002), and the presence of mammals that consume vegetation (Cadenasso *et al.*, 2002) sometimes play roles in determining successional sequences.

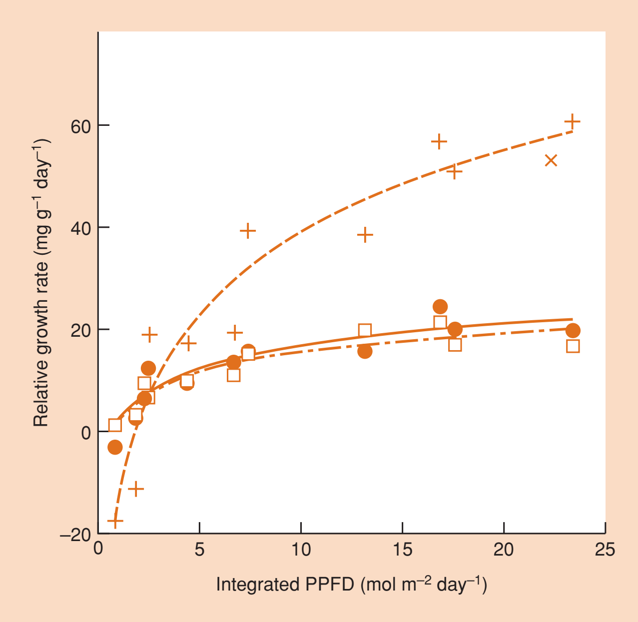


Figure 16.13 Relative growth rate (during the July–August 1994 growing season) of trembling aspen (+), northern red oak (●) and sugar maple (□) in relation to photosynthetic photon flux density (PPFD). (After Kaelke *et al.*, 2001.)

16.6.4 Resource-ratio hypothesis

Tilman's resource-ratio hypothesis emphasizes changing competitive abilities

A further example of a successional niche being responsible for species replacement is worth highlighting. Trembling aspen (*Populus tremuloides*) is a tree that appears earlier in successions in North America than northern red oak (*Quercus rubra*) or sugar maple (*Acer saccharum*). Kaelke *et al.* (2001) compared the growth of seedlings of all three species when planted along a gradient of light availability ranging from forest understory (2.6% of full light) to small clearings (69% of full light). The aspen outgrew the others when relative light availability exceeded 5%. However, there was a rank reversal in relative growth rate in deep shade; here the oak and maple, typical of later stages of succession, grew more strongly and survived better than aspen (Figure 16.13). In his *resource-ratio* hypothesis of succession, Tilman (1988) places strong emphasis on the role of changing relative competitive abilities of plant species as conditions slowly change with time. He hypothesized that species dominance at any point in a terrestrial succession is strongly influenced by the relative availability of two resources: not just by light (as demonstrated by Kaelke *et al.*, 2001) but also by a limiting soil nutrient (often nitrogen). Early in succession, the habitat experienced by seedlings has low nutrient but high light availability. As a result of litter input and the activities of decomposer organisms, nutrient availability increases with time – this can be expected to be particularly marked in primary successions that begin with a very poor soil (or no soil at all). But total plant biomass also increases with time and, in consequence, light penetration to the soil surface decreases. Tilman's ideas are illustrated in Figure 16.14 for five hypothetical species. Species A has the lowest requirement for the nutrient and the highest requirement for light at the soil surface. It has a short, prostrate growth form. Species E, which is the superior competitor in high-nutrient, low-light habitats, has the lowest requirement for light and the highest for the nutrient. It is a tall, erect species. Species B, C and D are intermediate in their requirements and each reaches its peak abundance at a different point along the soil nutrient–light gradient. There is scope for further experimental testing of Tilman's hypothesis.

16.6.5 Vital attributes

beyond just competitive ability: Noble and Slatyer's 'vital attributes'

Noble and Slatyer (1981) were also interested in defining the qualities that determine the place of a species in a succession. They called these properties *vital attributes*. The two most important relate to: (i) the method of recovery after

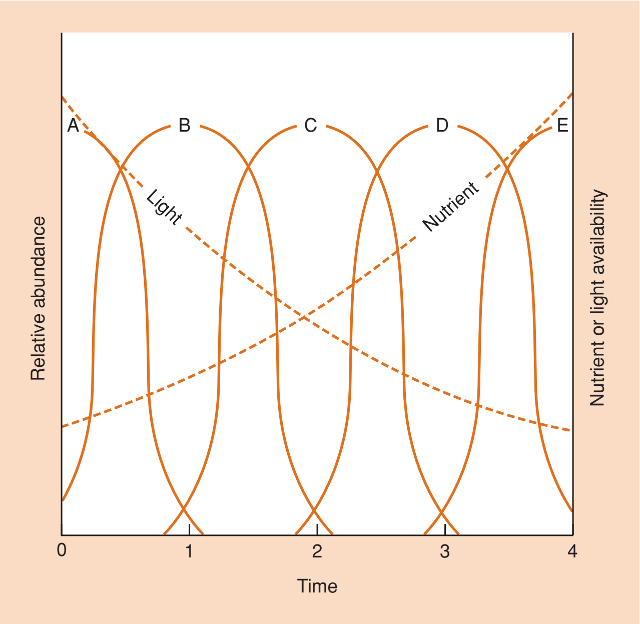


Figure 16.14 Tilman's (1988) resource-ratio hypothesis of succession. Five hypothetical plant species are assumed to be differentiated in their requirements for a limiting soil nutrient and light. During the succession, the habitat starts with a nutrient-poor soil but high light availability, changing gradually into a habitat with a rich soil but low availability of light at the soil surface. Relative competitive abilities change as conditions vary, and first one species and then another comes to dominate.

disturbance (four classes are defined: vegetative spread, V; seedling pulse from a seed bank, S; seedling pulse from abundant dispersal from the surrounding area, D; no special mechanism with just moderate dispersal from only a small seed bank, N); and (ii) the ability of individuals to reproduce in the face of competition (defined in terms of tolerance T at one extreme and intolerance I at the other). Thus, for example, a species may be classed as SI if disturbance releases a seedling pulse from a seed bank, and if the plants are intolerant of competition (being unable to germinate or grow in competition with older or more advanced individuals of either their own or another species). Seedlings of such a species could establish themselves only immediately after a disturbance, when competitors are rare. Of course, a seedling pulse fits well with such a pioneer existence. An example is the annual *Ambrosia artemisiifolia* which often figures early in old-field successions. In contrast, the American beech (*Fagus grandifolia*) could be classed as VT (being able to regenerate vegetatively from root stumps, and tolerant of competition since it is able to establish itself and reproduce in competition with older or more advanced individuals of either its own or another species) or NT (if no stumps remain, it would invade slowly via seed dispersal). In either case, it would eventually displace other species and form part of the 'climax' vegetation. Noble and Slatyer argue that it should be possible to classify all the species in an area according to these two vital attributes (to which relative longevity might be added as a third). Given this information, quite precise predictions about successional sequences should be possible.

Lightning-induced fires produce regular and natural disturbances in many ecosystems in arid parts of the world and two fire-response syndromes, analogous to two of Noble and Slatyer's disturbance recovery classes, can be identified. Resprouters have massive, deeply penetrating root systems, and survive fires as individuals, whereas reseeders are killed by the fire but re-establish through heat-stimulated germination and growth of seedlings (Bell, 2001). The proportion of species that can be classified as resprouters is higher in forest and shrubland vegetation of southwest Western Australia (Mediterranean-type climate) than in more arid areas of the continent. Bell suggests that this is because the Western Australian communities have been subject to more frequent fires than other areas, conforming to the hypothesis that short intervals between fires (averaging 20 years or less in many areas of Western Australia) promote the success of resprouters. Longer intervals between fires, on the other hand, allow fuel loads to build up so that fires are more intense, killing resprouters and favoring the reseeding strategy.

r and *K* species and succession

The consideration of vital attributes from an evolutionary point of view suggests that certain attributes are likely to occur together more often than by chance. We can envisage two alternatives that might increase the fitness of an organism in a succession (Harper, 1977), either: (i) the species reacts to the competitive selection pressures and evolves characteristics that enable it to persist longer in the succession, i.e. it responds to *K* selection; or (ii) it may develop more efficient mechanisms of escape from the succession, and discover and colonize suitable early stages of succession elsewhere, i.e. it responds to *r* selection (see Section 4.12). Thus, from an evolutionary point of view, good colonizers can be expected to be poor competitors and vice versa. This is evident in Table 16.3, which lists some physiological characteristics that tend to go together in early and late successional plants.

16.6.6 The role of animals in successions

necromass and the late successional role of trees

The structure of communities and the successions within them have most often been treated as essentially botanical matters. There are obvious reasons for this. Plants commonly provide most of the biomass and the physical structure of communities; moreover, plants do not hide or run away and this makes it rather easy to assemble species lists, determine abundances and detect change. The massive contribution that plants make to

Table 16.3 Physiological characteristics of early and late successional plants. (After Bazzaz, 1979.)

Attribute	*Early successional plants*	*Late successional plants*
Seed dispersal in time	Well dispersed	Poorly dispersed
Seed germination:		
enhanced by		
light	Yes	No
fluctuating temperatures	Yes	No
high NO_3^-	Yes	No
inhibited by		
far-red light	Yes	No
high CO_2 concentration	Yes	No?
Light saturation intensity	High	Low
Light compensation point	High	Low
Efficiency at low light	Low	High
Photosynthetic rates	High	Low
Respiration rates	High	Low
Transpiration rates	High	Low
Stomatal and mesophyll resistances	Low	High
Resistance to water transport	Low	High
Recovery from resource limitation	Fast	Slow
Resource acquisition rates	Fast	Slow?

determining the character of a community is not just a measure of their role as the primary producers, it is also a result of their slowness to decompose. The plant population not only contributes biomass to the community, but is also a major contributor of *necromass*. Thus, unless microbial and detritivore activity is fast, dead plant material accumulates as leaf litter or as peat. Moreover, the dominance of trees in so many communities comes about because they accumulate dead material; the greater part of a tree's trunk and branches is dead. The tendency in many habitats for shrubs and trees to succeed herbaceous vegetation comes largely from their ability to hold leaf canopies (and root systems) on an extending skeleton of predominantly dead support tissue (the heart wood).

animals are often affected by, but may also affect, successions

Animal bodies decompose much more quickly, but there are situations where animal remains, like those of plants, can determine the structure and succession of a community. This happens when the animal skeleton resists decomposition, as is the case in the accumulation of calcified skeletons during the growth of corals. A coral reef, like a forest or a peat bog, gains its structure, and drives its successions, by accumulating its dead past. Reef-forming corals, like forest trees, gain their dominance in their respective communities by holding their assimilating parts progressively higher on predominantly dead support. In both cases, the organisms have an almost overwhelming effect on the abiotic environment, and they 'control' the lives of other organisms within it. The coral reef community (dominated by an animal, albeit one with a plant symbiont) is as structured, diverse and dynamic as a tropical rainforest.

The fact that plants dominate most of the structure and succession of communities does not mean that animals always follow the communities that plants dictate. This will often be the case, of course, because the plants provide the starting point for all food webs and determine much of the character of the physical environment in which animals live. But it is also sometimes the animals that determine the nature of the plant community. We have already seen how seed-eating insects and rodents can slow successions in old fields and sand dunes by causing a higher seed mortalilty of later successional species. A particularly dramatic example of a role for animals, and on a much larger scale, comes from the savanna at Ndara in Kenya. The vegetation in savannas is often held in check by grazers. The experimental exclusion of elephants from a plot of savanna led to a more than threefold increase in the density of trees over a 10-year period (work by Oweyegha-Afundaduula, reported in Deshmukh, 1986).

More often though, animals are passive followers of successions amongst the plants. This is certainly the case for passerine bird species in an old-field succession (Figure 16.15). Arbuscular mycorrhizal fungi (see Section 13.8.2), which show a clear sequence of species replacement in the soils associated with an old-field succession (Johnson *et al.*, 1991), may also be passive followers of the plants. But this does not mean that the birds, which eat seeds, or the fungi, which affect plant growth and survival, do not influence the succession in its course. They probably do.

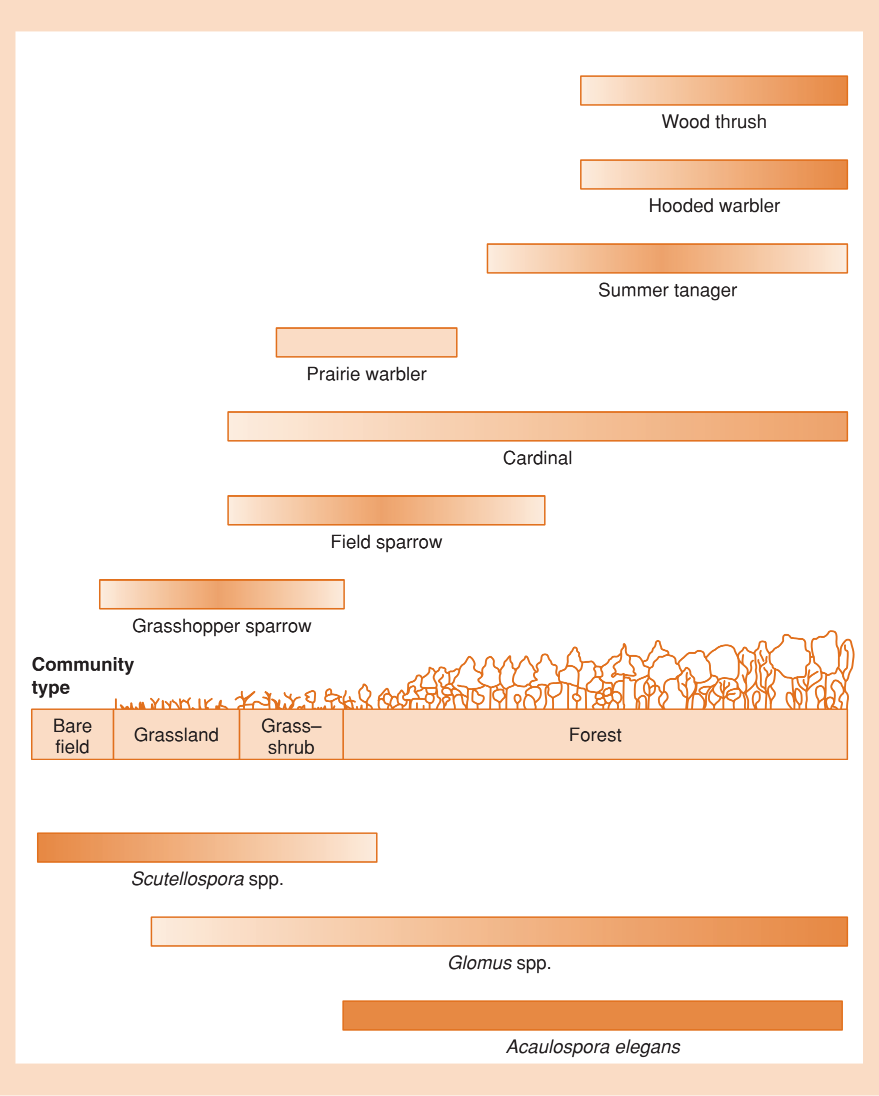


Figure 16.15 Top: bird species distributions along a plant succession gradient in the Piedmont region of Georgia, USA. Differential shading indicates relative abundance of the birds. (After Johnston & Odum, 1956; from Gathreaux, 1978.) Bottom: distributions of vesicular–arbuscular mycorrhizae in the soils associated with an old-field succession in Minnesota. Differential shading indicates relative abundance of spores of species in the genera *Scutellospora, Glomus* and *Acaulospora*. (After Johnson *et al.*, 1991).

16.6.7 Concept of the climax

Do successions come to an end? It is clear that a stable equilibrium will occur if individuals that die are replaced on a one-to-one basis by young of the same species. At a slightly more complex level, Markov models (see Section 16.5) tell us that a stationary species composition should, in theory, occur whenever the replacement probabilities (of one species by itself or by any one of several others) remain constant through time.

The concept of the climax has a long history. One of the earliest students of succession, Frederic Clements (1916), is associated with the idea that a single climax will dominate in any given climatic region, being the endpoint of all successions, whether they happened to start from a sand dune, an abandoned old field or even a pond filling in and progressing towards a terrestrial climax. This *monoclimax* view was challenged by many ecologists, amongst whom Tansley (1939) was prominent. The *polyclimax* school of thought recognized that a local climax may be governed by one factor or a combination of factors: climate, soil conditions, topography, fire and so on. Thus, a single climatic area could easily contain a number of specific climax types. Later still, Whittaker (1953) proposed his climax pattern hypothesis. This conceives a continuity of climax types, varying gradually along environmental gradients and not necessarily separable into discrete climaxes. (This is an extension of Whittaker's approach to gradient analysis of vegetation, discussed in Section 16.3.1.)

climaxes may be approached rapidly – or, so slowly that they are rarely ever reached

In fact, it is very difficult to identify a stable climax community in the field.

Usually, we can do no more than point out that the rate of change of succession slows down to the point where any change is imperceptible to us. In this context, the subtidal rockface succession illustrated in Figure 16.12 is unusual in that convergence to a climax took only a few years. Old-field successions might take 100–500 years to reach a 'climax', but in that time the probabilities of further fires or hurricanes are so high that a process of succession may rarely go to completion. If we bear in mind that forest communities in northern temperate regions, and probably also in the tropics, are still recovering from the last glaciation (see Chapter 1), it is questionable whether the idealized climax vegetation is often reached in nature.

16.7 Communities in a spatiotemporal context: the patch dynamics perspective

the idea of a successional mosaic

A forest, or a rangeland, that appears to have reached a stable community structure when studied on a scale of hectares, will always be a mosaic of miniature successions. Every time a tree falls or a grass tussock dies, an opening is created in which a new succession starts. One of the most seminal papers in the history of ecology was entitled 'Pattern and process in the plant community' (Watt, 1947). Part of the pattern of a community is caused by the dynamic processes of deaths, replacements and microsuccessions that the broad view may conceal. Thus, although we can point to patterns in community composition in space (see Section 16.3) and in time (see Section 16.4), it is often more meaningful to consider space and time together.

disturbance . . . gaps . . . dispersal . . . recruitment

We have already seen that disturbances that open up gaps are common in all kinds of community. The formation of gaps is obviously of considerable significance to sessile or sedentary species that have a requirement for open space, but gaps have also proved to be important for mobile species such as invertebrates on the beds of streams (Matthaei & Townsend, 2000). The patch dynamics concept of communities views the habitat as patchy, with patches being disturbed and recolonized by individuals of various species. Implicit in the patch dynamics view is a critical role for disturbance as a reset mechanism (Pickett & White, 1985). A single patch without migration is, by definition, a closed system, and any extinction caused by disturbance would be final. However, extinction within a patch in an open system is not necessarily the end of the story because of the possibility of reinvasion from other patches.

Fundamental to the patch dynamics perspective is recognition of the importance of migration between habitat patches. This may involve adult individuals, but very often the process of most significance is the dispersal of immature propagules (seeds, spores, larvae) and their recruitment to populations within habitat patches. The order of arrival and relative recruitment levels of individual species may determine or modify the nature and outcome of population interactions in the community (Booth & Brosnan, 1995).

In Section 16.4.1 we identified two fundamentally different kinds of situations within communities: those in which some species are strongly competitively superior are *dominance controlled* (equivalent to succession) and those in which all species have similar competitive abilities are *founder controlled*. Within the patch dynamics framework, the dynamics of these two situations are different and we deal with them in turn.

16.7.1 Dominance-controlled communities

dominance control and succession

In patch dynamics models where some species are competitively superior to others, the effect of the disturbance is to knock the community back to an earlier stage of succession (Figure 16.16). The open space is colonized by one or more of a group of opportunistic, early successional species (p_1, p_2, etc., in Figure 16.16). As time passes, more species invade, often those with poorer powers of dispersal. These eventually reach maturity, dominating mid-succession (m_1, m_2, etc.) and many or all of the pioneer species are driven to extinction. Later still, the community regains the climax stage when the most efficient competitors (c_1, c_2, etc.) oust their neighbors. In this sequence, diversity starts at a low level, increases at the mid-successional stage and usually declines again at the climax. The gap essentially undergoes a minisuccession.

disturbance scale and phasing

Some disturbances are synchronized, or phased, over extensive areas. A forest fire may destroy a large tract of a climax community. The whole area then proceeds through a more or less synchronous succession, with diversity increasing through the early colonization phase and falling again through competitive exclusion as the climax is approached. Other disturbances are much smaller and produce a patchwork of habitats. If these disturbances are unphased, the resulting community comprises a mosaic of patches at different stages of succession. A climax mosaic, produced by unphased disturbances, is much richer in species than an extensive area undisturbed for a very long period and occupied by just one or a few dominant climax species. Towne (2000) monitored the plant species that established in prairie grassland where large ungulates had died (mainly bison, *Bos bison*). Scavengers remove most of the body tissue but copious amounts of body fluids and decomposition products seep into the soil. The flush of nutrients combined with death of the previous vegetation produces a competitor-free, disturbed area where resources are unusually abundant. The patches are also exceptional because the soil has not been disturbed (as it would be after a ploughed field is abandoned or a badger makes a burrow); thus,

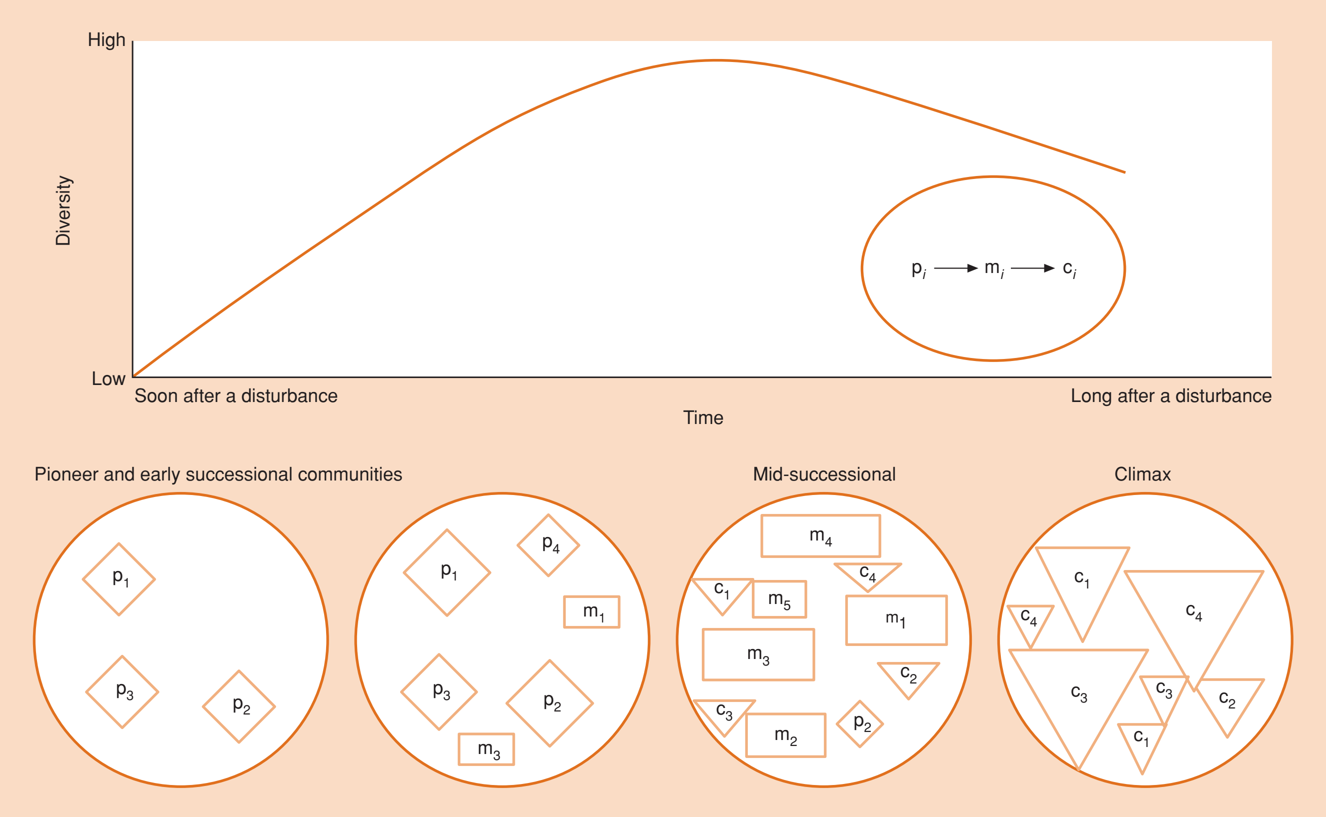


Figure 16.16 Hypothetical minisuccession in a gap. The occupancy of gaps is reasonably predictable. Diversity begins at a low level as a few pioneer (p_i) species arrive; reaches a maximum in mid-succession when a mixture of pioneer, mid-successional (m_i) and climax (c_i) species occur together; and drops again as competitive exclusion by the climax species takes place.

the colonizing plants do not derive from the local seed bank. The unusual nature of the disturbed patches means that many of the pioneer species are rare in the prairie as a whole, and carcass sites contribute to species diversity and community heterogeneity for many years.

16.7.2 Frequency of gap formation

Connell's 'intermediate disturbance hypothesis'

The influence that disturbances have on a community depends strongly on the frequency with which gaps are opened up. In this context, the intermediate disturbance hypothesis (Connell, 1978; see also the earlier account by Horn, 1975) proposes that the highest diversity is maintained at intermediate levels of disturbance. Soon after a severe disturbance, propagules of a few pioneer species arrive in the open space. If further disturbances occur frequently, gaps will not progress beyond the pioneer stage in Figure 16.16, and the diversity of the community as a whole will be low. As the interval between disturbances increases, the diversity will also increase because time is available for the invasion of more species. This is the situation at an intermediate frequency of disturbance. At very low frequencies of disturbance, most of the community for most of the time will reach and remain at the climax, with competitive exclusion having reduced diversity. This is shown diagrammatically in Figure 16.17, which plots the pattern of species richness to be expected as a result of unphased high, intermediate and low frequencies of gap formation, in separate patches and for the community as a whole.

boulders on a rocky shore that vary in disturbability . . .

The influence of the frequency of gap formation was studied in southern California by Sousa (1979a, 1979b), in an intertidal algal community associated with boulders of various sizes. Wave action disturbs small boulders more often than large ones. Using a sequence of photographs, Sousa estimated the probability that a given boulder would be moved during the course of 1 month. A class of mainly small boulders (which required a force of less than 49 Newtons to move them) had a monthly probability of movement of 42%. An intermediate class (which required a force of 50–294 N) had a much smaller monthly probability of movement,

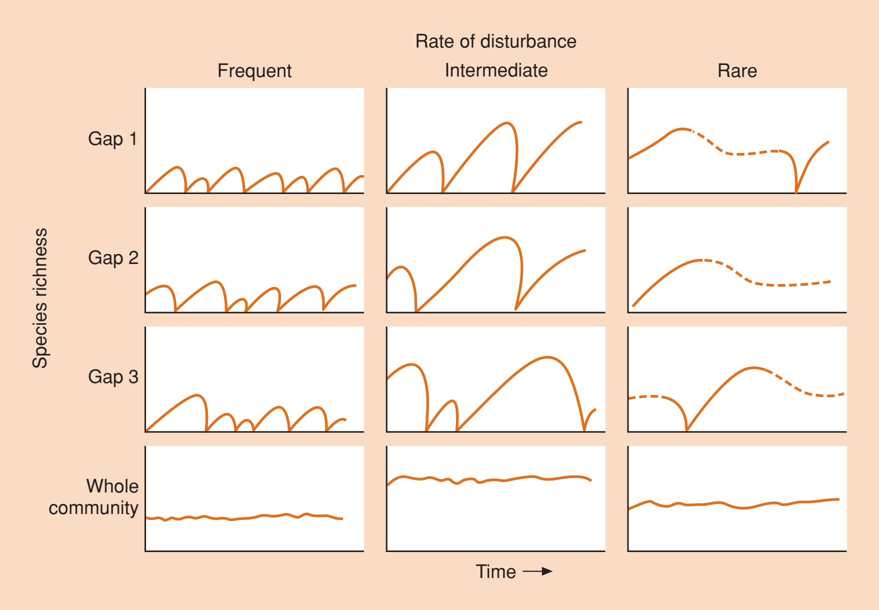


Figure 16.17 Diagrammatic representation of the time course of species richness in three gaps, and in the community as a whole, at three frequencies of disturbance. The disturbance is unphased. Dashed lines indicate the phase of competitive exclusion as the climax is approached.

9%. Finally, the class of mainly large boulders (which required a force >294 N) moved with a probability of only 0.1% per month. The 'disturbability' of the boulders had to be assessed in terms of the force required to move them, rather than simply in terms of top surface area, because some rocks which appeared to be small were actually stable portions of larger, buried boulders, and a few large boulders with irregular shapes moved when a relatively small force was applied. The three classes of boulder (<49, 50–294 and >294 N) can be viewed as patches exposed to a decreasing frequency of disturbance when waves caused by winter storms overturn them.

Species richness increased during early stages of succession through a process of colonization by the pioneer green alga *Ulva* spp. and various other algae, but declined again at the climax because of competitive exclusion by the perennial red alga *Gigartina canaliculata*. It is important to note that the same succession occurred on small boulders that had been artificially made stable. Thus, variations in the communities associated with the surfaces of boulders of different size were not simply an effect of size, but rather of differences in the frequency with which they were disturbed.

. . . provide support for the hypothesis

Communities on unmanipulated boulders in each of the three size/disturbability classes were assessed on four occasions. Table 16.4 shows that the percentage of bare space decreased from small to large boulders, indicating the effects of the greater frequency of disturbance of small boulders. Mean species richness was lowest on the regularly disturbed small boulders. These were dominated most commonly by *Ulva* spp. (and barnacles, *Chthamalus fissus*). The highest levels of species richness were consistently recorded on the intermediate boulder class. Most held mixtures of three to five abundant species from all successional stages. The largest boulders had a lower mean species richness than the intermediate class, although a monoculture was achieved on only a few boulders. *G. canaliculata* covered most of the rock surfaces.

These results offer strong support for the intermediate disturbance hypothesis as far as frequency of appearance of gaps is concerned. However, we must be careful not to lose sight of the fact that this is a highly stochastic process. By chance, some small boulders were not overturned during the period of study. These few were dominated by the climax species *G. canaliculata*. Conversely, two large boulders in the May census had been overturned, and these became dominated by the pioneer *Ulva*. On average, however, species richness and species composition followed the predicted pattern.

This study deals with a single community conveniently composed of identifiable patches (boulders) that become gaps (when overturned by waves) at short, intermediate or long intervals. Recolonization occurs mainly from propagules derived from other patches in the community. Because of the pattern of disturbance, this mixed boulder community is more diverse than would be one with only large boulders.

further support from a study of streams

Disturbances in small streams often take the form of bed movements during periods of high discharge. Because of differences in flow regimes and in the substrates of stream beds, some stream communities are disturbed more frequently and to a larger extent than others. This variation was assessed in 54 stream sites in the Taieri River in New Zealand (Townsend *et al.*, 1997) by recording the frequency at which at least 40% (chosen arbitrarily) of the bed moved and the average percentage that

Census date	*Boulder class (N)*	*Percentage bare space*	*Species richness*		
			Mean	*Standard error*	*Range*
November 1975	< 49	78.0	1.7	0.18	1–4
	50–294	26.5	3.7	0.28	2–7
	> 294	11.4	2.5	0.25	1–6
May 1976	< 49	66.5	1.9	0.19	1–5
	50–294	35.9	4.3	0.34	2–6
	> 294	4.7	3.5	0.26	1–6
October 1976	< 49	67.7	1.9	0.14	1–4
	50–294	32.2	3.4	0.40	2–7
	> 294	14.5	2.3	0.18	1–6
May 1977	< 49	49.9	1.4	0.16	1–4
	50–294	34.2	3.6	0.20	2–5
	> 294	6.1	3.2	0.21	1–5

Table 16.4 Seasonal patterns in bare space and species richness on boulders in each of three classes, categorized according to the force (in Newtons) required to move them. (After Sousa, 1979b.)

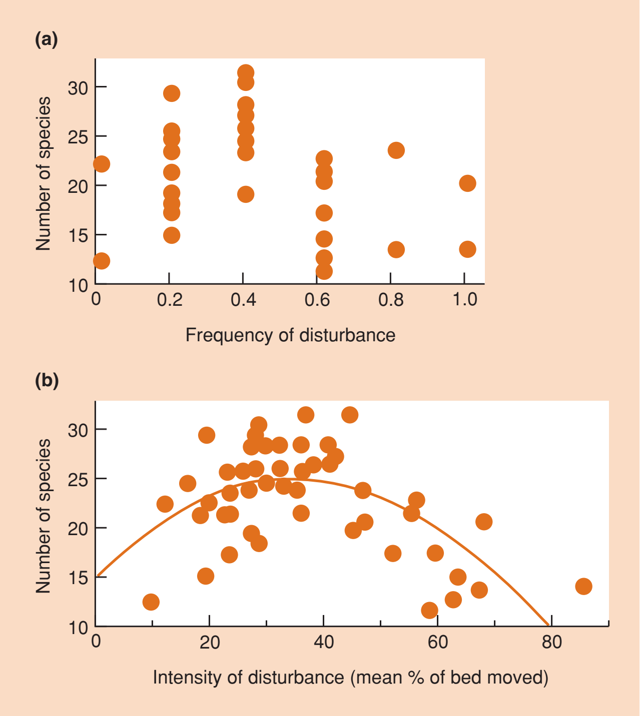


Figure 16.18 Relationship between invertebrate species richness and: (a) frequency of disturbance – assessed as the number of occasions in 1 year when more than 40% of the bed moved (analysis of variance significant at $P < 0.0001$), and (b) intensity of disturbance – average percentage of the bed that moved (polynomial regression fitted, relationship significant at $P < 0.001$) assessed at 54 stream sites in the Taieri River, New Zealand. The patterns are essentially the same; intensity and frequency of disturbance are strongly correlated. (After Townsend *et al*., 1997.)

moved (assessed on five occasions during 1 year, using painted particles of sizes characteristic of the stream bed in question). The pattern of richness of insect species conformed to the intermediate disturbance hypothesis (Figure 16.18). It is likely that low richness at high frequencies and intensities of disturbance reflects the inability of many species to persist in such situations. Whether low richness at low frequencies and intensities of disturbance is due to competitive exclusion, as proposed in the intermediate disturbance hypothesis, remains to be tested.

16.7.3 Formation and filling of gaps

influence of gap size . . .

Gaps of different sizes may influence community structure in different ways because of contrasting mechanisms of recolonization. The centers of very large gaps are most likely to be colonized by species producing propagules that travel relatively great distances. Such mobility is less important in small gaps, since most recolonizing propagules will be produced by adjacent established individuals. The smallest gaps of all may be filled simply by lateral movements of individuals around the periphery.

Intertidal beds of mussels provide excellent opportunities to study the processes of formation and filling-in of gaps. In the absence of disturbance, mussel beds may persist as extensive monocultures. More often, they are an ever-changing mosaic of many species that inhabit gaps formed by the action of waves. Gaps can appear virtually anywhere, and may exist for years as islands in a sea of mussels. The size of these gaps at the time of formation ranges from the dimensions of a single mussel to hundreds of square meters. In general, a mussel or group of mussels becomes infirm or damaged through disease, predation, old age or, most often, the effects of storm waves or battering by logs. Gaps begin to fill as soon as they are formed.

Table 16.5 Measures of area, perimeter and perimeter : area ratio for the experimental gaps created in two experiments on semiexposed shores in southeast Brazil. (From Tanaka & Magalhaes, 2002.)

	Area (cm^2)	*Perimeter (cm)*	*Perimeter : area ratio*
Patch size effects			
Square	25	20	0.8
Square	100	40	0.2
Square	400	80	0.2
Patch shape effects			
Square	100.0	40.0	0.4
Circle	78.5	31.4	0.4
Rectangle	112.5	45.0	0.4
Sector	190.1	78.6	0.4

. . . and gap shape

In their experimental study of mussel beds of *Brachidontes solisianus* and *B. darwinius* in Brazil, Tanaka and Magalhaes (2002) aimed to determine the differential effects of patch size and perimeter : area ratio on the dynamics of succession. In an experiment on one moderately exposed shoreline, they created square gaps with different areas (because of identical shapes, the bigger squares had smaller perimeter : area ratios) (Table 16.5). On a nearby and physically very similar shore, they created patches of four different shapes and chose areas for each that produced identical perimeter : area ratios (Figure 16.19a). Note that a circle has the most perimeter per unit area of any shape. The gap sizes were within the range observed for natural gaps, which did not differ on the two shores (Figure 16.19b).

colonization of gaps . . .
. . . in mussel beds, . . .

Higher densities of the herbivorous limpet *Collisella subrugosa* occurred in the small gaps in the first 6 months after gap formation (Figure 16.19c). Small gaps, compared to medium and large gaps, were also most quickly colonized by lateral migration of the two mussel species, but with *B. darwinius* predominating. The larger gaps had higher densities of the barnacle *Chthamalus bisinuatus* and sheltered more limpets at their edges, while central areas had more *Brachiodontes* recruited from larvae after 6 months (Figure 16.19d). The gaps with identical perimeter : area ratios showed very similar patterns of colonization despite their different sizes, emphasizing that colonization dynamics are mainly determined by distance from adjacent sources of colonists.

The limpet is probably associated with patch edges because here they are less vulnerable to visually hunting predators. The negative relationship between distributions of the limpet and the barnacle may be due to the former dislodging the latter from the substrate. Tanaka and Magalhaes conclude that the mussel *B. darwinius* is a more effective colonist of disturbed patches than *B. solisianus*, and suggest that *B. darwinius* would gradually come to dominate the whole of the shoreline if it were not for occasional massive recruitment events of *B. solisianus*.

. . . in grassland . . .

The pattern of colonization of gaps in mussel beds is repeated in almost every detail in the colonization of gaps in grassland caused by burrowing animals or patches killed by urine. Initially, leaves lean into the gap from plants outside it. Then colonization begins by clonal spread from the edges, and a very small gap may close up quickly. In larger gaps, new colonists may enter as dispersed seed, or germinate from the seed bank in the soil. Over 2–3 years the vegetation begins to acquire the character that it had before the gap was formed.

. . . and in mangrove forest

The gaps produced in forests vary greatly in size. Lightning-induced gaps in mangrove forest in the Dominican Republic, for example, range from 200 to 1600 m^2 or more (Figure 16.20). Lightning almost always kills groups of trees in a 20–30 m circle, and the trees remain as standing dead for several years. In a forest dominated by red mangrove *Rhizophora mangle* and white mangrove *Laguncularia racemosa*, and with some black mangrove *Avicennia germinans*, Sherman *et al.* (2000) compared the performance of the three species in lightning gaps and under forest canopy. Seedling density did not differ in gaps and intact forest, but sapling density and the growth rates of all three species were much higher in the gaps (Table 16.6). However, gap regeneration was dominated by *R. mangle* because its mortality rate was much lower in gaps than was the case for the other species. Sherman *et al.* (2000) note that the peat mat on the forest floor usually collapses after lightning damage, resulting in increased levels of standing water. They suggest that the success of *R. mangle* in gaps is due to their higher tolerance of flooding conditions.

Organisms other than plants can also be overrepresented in gaps. In a study of tropical rainforest in Costa Rica, Levey (1988) found that nectarivorous and frugivorous birds were much more abundant in treefall gaps, reflecting the fact that understory plants in gaps tend to produce more fruit over a longer period than conspecifics fruiting under a closed canopy.

16.7.4 Founder-controlled communities

founder-controlled communities: a competitive lottery not a predictable succession

In the dominance-controlled communities discussed in Section 16.7.1 there was the familiar *r* and *K* selection dichotomy in which colonizing ability and competitive status are inversely related. In founder-controlled communities, on the other hand, all species are both good colonists and essentially equal competitors; thus, within a patch opened by disturbance, a competitive lottery rather than a predictable succession is to

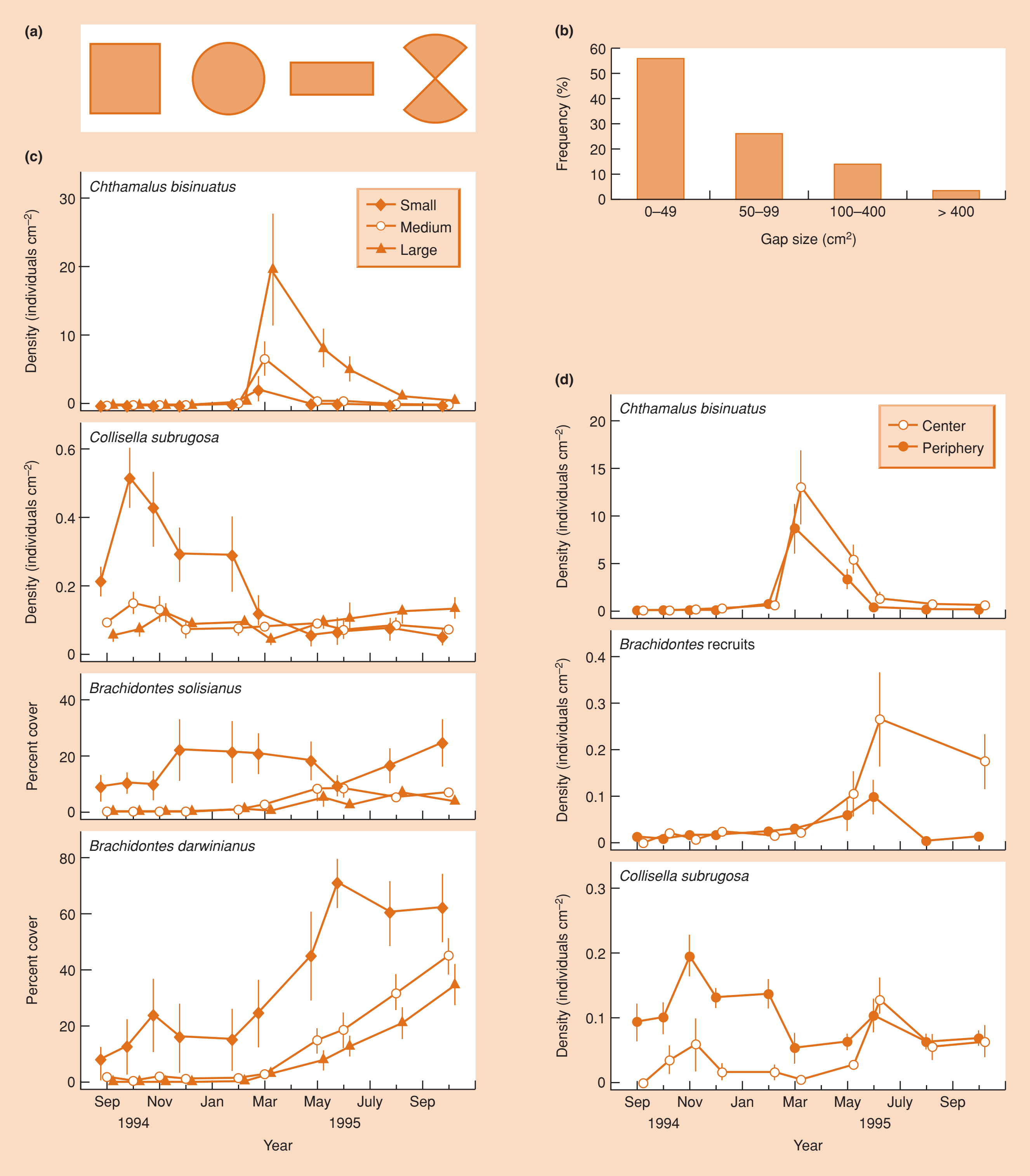


Figure 16.19 (a) The four shapes used in patch-shape experiments: square, circle, rectangle and 'sector' (see Table 16.5). (b) Size distribution of natural gaps in the mussel beds. (c) Mean abundances (±SE) of four colonizing species in experimentally cleared small, medium and large square gaps. (d) Recruitment of three species at the periphery (within 5 cm of the gap edge) and in the center of 400 cm^2 square gaps. (After Tanaka & Magalhaes, 2002.)

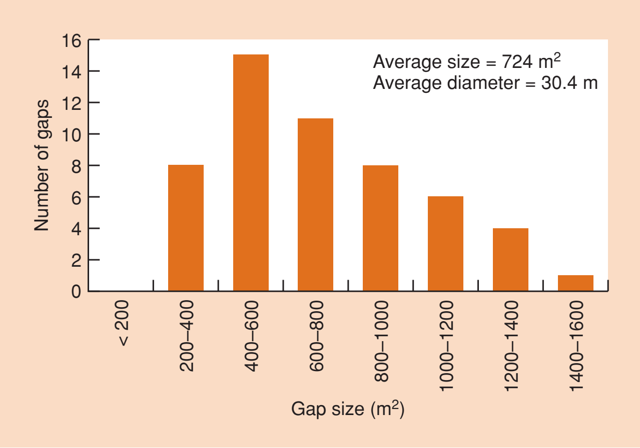


Figure 16.20 Frequency distribution of gaps created by lightning in a tropical mangrove forest in the Dominican Republic. (After Sherman *et al.*, 2000.)

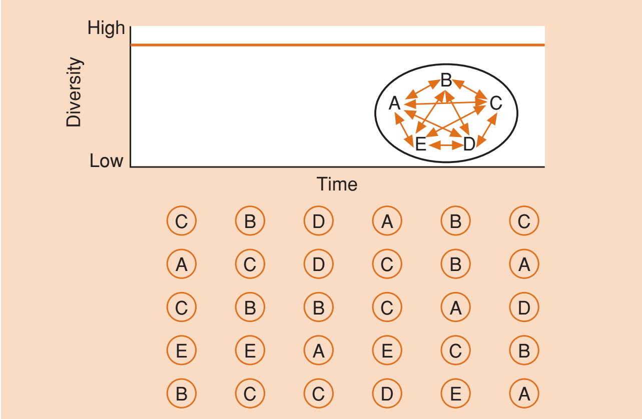


Figure 16.21 Hypothetical competitive lottery: occupancy of gaps which periodically become available. Each of species A–E is equally likely to fill a gap, regardless of the identity of its previous occupant. Species richness remains high and relatively constant.

be expected. If a large number of species are approximately equivalent in their ability to invade gaps, are equally tolerant of the abiotic conditions and can hold the gaps against all comers during their lifetime, then the probability of competitive exclusion may be much reduced in an environment where gaps are appearing continually and randomly. A further condition for coexistence is that the number of young that invade and occupy the gaps should not be consistently greater for parent populations that produce more offspring, otherwise the most productive species would come to monopolize space even in a continuously disturbed environment.

fish coexisting on coral reefs

If these idealized conditions are met, it is possible to envisage how the occupancy of a series of gaps will change through time (Figure 16.21). On each occasion that an organism dies (or is killed) the gap is reopened for invasion. All conceivable replacements are possible and species richness will be maintained at a high level. Some tropical reef communities of fish may conform to this model (Sale, 1977, 1979). They are extremely diverse. For example, the number of species of fish on the Great Barrier Reef ranges from 900 in the south to 1500 in the north, and more than 50 resident species may be recorded on a single patch of reef 3 m in diameter. Only a proportion of this diversity is likely to be attributable to resource partitioning of food and space – indeed, the diets of many of the coexisting species are very similar. In this community, vacant living space seems to be a crucial limiting factor, and it is generated unpredictably in space and time when a resident dies or is killed. The lifestyles of the species match this state of affairs. They breed often, sometimes year-round, and produce numerous clutches of dispersive eggs or larvae. It can be argued that the species compete in a lottery for living space in which larvae are the tickets, and the first arrival at the vacant space wins the site, matures quickly and holds the space for its lifetime.

Three species of herbivorous pomacentrid fish co-occur on the upper slope of Heron Reef, part of the Great Barrier Reef off eastern Australia. Within rubble patches, the available space is occupied by a series of contiguous and usually nonoverlapping territories, each up to 2 m² in area, held by individuals of *Eupomacentrus apicalis*, *Plectroglyphidodon lacrymatus* and *Pomacentrus wardi*. Individuals hold territories throughout their juvenile and adult life and defend them against a broad range of chiefly herbivorous species, including conspecifics. There seems to be no particular tendency for space initially held by one species to be

Table 16.6 Initial size, and growth and mortality rates over a 1-year period of saplings of three mangrove species in lightning-induced gaps and under intact forest canopy. (After Sherman *et al.*, 2000.)

	Initial sapling diameter (cm ± SE)		*Growth rate–diameter increment (cm ± SE)*		*Mortality (%)*	
	Gaps	*Canopy*	*Gaps*	*Canopy*	*Gaps*	*Canopy*
Rhizophora mangle	1.9 ± 0.06	2.3 ± 0.06	0.58 ± 0.03	0.09 ± 0.01	9	16
Laguncularia racemosa	1.7 ± 0.11	1.8 ± 0.84	0.46 ± 0.04	0.11 ± 0.06	32	40
Avicennia germinans	1.3 ± 0.25	1.7 ± 0.45	0.51 ± 0.04	–	56	88

Table 16.7 Numbers of individuals of each species observed occupying sites, or parts of sites, that had been vacated during the immediately prior interperiod between censuses through the loss of residents of each species. The sites vacated through loss of 120 residents have been reoccupied by 131 fish; the species of the new occupant is not dependent on the species of the previous resident.

	Reoccupied by:		
Resident lost	*E. apicalis*	*P. lacrymatus*	*P. wardi*
Eupomacentrus apicalis	9	3	19
Plectroglyphidodon lacrymatus	12	5	9
Pomacentrus wardi	27	18	29

taken up, following mortality, by the same species. Nor is any successional sequence of ownership evident (Table 16.7). *P. wardi* both recruited and lost individuals at a higher rate than the other two species, but all three species appear to have recruited at a sufficient level to balance their rates of loss and maintain a resident population of breeding individuals.

plants in grassland or forest

Thus, the maintenance of high reef diversity depends, at least in part, on the unpredictability of the supply of living space; and as long as all species win some of the time and in some places, they will continue to put larvae into the plankton, and hence, into the lottery for new sites. An analogous situation has been postulated for the highly diverse chalk grasslands of Great Britain (Grubb, 1977) and even for trees in temperate and tropical forest gaps (Busing & Brokaw, 2002). Any small gap that appears is rapidly exploited, by a seed in grassland and very often by a sapling in a forest gap. In these cases, the tickets in the lottery are saplings or seeds (either in the act of dispersal or as components of a persistent seed bank in the soil). Which seeds or saplings develop to established plants, and therefore which species comes to occupy the gap, may depend on a strong random element since many species overlap in their requirements for successful growth. The successful plant rapidly establishes itself and retains the patch for its lifetime, in a similar way to the reef fish described above.

16.8 Conclusions: the need for a landscape perspective

founder and dominance control as a continuum of possibilities

The lottery hypothesis and the notion of the founder-controlled community were important steps in the development of our understanding of the range of community dynamics that can occur. However, these should be viewed not as hard and fast rules to which some communities are subject, but rather as extremes on a continuum from dominance to founder control. Real communities may be closer to one or other end of this continuum, but in reality component species or component patches may be dominance controlled or founder controlled within the same community. Syms and Jones (2000), for example, acknowledge that more than half of within-reef variation in fish species composition in their study of patch reefs in the Great Barrier Reef was attributable to unexplained, and thus possibly stochastic, factors such as those emphasized in the lottery hypothesis. But a significant proportion of variation could be explained by specific habitat requirements of the constituent species.

importance of a 'landscape ecology' perspective

More generally, no community is truly the homogeneous, temporally invariant system described by simple Lotka–Volterra mathematics and exemplified by laboratory microcosms, although some are less variable than others. In most real communities, population dynamics will be spatially distributed and temporal variation will be present. In a closed system, composed of a single patch, species extinctions can occur for two very different reasons: (i) as a result of biotic instability caused by competitive exclusion, overexploitation and other strongly destabilizing species interactions; or (ii) as a result of environmental instability caused by unpredictable disturbances and changes in conditions. By integrating unstable patches of either of these types into the open system of a larger landscape (consisting of many patches out of phase with each other), persistent species-rich communities can result (DeAngelis & Waterhouse, 1987). This is the principal message to emerge from the patch dynamics perspective, and its larger scale counterpart, 'landscape ecology' (Wiens *et al.*, 1993), stressing the importance of the spatial scale at which we view communities and the open nature of most of them. Note the strong link between the patch dynamics view of community organization and metapopulation theory, which deals with the effects on the dynamics of populations of dividing them into fragments (see Section 6.9). In a model that combines extinction–colonization dynamics (the metapopulation approach) with the dynamics of patch succession, Amarasekare and Possingham (2001) show that persistence of a species in the landscape depends: (i) on the net rate at which suitable patches arise relative to the species' colonization ability; as well as (ii) the longevity of the dormant stages (e.g. seed bank) relative to disturbance frequency.

multiple classes of disturbance . . .

Future development of ideas about patch dynamics is likely to concern the consequences of multiple classes of disturbance. Steinauer and Collins (2001) have made a start by showing that disturbances caused by urine deposition and grazing by bison (*Bos bison*) interact with each other. The abundance of four common grass species, and of all of them combined, increased on urine patches in ungrazed prairie grassland. However, the abundance of the grass *Andropogon gerardii*, and all grasses combined, decreased on urine patches in grazed prairie. The changed dynamics reflect the fact that bison preferentially graze on urine patches. In addition, grazed areas initiated on urine patches tend to expand well beyond the area of urine deposition, increasing the size and severity of disturbance by grazing.

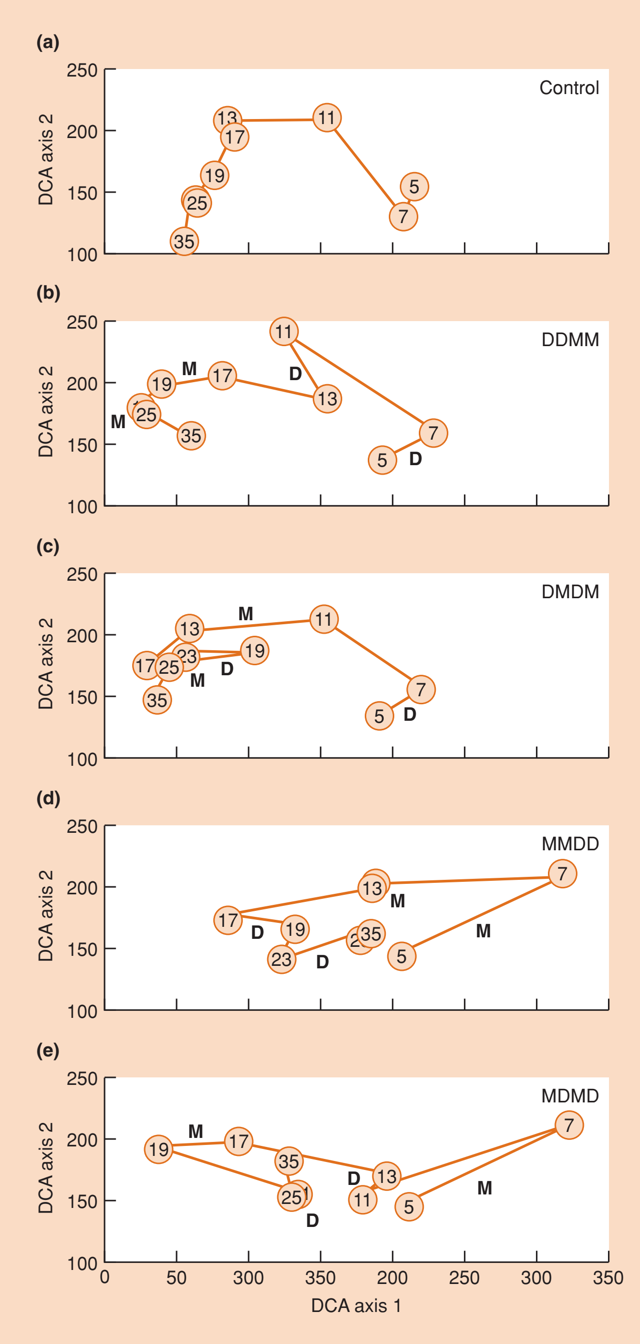


Figure 16.22 (*left*) Temporal changes in species composition and relative abundance of microcosms composed of a specific mix of protists and metazoans. The change is expressed in ordination plots based on a procedure called detrended correspondence analysis (DCA). (Recall that ordination is a mathematical treatment that allows communities to be organized on a graph so that those that are most similar in species composition and relative abundance appear closest together, whilst communities that differ greatly in the relative importance of a similar set of species, or that possess quite different species, appear far apart.) Data points are the mean ordination scores on different days in the experiment (from day 5 to day 35). The letter D indicates periods of drought disturbance, and the letter M, mosquito disturbance. (a–e) The results of the control and disturbances imposed in different sequences. (After Fukami, 2001.)

. . . may interact to determine community patterns

Finally, just as we can readily see how community dynamics may vary according to the order in which colonizing species happen to appear after a disturbance, it is equally the case that the order in which different kinds of disturbance occur may affect the outcome. Fukami (2001) addressed this issue by introducing two classes of disturbance (drought or the addition of predatory mosquito larvae) in various sequences to laboratory micrososms of protists and small metazoans (analogous to natural communities in water-filled bamboo stumps). Different disturbance sequences drove the microcosms into different successional trajectories, sometimes leading to divergence in final community composition (both in terms of species richness and relative abundance of the component species). This is illustrated graphically by ordination diagrams (see Section 16.3.2) that show the sequence of positions of communities in the same ordination space through experiments where disturbances were imposed in different sequences (Figure 16.22). It may often be the case that a knowledge of the disturbance history will be needed to predict the responses of communities to disturbances imposed in the future (such as global climate change).

Summary

The community is an assemblage of species populations that occur together in space and time. Community ecology seeks to understand the manner in which groupings of species are distributed in nature, and how they are influenced by their abiotic environment and by species interactions.

We begin by explaining how the structure of communities can be measured and described, in terms of species composition, species richness, diversity, equitability (evenness) and rank–abundance diagrams.

The assessment of community patterns in space has progressed from subjective 'gradient analysis' to objective mathematical approaches ('classification' and 'ordination') that permit relationships between community composition and abiotic factors to be systematically explored. We note that most communities are not delimited by sharp boundaries, where one group of species is abruptly replaced by another. Moreover a given species that occurs in one predictable association is also quite likely to occur with another group of species under different conditions elsewhere.

Just as the relative importance of species varies in space, so their patterns of abundance may change with time. A particular species can occur where it is capable of reaching a location, appropriate conditions and resources exist, and competitors, predators and parasites do not preclude it. A temporal sequence in the appearance and disappearance of species therefore requires that conditions, resources and/or the influence of enemies themselves vary with time. We emphasize and explain patterns of community change that follow a disturbance. Sometimes these patterns are predictable (succession; dominance control), in other cases highly stochastic (founder control).

Although we can discern and often explain patterns in community composition in space and in time, it is often more meaningful to consider space and time together. The patch dynamics concept of communities views the landscape as patchy, with patches being disturbed and recolonized by individuals of various species. Implicit in this view are critical roles for disturbance as a reset mechanism, and of migration between habitat patches. The community dynamics of patchy landscapes are strongly influenced by the frequency of gap formation and the sizes and shapes of these gaps in relation to the colonization and competitive properties of the species concerned.

Chapter 17

The Flux of Energy through Ecosystems

17.1 Introduction

All biological entities require matter for their construction and energy for their activities. This is true not only for individual organisms, but also for the populations and communities that they form in nature. The intrinsic importance of fluxes of energy (this chapter) and of matter (see Chapter 18) means that community processes are particularly strongly linked with the abiotic environment. The term *ecosystem* is used to denote the biological community *together with* the abiotic environment in which it is set. Thus, ecosystems normally include primary producers, decomposers and detritivores, a pool of dead organic matter, herbivores, carnivores and parasites *plus* the physicochemical environment that provides the living conditions and acts both as a source and a sink for energy and matter. Thus, as is the case with all chapters in Part 3 of this book, our treatment calls upon knowledge of individual organisms in relation to conditions and resources (Part 1) together with the diverse interactions that populations have with one another (Part 2).

Lindemann laid the foundations of ecological energetics

A classic paper by Lindemann (1942) laid the foundations of a science of ecological energetics. He attempted to quantify the concept of food chains and food webs by considering the efficiency of transfer between trophic levels – from incident radiation received by a community through its capture by green plants in photosynthesis to its subsequent use by herbivores, carnivores and decomposers. Lindemann's paper was a major catalyst for the International Biological Programme (IBP), which, with a view to human welfare, aimed to understand the biological basis of productivity of areas of land, fresh waters and the seas (Worthington, 1975). The IBP provided the first occasion on which biologists throughout the world were challenged to work together towards a common end. More recently, a further pressing issue has again galvanized the community of ecologists into action. Deforestation, the burning of fossil fuels and other pervasive human influences are causing dramatic changes to global climate and atmospheric composition, and can be expected in turn to influence patterns of productivity on a global scale. Much of the current work on productivity has a prime objective of providing the basis for predicting the effects of changes in climate, atmospheric composition and land use on terrestrial and aquatic ecosystems (aspects that will be dealt with in Chapter 22).

progressive improvements in technology to assess productivity

The decades since Lindemann's classic work have seen a progressive improvement in technology to assess productivity. Early calculations in terrestrial ecosystems involved sequential measurements of biomass of plants (usually just the aboveground parts) and estimates of energy transfer efficiency between trophic levels. In aquatic ecosystems, production estimates relied on changes in the concentrations of oxygen or carbon dioxide measured in experimental enclosures. Increasing sophistication in the measurement, *in situ*, of chlorophyll concentrations and of the gases involved in photosynthesis, coupled with the development of satellite remote-sensing techniques, now permit the extrapolation of local results to the global scale (Field *et al.*, 1998). Thus, satellite sensors can measure vegetation cover on land and chlorophyll concentrations in the sea, from which rates of light absorption are calculated and, based on our understanding of photosynthesis, these are converted to estimates of productivity (Geider *et al.*, 2001).

some definitions: standing crop and biomass, . . .

Before proceeding further it is necessary to define some new terms. The bodies of the living organisms within a unit area constitute a *standing crop* of biomass. By *biomass* we mean the mass of organisms per unit area of ground (or per unit area or unit volume of water) and this is usually expressed in units of energy (e.g. J m^{-2}) or dry organic matter (e.g. t ha^{-1}) or carbon (e.g. g C m^{-2}). The great bulk of the biomass in communities is almost always formed by plants, which are the primary producers of biomass because of their almost unique ability to fix carbon in photosynthesis. (We have to say 'almost unique' because bacterial photosynthesis and chemosynthesis may also contribute to forming new biomass.) Biomass includes the whole bodies of the organisms even though parts of them may be dead. This needs to be borne in mind, particularly when considering woodland and forest communities in which the bulk of the biomass is dead heartwood and bark. The living fraction of biomass represents active capital capable of generating interest in the form of new growth, whereas the dead fraction is incapable of new growth. In practice we include in biomass all those parts, living or dead, which are attached to the living organism. They cease to be biomass when they fall off and become litter, humus or peat.

. . . primary and secondary productivity, autotrophic respiration, . . .

The *primary productivity* of a community is the rate at which biomass is produced per unit area by plants, the primary producers. It can be expressed either in units of energy (e.g. J m^{-2} day^{-1}) or dry organic matter (e.g. kg ha^{-1} $year^{-1}$) or carbon (e.g. g C m^{-2} $year^{-1}$). The total fixation of energy by photosynthesis is referred to as *gross primary productivity* (GPP). A proportion of this is respired away by the plants (autotrophs) and is lost from the community as respiratory heat (RA – *autotrophic respiration*). The difference between GPP and RA is known as *net primary productivity* (NPP) and represents the actual rate of production of new biomass that is available for consumption by heterotrophic organisms (bacteria, fungi and animals). The rate of production of biomass by heterotrophs is called *secondary productivity*.

. . . net ecosystem productivity, and heterotrophic and ecosystem respiration

Another way to view energy flux in ecosystems involves the concept of *net ecosystem productivity* (NEP, using the same units as GPP or NPP). This acknowledges that the carbon fixed in GPP can leave the system as inorganic carbon (usually carbon dioxide) via either autotrophic respiration (RA) or, after consumption by heterotrophs, via *heterotrophic respiration* (RH)—the latter consisting of respiration by bacteria, fungi and animals. Total *ecosystem respiration* (RE) is the sum of RA and RH. NEP then is equal to GPP – RE. When GPP exceeds RE, the ecosystem is fixing carbon faster than it is being released and thus acts as a carbon sink. When RE exceeds GPP, carbon is being released faster than it is fixed and the ecosystem is a net carbon source. That the rate of ecosystem respiration can exceed GPP may seem paradoxical. However, it is important to note that an ecosystem can receive organic matter from sources other than its own photosynthesis – via the import of dead organic matter that has been produced elsewhere. Organic matter produced by photosynthesis within an ecosystem's boundaries is known as *autochthonous*, whereas that imported from elsewhere is called *allochthonous*.

In what follows we deal first with large-scale patterns in primary productivity (Section 17.2) before considering the factors that limit productivity in terrestrial (Section 17.3) and aquatic (Section 17.4) settings. We then turn to the fate of primary productivity and consider the flux of energy through food webs (Section 17.5), placing particular emphasis on the relative importance of grazer and decomposer systems (we return to food webs and their detailed population interactions in Chapter 20). We finally turn to seasonal and longer term variations in energy flux through ecosystems.

17.2 Patterns in primary productivity

primary productivity depends on, but is not solely determined by, solar radiation

The net primary production of the planet is estimated to be about 105 petagrams of carbon per year (1 Pg = 10^{15} g) (Geider *et al.*, 2001). Of this, 56.4 Pg C $year^{-1}$ is produced in terrestrial ecosystems and 48.3 Pg C $year^{-1}$ in aquatic ecosystems (Table 17.1). Thus, although oceans

Marine	*NPP*	*Terrestrial*	*NPP*
Tropical and subtropical oceans	13.0	Tropical rainforests	17.8
Temperate oceans	16.3	Broadleaf deciduous forests	1.5
Polar oceans	6.4	Mixed broad/needleleaf forests	3.1
Coastal	10.7	Needleleaf evergreen forests	3.1
Salt marsh/estuaries/seaweed	1.2	Needleleaf deciduous forests	1.4
Coral reefs	0.7	Savannas	16.8
		Perennial grasslands	2.4
		Broadleaf shrubs with bare soil	1.0
		Tundra	0.8
		Desert	0.5
		Cultivation	8.0
Total	48.3	Total	56.4

Table 17.1 Net primary production (NPP) per year for major biomes and for the planet in total (in units of petragrams of C). (From Geider *et al.*, 2001.)

cover about two-thirds of the world's surface, they account for less than half of its production. On the land, tropical rainforests and savannas account between them for about 60% of terrestrial NPP, reflecting the large areas covered by these biomes and their high levels of productivity. All biological activity is ultimately dependent on received solar radiation but solar radiation alone does not determine primary productivity. In very broad terms, the fit between solar radiation and productivity is far from perfect because incident radiation can be captured efficiently only when water and nutrients are available and when temperatures are in the range suitable for plant growth. Many areas of land receive abundant radiation but lack adequate water, and most areas of the oceans are deficient in mineral nutrients.

17.2.1 Latitudinal trends in productivity

the productivity of forests, grasslands and lakes follows a latitudinal pattern

In the forest biomes of the world a general latitudinal trend of increasing productivity can be seen from boreal, through temperate, to tropical conditions (Table 17.2). However, there is also considerable variation, much of it due to differences in water availability, local topography and associated variations in microclimate. The same latitudinal trend (and local variations) exists in the above-ground productivity of grassland communities (Figure 17.1). Note the considerable differences in the relative importance of above-ground and below-ground productivity in the different grassland biomes. It is technically difficult to estimate below-ground productivity and early reports of NPP often ignored or underestimated the true values. As far as aquatic communities are concerned, a latitudinal trend is clear in lakes (Brylinski & Mann, 1973) but not in the oceans, where productivity may more often be limited by a shortage of nutrients – very high productivity occurs in marine communities where there are upwellings of nutrient-rich waters, even at high latitudes and low temperatures.

Table 17.2 Gross primary productivity (GPP) of forests at various latitudes in Europe and North and South America, estimated as the sum of net ecosystem productivity and ecosystem respiration (calculated from CO_2 fluxes measured in the forest canopies – only one estimate for tropical forest was included by the reviewers). (From data in Falge *et al.*, 2002.)

Forest type	*Range of GPP estimates (g C m^{-2} year^{-1})*	*Mean of estimates (g C m^{-2} year^{-1})*
Tropical rainforest	3249	3249
Temperate deciduous	1122–1507	1327
Temperate coniferous	992–1924	1499
Cold temperate deciduous	903–1165	1034
Boreal coniferous	723–1691	1019

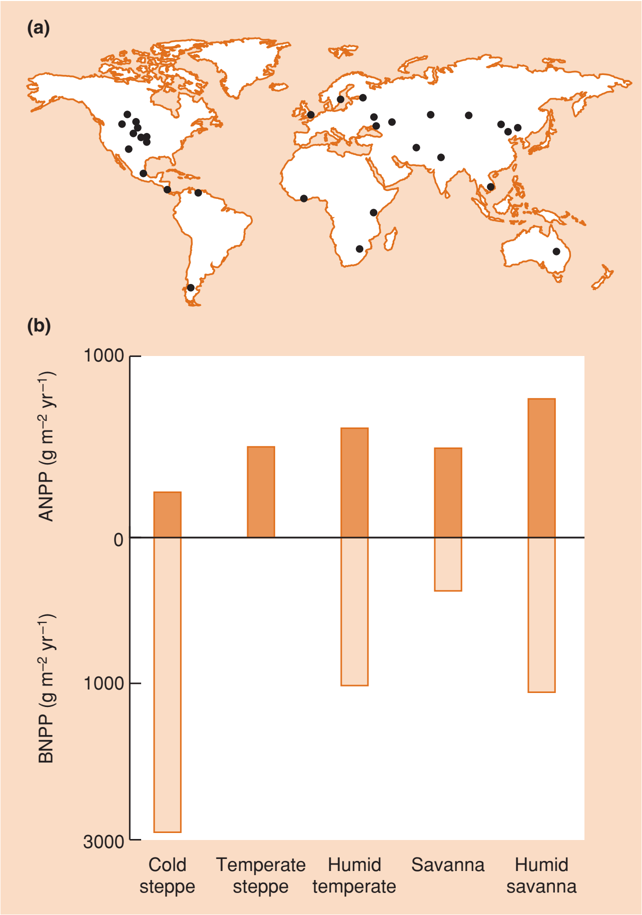


Figure 17.1 (a) The location of 31 grassland study sites included in this analysis. (b) Above-ground net primary productivity (ANPP) and below-ground net primary productivity (BNPP) for five categories of grassland biomes (BNPP not available for temperate steppe). The values in each case are averages for 4–8 grassland studies. The technique involved summing increments in the biomass of live plants, standing dead matter and litter between successive samples in the study period (average 6 years). (From Scurlock *et al.*, 2002.)

The overall trends with latitude suggest that radiation (a resource) and temperature (a condition) may often limit the productivity of communities. But other factors frequently constrain productivity within even narrower limits.

17.2.2 Seasonal and annual trends in primary productivity

productivity shows considerable temporal variation

The large ranges in productivity in Table 17.2 and the wide confidence intervals in Figure 17.1 emphasize the

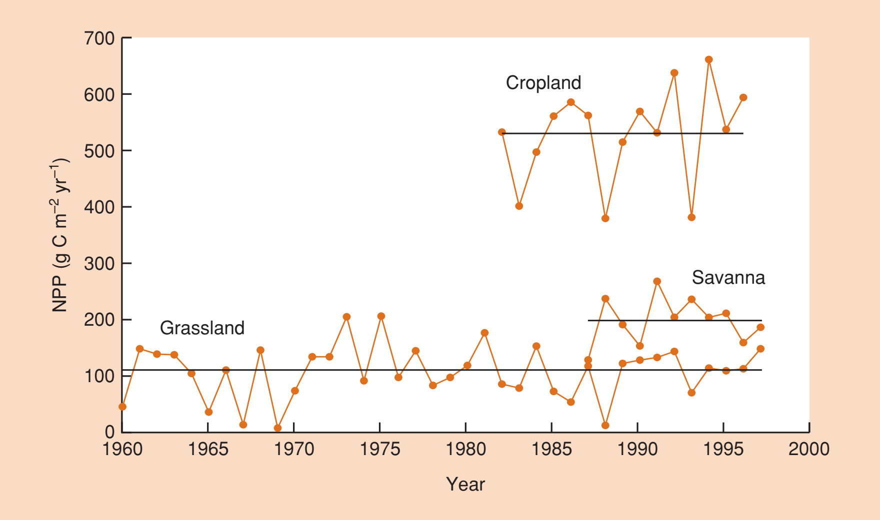


Figure 17.2 Interannual variation in net primary productivity (NPP) in a grassland in Queensland, Australia (above-ground NPP), a cropland in Iowa, USA (total above- and below-ground NPP) and a tropical savanna in Senegal (above-ground NPP). Black horizontal lines show the mean NPP for the whole study period. (After Zheng *et al*., 2003.)

considerable variation that exists within a given class of ecosystems. It is important to note also that productivity varies from year to year in a single location (Knapp & Smith, 2001). This is illustrated for a temperate cropland, a tropical grassland and a tropical savanna in Figure 17.2. Such annual fluctuations no doubt reflect year-to-year variation in cloudless days, temperature and rainfall. At a smaller temporal scale, productivity reflects seasonal variations in conditions, particularly in relation to the consequences of temperature for the length of the growing season. For example, the period when daily GPP is high persists for longer in temperate than in boreal situations (Figure 17.3). Moreover, the growing season is more extended but the amplitude of seasonal change is smaller in evergreen coniferous forests than in their deciduous counterparts (where the growing season is curtailed by the shedding of leaves in the fall).

17.2.3 Autochthonous and allochthonous production

autochthonous and allochthonous production . . .

All biotic communities depend on a supply of energy for their activities. In most terrestrial systems this is contributed *in situ* by the photosynthesis of green plants – this is autochthonous production. Exceptions exist, however, particularly where colonial animals deposit feces derived from food consumed at a distance from the colony (e.g. bat colonies in caves, seabirds on coastland) – guano is an example of allochthonous organic matter (dead organic material formed outside the ecosystem).

. . . vary in systematic ways in lakes, rivers and estuaries

In aquatic communities, the autochthonous input is provided by the photosynthesis of large plants and attached algae in shallow waters (littoral zone) and by microscopic phytoplankton in the open water. However, a substantial proportion of the organic matter in aquatic communities comes from allochthonous material that arrives in rivers, via groundwater or is blown in by the wind. The relative importance of the two autochthonous sources (littoral and planktonic) and the allochthonous source of organic material in an aquatic system depends on the dimensions of the body of water and the types of terrestrial community that deposit organic material into it.

A small stream running through a wooded catchment derives most of its energy input from litter shed by surrounding vegetation (Figure 17.4). Shading from the trees prevents any significant growth of planktonic or attached algae or aquatic higher plants. As the stream widens further downstream, shading by trees is restricted to the margins and autochthonous primary production increases. Still further downstream, in deeper and more turbid waters, rooted higher plants contribute much less, and the role of the microscopic phytoplankton becomes more important. Where large river channels are characterized by a flood plain, with associated oxbow lakes, swamps and marshes, allochthonous dissolved and particulate organic may be carried to the river channel from its flood plain during episodes of flooding (Junk *et al*., 1989; Townsend 1996).

The sequence from small, shallow lakes to large, deep ones shares some of the characteristics of the river continuum just discussed (Figure 17.5). A small lake is likely to derive quite a large proportion of its energy from the land because its periphery is large in relation to its area. Small lakes are also usually shallow, so internal littoral production is more important than that by phytoplankton. In contrast, a large, deep lake will derive only limited organic matter from outside (small periphery relative to lake surface area) and littoral production, limited to the shallow margins, may also be low. The organic inputs to the community may then be due almost entirely to photosynthesis by the phytoplankton.

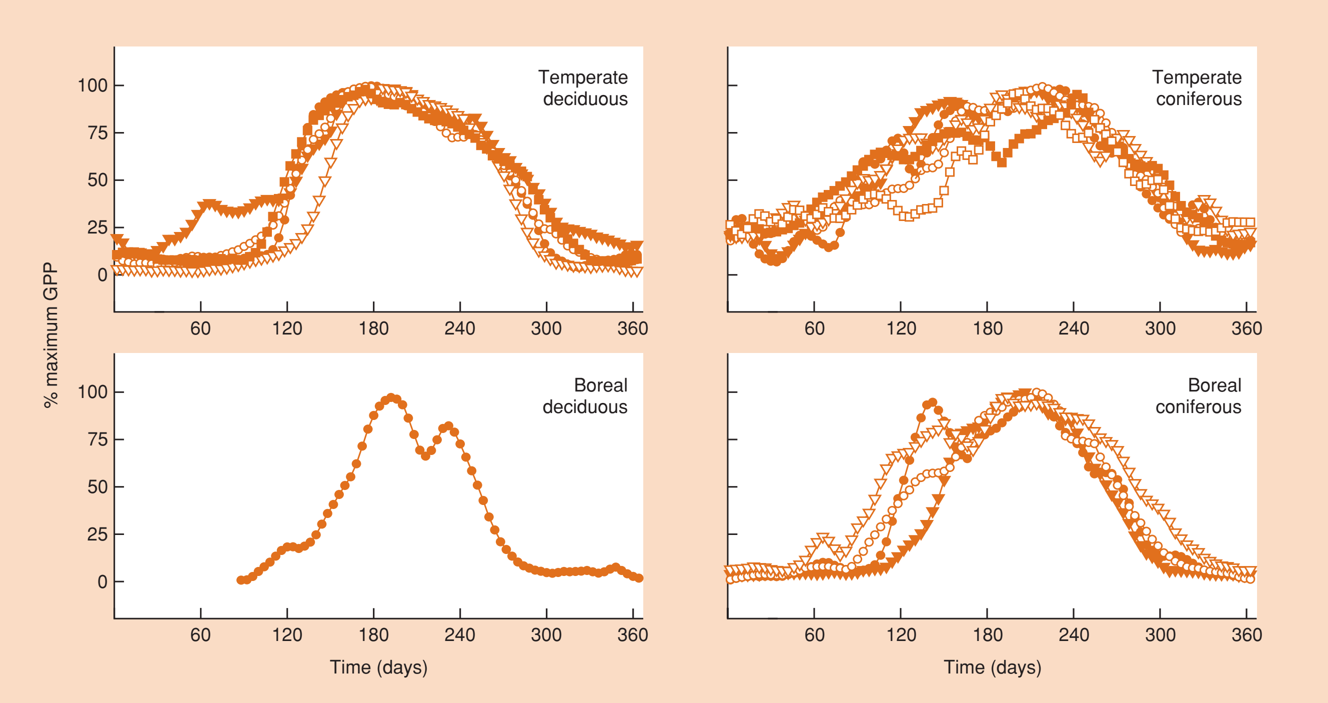


Figure 17.3 Seasonal development of maximum daily gross primary productivity (GPP) for deciduous and coniferous forests in temperate (Europe and North America) and boreal locations (Canada, Scandinavia and Iceland). The different symbols in each panel relate to different forests. Daily GPP is expressed as the percentage of the maximum achieved in each forest during 365 days of the year. (After Falge *et al.*, 2002.)

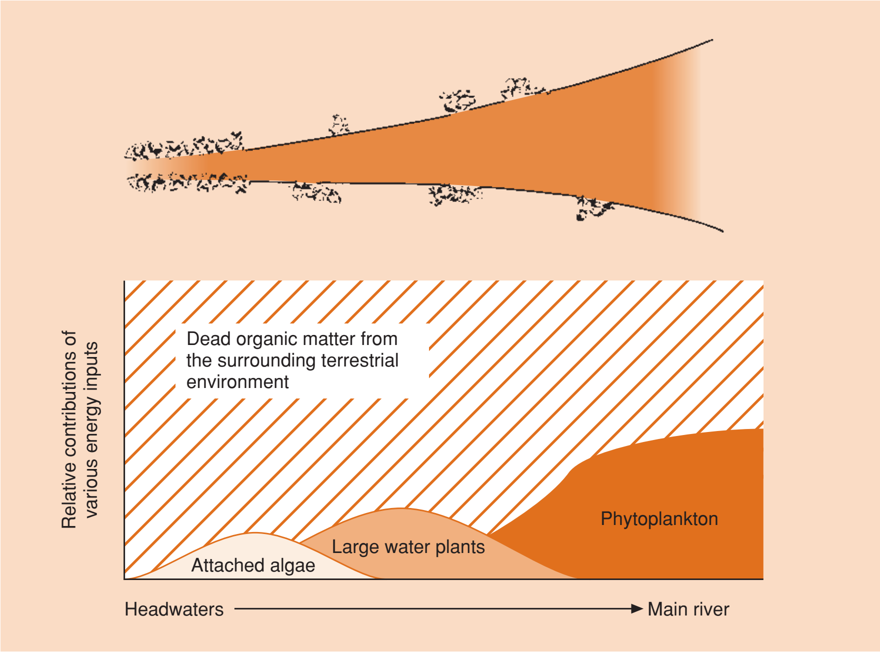


Figure 17.4 Longitudinal variation in the nature of the energy base in stream communities.

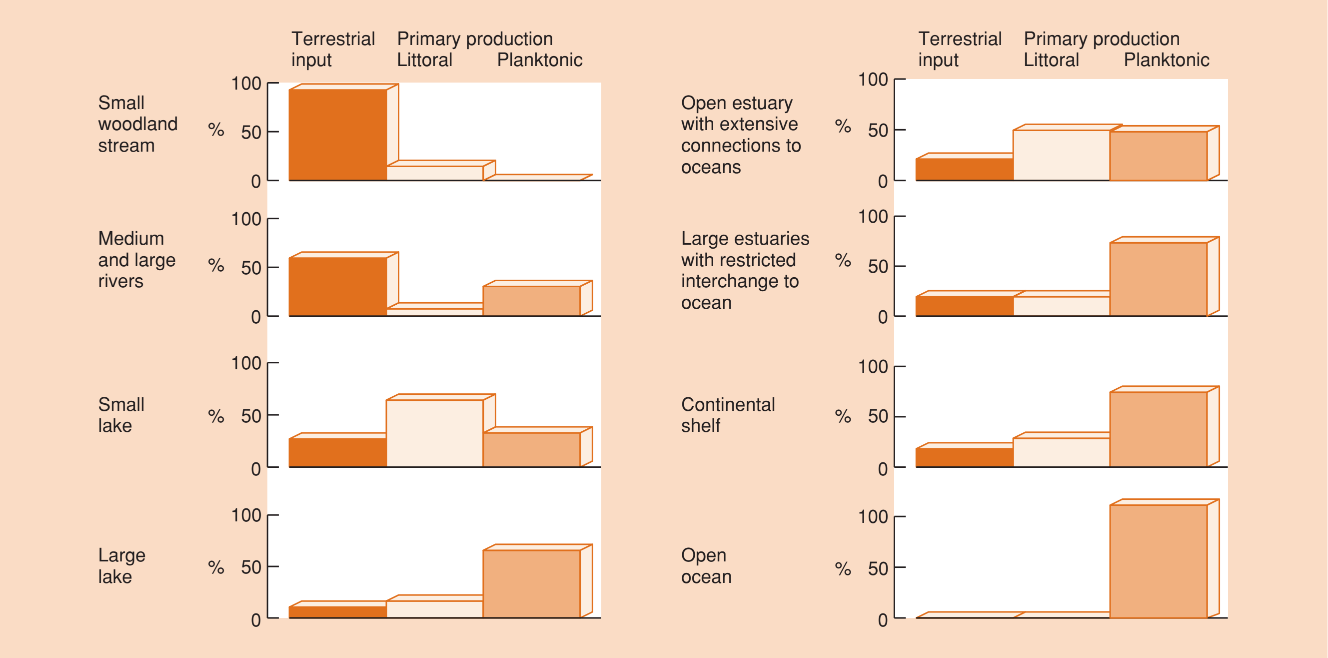


Figure 17.5 Variation in the importance of terrestrial input of organic matter and littoral and planktonic primary production in contrasting aquatic communities.

Estuaries are often highly productive systems, receiving allochthonous material and a rich supply of nutrients from the rivers that feed them. The most important autochthonous contribution to their energy base varies. In large estuarine basins, with restricted interchange with the open ocean and with small marsh peripheries relative to basin area, phytoplankton tend to dominate. By contrast, seaweeds dominate in some open basins with extensive connections to the sea. In turn, continental shelf communities derive a proportion of their energy from terrestrial sources (particularly via estuaries) and their shallowness often provides for significant production by littoral seaweed communities. Indeed, some of the most productive systems of all are to be found among seaweed beds and reefs.

Finally, the open ocean can be described in one sense as the largest, deepest 'lake' of all. The input of organic material from terrestrial communities is negligible, and the great depth precludes photosynthesis in the darkness of the sea bed. The phytoplankton are then all-important as primary producers.

17.2.4 Variations in the relationship of productivity to biomass

NPP : B ratios are very low in forests and very high in aquatic communities

We can relate the productivity of a community to the standing crop biomass that produces it (the interest rate on the capital). Alternatively, we can think of the standing crop as the biomass that is sustained by the productivity (the capital resource that is sustained by earnings). Overall, there is a dramatic difference in the total biomass that exists on land (800 Pg) compared to the oceans (2 Pg) and fresh water (< 0.1 Pg) (Geider *et al.*, 2001). On an areal basis, biomass on land ranges from 0.2 to 200 kg m^{-2}, in the oceans from less than 0.001 to 6 kg m^{-2} and in freshwater biomass is generally less than 0.1 kg m^{-2} (Geider *et al.*, 2001). The average values of net primary productivity (NPP) and standing crop biomass (B) for a range of community types are plotted against each other in Figure 17.6. It is evident that a given value of NPP is produced by a smaller biomass when nonforest terrestrial systems are compared with forests, and the biomass involved is smaller still when aquatic systems are considered. Thus NPP : B ratios (kilograms of dry matter produced per year per kilogram of standing crop) average 0.042 for forests, 0.29 for other terrestrial systems and 17 for aquatic communities. The major reason for this is almost certainly that a large proportion of forest biomass is dead (and has been so for a long time) and also that much of the living support tissue is not photosynthetic. In grassland and scrub, a greater proportion of the biomass is alive and involved in photosynthesis, though half or more of the biomass may be roots. In aquatic communities, particularly where productivity is due mainly to phytoplankton, there is no support tissue, there is no need for roots to absorb water and nutrients, dead cells do not accumulate (they are usually eaten before they die) and the photosynthetic output per kilogram of biomass is thus very high indeed. Another factor that helps to account for high NPP : B ratios in phytoplankton communities is

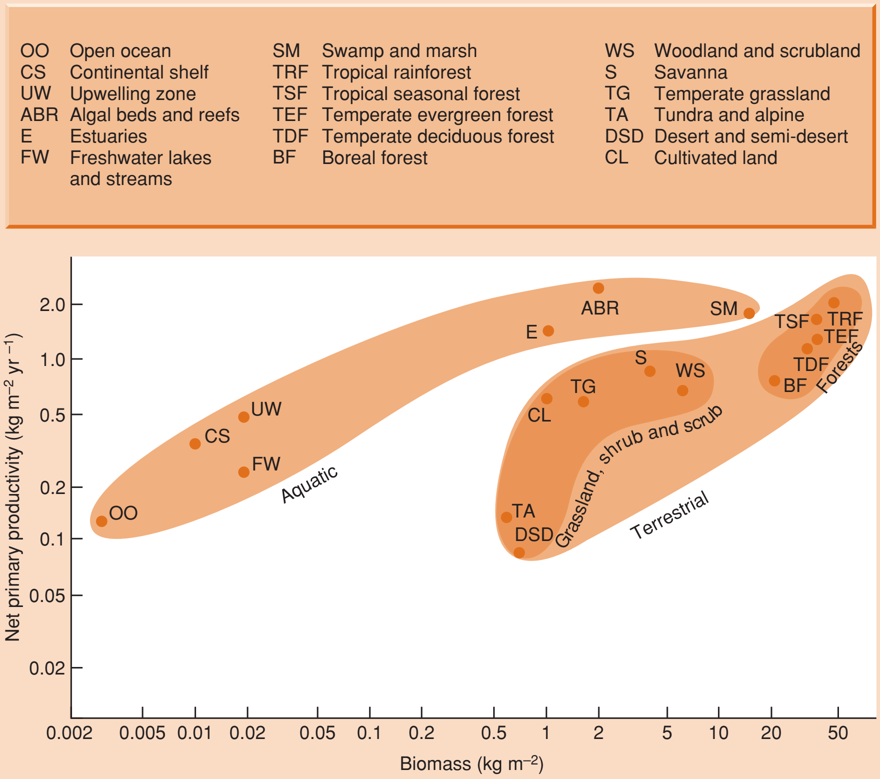


Figure 17.6 The relationship between average net primary productivity and average standing crop biomass for a range of ecosystems. (Based on data in Whittaker, 1975.)

the rapid turnover of biomass (turnover times of biomass in oceans and fresh waters average 0.02–0.06 years, compared to 1–20 years on land; Geider *et al.*, 2001). The annual NPP shown in the figure is actually produced by a number of overlapping phytoplankton generations, while the standing crop biomass is only the average present at an instant.

NPP : B ratios tend to decrease during successions

Ratios of NPP to biomass tend to decrease during successions. This is because the early successional pioneers are rapidly growing herbaceous species with relatively little support tissue (see Section 16.6). Thus, early in the succession the NPP : B ratio is high. However, the species that come to dominate later are generally slow growing, but eventually achieve a large size and come to monopolize the supply of space and light. Their structure involves considerable investment in nonphotosynthesizing and dead support tissues, and as a consequence their NPP : B ratio is low.

When attention is focused on trees, a common pattern is for above-ground NPP to reach a peak early in succession and then gradually decline by as much as 76%, with a mean reduction of 34% (Table 17.3). The reductions are no doubt partly due to a shift from photosynthesizing to respiring tissues. In addition, nutrient limitation may become more significant later in the succession or the longer branches and taller stems of older trees may increase resistance to the transpiration stream and thus limit photosynthesis (Gower *et al.*, 1996). Trees characteristic of different stages in succession show different patterns of NPP with stand age. In a subalpine coniferous forest, for example, the early successional whitebark pine (*Pinus albicaulis*) reached a peak above-ground NPP at about 250 years and then declined, whereas the late successional, shade-tolerant subalpine fir (*Abies lasiocarpa*) continued towards a maximum beyond 400 years (Figure 17.7). The late successional species allocated almost twice as much biomass to leaves as its early successional counterpart, and maintained a high photosynthesis : respiration ratio to a greater age (Callaway *et al.*, 2000).

17.3 Factors limiting primary productivity in terrestrial communities

Sunlight, carbon dioxide (CO_2), water and soil nutrients are the resources required for primary production on land, while temperature, a condition, has a strong influence on the rate

Table 17.3 Above-ground net primary productivity (ANPP) for forest age sequences in contrasting biomes. (After Gower *et al*., 1996.)

Biome/species	*Location*	*Range of stand ages, in years (no. of stands shown in brackets)*	*ANPP (t dry mass ha^{-1} $year^{-1}$)* Peak	Oldest	% change
Boreal					
Larix gmelinii	Yakutsk, Siberia	50–380 (3)	4.9	2.4	−51
Picea abies	Russia	22–136 (10)	6.2	2.6	−58
Cold temperate					
Abies baisamea	New York, USA	0–60 (6)	3.2	1.1	−66
Pinus contorta	Colorado, USA	40–245 (3)	2.1	0.5	−76
Pinus densiflora	Mt Mino, Japan	16–390 (7)	16.1	7.4	−54
Populus tremuloides	Wisconsin, USA	8–83 (5)	11.1	10.7	−4
Populus grandidentata	Michigan, USA	10–70	4.6	3.5	−24
Pseudotsuga menziesii	Washington, USA	22–73 (4)	9.9	5.1	−45
Warm temperate					
Pinus elliottii	Florida, USA	2–34 (6)	13.2	8.7	−34
Pinus radiata	Puruki, NZ (Tahi)	2–6 (5)	28.5	28.5	0
	(Rue)	2–7 (6)	29.2	23.5	−20
	(Toru)	2–8 (7)	31.1	31.1	0
Tropical					
Pinus caribaea	Afaka, Nigeria	5–15 (4)	19.2	18.5	−4
Pinus kesiya	Meghalaya, India	1–22 (9)	30.1	20.1	−33
Tropical rainforest	Amazonia	1–200 (8)	13.2	7.2	−45

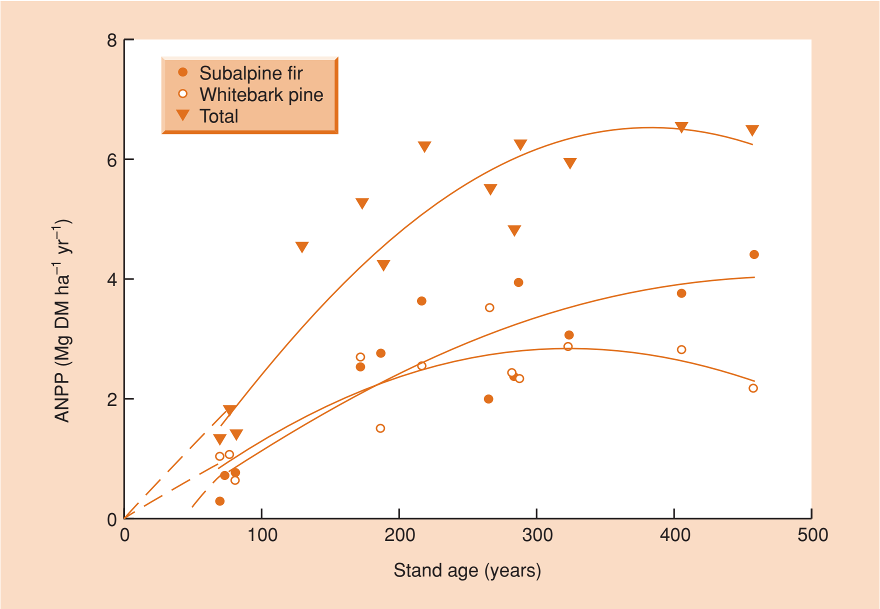


Figure 17.7 Annual above-ground net primary productivity (ANPP) (Mg dry matter ha^{-1} $year^{-1}$) in stands of different ages in a subalpine coniferous forest in Montana, USA: early successional whitebark pine, late successional subalpine fir, and total ANPP. (After Callaway *et al*., 2000.)

of photosynthesis. CO_2 is normally present at a level of around 0.03% of atmospheric gases. Turbulent mixing and diffusion prevent the CO_2 concentration from varying much from place to place, except in the immediate neighborhood of a leaf, and CO_2 probably plays little role in determining differences between the productivities of different communities (although global increases in CO_2 concentration are expected to have profound effects (e.g. DeLucia *et al*., 1999). On the other hand, the quality and quantity of light, the availability of water and nutrients, and temperature all vary dramatically from place to place. They are all candidates for the role of limiting factor. Which of them actually sets the limit to primary productivity?

17.3.1 Inefficient use of solar energy

terrestrial communities use radiation inefficiently

Depending on location, something between 0 and 5 joules of solar energy strikes each square meter of the earth's surface every minute. If all this were converted by photosynthesis to plant biomass (that is, if photosynthetic efficiency were 100%) there would be a prodigious generation of plant material, one or two orders of magnitude greater than recorded values. However, much of this solar energy is unavailable for use by plants. In particular, only about 44% of incident shortwave radiation occurs at wavelengths suitable for photosynthesis. Even when this is taken into account, though, productivity still falls well below the maximum possible. Photosynthetic efficiency has two components – the efficiency with which light is intercepted by leaves and the efficiency with which intercepted light is converted by photosynthesis to new biomass (Stenberg *et al.*, 2001). Figure 17.8 shows the range in overall net photosynthetic efficiencies (percentage of incoming photosynthetically active radiation (PAR) incorporated into above-ground NPP) in seven coniferous forests, seven deciduous forests and eight desert communities studied as part of the International Biological Programme (see Section 17.1). The conifer communities had the highest efficiencies, but these were only between 1 and 3%. For a similar level of incoming radiation, deciduous forests achieved 0.5–1%, and, despite their greater energy income, deserts were able to convert only 0.01–0.2% of PAR to biomass.

productivity may still be limited by a shortage of PAR

However, the fact that radiation is not used efficiently does not in itself imply that it does not limit community productivity. We would need to know whether at increased intensities of radiation the productivity increased or remained unchanged. Some of the evidence given in Chapter 3 shows that the intensity of light during part of the day is below the optimum for canopy photosynthesis. Moreover, at peak light intensities, most canopies still have their lower leaves in relative gloom, and would almost certainly photosynthesize faster if the light intensity were higher. For C_4 plants a saturating intensity of radiation never seems to be reached, and the implication is that productivity may in fact be limited by a shortage of PAR even under the brightest natural radiation.

There is no doubt, however, that what radiation is available would be used more efficiently if other resources were in abundant supply. The much higher values of community productivity recorded from agricultural systems bear witness to this.

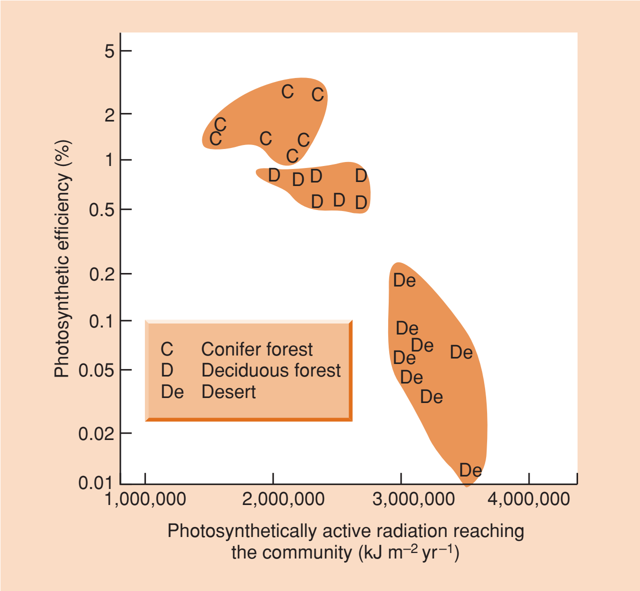


Figure 17.8 Photosynthetic efficiency (percentage of incoming photosynthetically active radiation converted to above-ground net primary productivity) for three sets of terrestrial communities in the USA. (After Webb *et al.*, 1983.)

17.3.2 Water and temperature as critical factors

shortage of water may be a critical factor

The relationship between the NPP of a wide range of ecosystems on the Tibetan Plateau and both precipitation and temperature is illustrated in Figure 17.9. Water is an essential resource both as a constituent of cells and for photosynthesis. Large quantities of water are lost in transpiration – particularly because the stomata need to be open for much of the time for CO_2 to enter. It is not surprising that the rainfall of a region is quite closely correlated with its productivity. In arid regions, there is an approximately linear increase in NPP with increase in precipitation, but in the more humid forest climates there is a plateau beyond which productivity does not continue to rise. Note that a large amount of precipitation is not necessarily equivalent to a large amount of water available for plants; all water in excess of field capacity will drain away if it can. A positive relationship between productivity and mean annual temperature can also be seen in Figure 17.9. However, the pattern can be expected to be complex because, for example, higher temperatures are associated with rapid water loss through evapotranspiration; water shortage may then become limiting more quickly.

interaction of temperature and precipitation

To unravel the relationships between productivity, rainfall and temperature, it is more instructive to concentrate on a single ecosystem

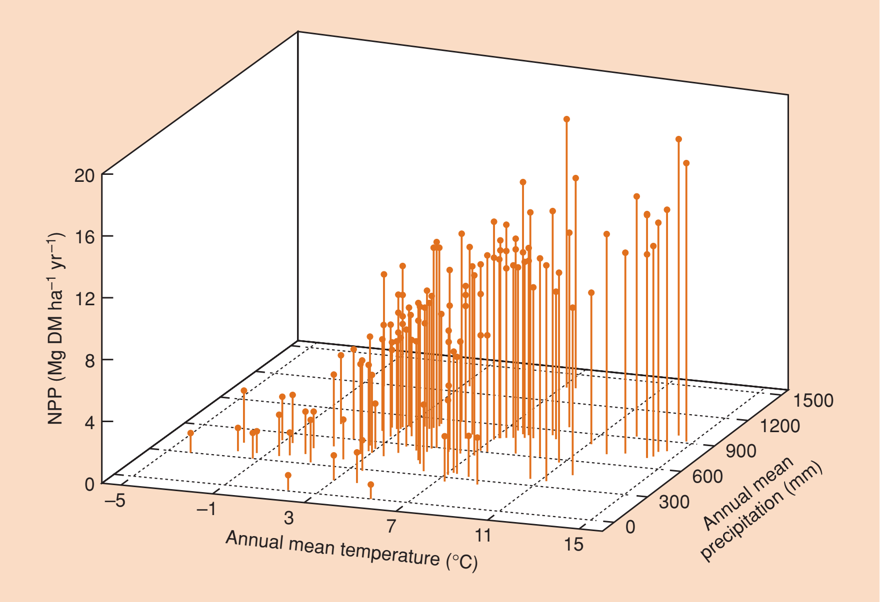


Figure 17.9 Relationship between total net primary productivity (Mg dry matter ha^{-1} year^{-1}) and annual precipitation and temperature for ecosystems on the Tibetan Plateau. The ecosystems include forests, woodlands, shrublands, grasslands and desert. (After Luo *et al.*, 2002.)

type. Above-ground NPP was estimated for a number of grassland sites along two west-to-east precipitation gradients in the Argentinian pampas. One of these gradients was in mountainous country and the other in the lowlands. Figure 17.10 shows the relationship between an index of above-ground NPP (ANPP) and precipitation and temperature for the two sets of sites. There are strong positive relationships between ANPP and precipitation but the slopes of the relationships differed between the two environmental gradients (Figure 17.10a).

The relationships between ANPP and temperature are similar for two further environmental gradients (both north-to-south elevation transects) in Figure 17.10b – both show a hump-shaped pattern. This probably results from the overlap of two effects of increasing temperature: a positive effect on the length of the

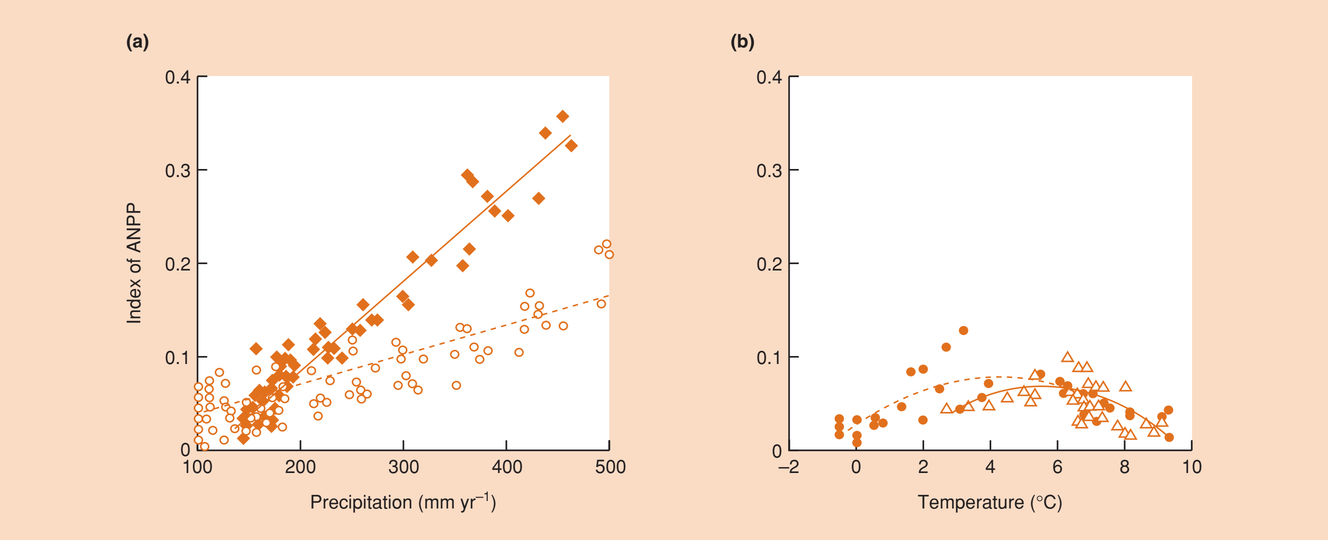


Figure 17.10 Annual above-ground net primary productivity (ANPP) of grasslands along two precipitation gradients in the Argentinian pampas. NPP is shown as an index based on satellite radiometric measurements with a known relationship to absorbed photosynthetically active radiation in plant canopies. (a) NPP in relation to annual precipitation. (b) NPP in relation to annual mean temperature. Open circles and diamonds represent sites along precipitation gradients in the lowland and mountainous regions respectively. Closed circles and triangles represent sites along two elevation transects. (After Jobbagy *et al.*, 2002.)

growing season and a negative effect through increased evapotranspiration at higher temperatures. Because temperature is the main constraint on productivity at the cool end of the gradients, an increase in NPP is observed as we move from the coolest to warmer sites. However, there is a temperature value above which the growing season does not lengthen and the dominating effect of increasing temperature is now to increase evapotranspiration, thus reducing water availability and curtailing NPP (Epstein *et al.*, 1997).

productivity and the structure of the canopy

Water shortage has direct effects on the rate of plant growth but also leads to the development of less dense vegetation. Vegetation that is sparse intercepts less light (much of which falls on bare ground). This wastage of solar radiation is the main cause of the low productivity in many arid areas, rather than the reduced photosynthetic rate of drought-affected plants. This point is made by comparing the productivity per unit weight of leaf biomass instead of per unit area of ground for the studies shown in Figure 17.8. Coniferous forest produced 1.64 g g^{-1} year^{-1}, deciduous forest 2.22 g g^{-1} year^{-1} and desert 2.33 g g^{-1} year^{-1}.

17.3.3 Drainage and soil texture can modify water availability and thus productivity

There was a notable difference in the slopes of the graphs of NPP against precipitation for the mountainous and lowland sites in Figure 17.10. The slope was much lower in the mountainous case and it seems likely that the steeper terrain in this region resulted in a higher rate of water runoff from the land and, thus, a lower efficiency in the use of precipitation (Jobbagy *et al.*, 2002).

soil texture can influence productivity

A related phenomenon has been observed when forest production on sandy, well-drained soils is compared with soils consisting of finer particle sizes. Data are available for the accumulation through time of forest biomass at a number of sites where all the trees had been removed by a natural disturbance or human clearance. For forests around the world, Johnson *et al.* (2000) have reported the relationship between above-ground biomass accumulation (a rough index of ANPP) and accumulated growing season degree-days (stand age in years × growing season temperature × growing season as a proportion of the year). In effect, 'growing season degree-days' combine the time for which the stand has been accumulating biomass with the average temperature at the site in question. Figure 17.11 shows that productivity of broadleaf forests is generally much lower, for a given value for growing season degree-days, when the forest is on sandy soil. Such soils have less favorable soil-moisture-holding capacities and this accounts in some measure for their poorer productivity. In addition, however, nutrient retention may be lower in coarse soils, further reducing productivity compared to soils with finer texture. This was confirmed by Reich *et al.* (1997) who, in their compilation of data for 50 North American forests, found that soil nitrogen availability (estimated as annual net nitrogen mineralization rate) was indeed lower in sandier soils and, moreover, that ANPP was lower per unit of available nitrogen in sandy situations.

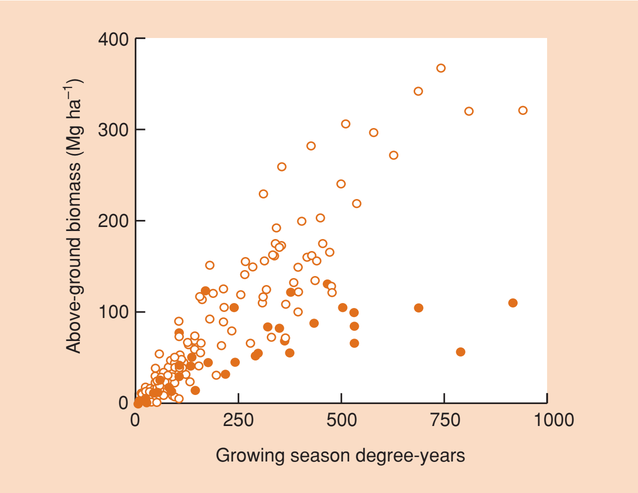


Figure 17.11 Above-ground biomass accumulation (a rough index of NPP) expressed as megagrams (= 10^6 g) per hectare in relation to accumulated growing season degree-days in broadleaf forest stands growing on sandy or nonsandy soils. ○, nonsandy soils; ●, sandy soils. (After Johnson *et al.*, 2000.)

17.3.4 Length of the growing season

The productivity of a community can be sustained only for that period of the year when the plants have photosynthetically active foliage. Deciduous trees have a self-imposed limit on the period when they bear foliage. In general, the leaves of deciduous species photosynthesize fast and die young, whereas evergreen species have leaves that photosynthesize slowly but for longer (Eamus, 1999). Evergreen trees hold a canopy throughout the year, but during some seasons they may barely photosynthesize at all or may even respire faster than they photosynthesize. Evergreen conifers tend to dominate in nutrient-poor and cold conditions, perhaps because in other situations their seedlings are outcompeted by their faster growing deciduous counterparts (Becker, 2000).

length of the growing season: a pervasive influence on productivity

The latitudinal patterns in forest productivity seen earlier (see Table 17.2) are largely the result of differences in the number of days when there is active photosynthesis. In this context, Black *et al.* (2000) measured net ecosystem productivity (NEP) in a boreal deciduous forest in Canada for 4 years. First leaf emergence occurred considerably earlier in 1998 when

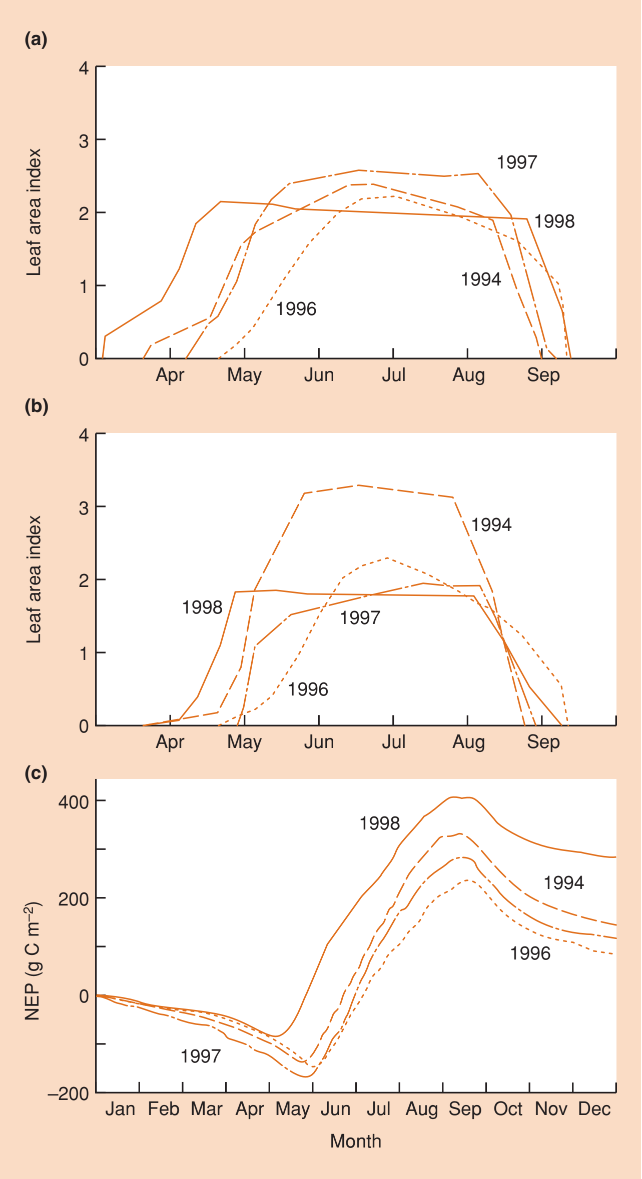


Figure 17.12 Seasonal patterns in leaf area index (area of leaves divided by ground area beneath the foliage) of (a) overstory aspen (*Populus tremuloides*) and (b) understory hazelnut (*Corylus cornuta*) in a boreal deciduous forest during four study years with contrasting spring temperatures. (c) Cumulative net ecosystem productivity (NEP). (After Black *et al.*, 2000.)

the April/May temperature was warmest (9.89°C) and a month later in 1996 when the April/May temperature was coldest (4.24°C) (Figure 17.12a, b). Equivalent spring temperatures in 1994 and 1997 were 6.67 and 5.93°C. The difference in the length of the growing season in the four study years can be gauged from the pattern of cumulative NEP (Figure 17.12c). During winter and early spring, NEP was negative because ecosystem respiration exceeded gross ecosystem productivity. NEP became positive earlier in warmer years (particularly 1998) so that overall total carbon sequestered by the ecosystem in the four years was 144, 80, 116 and 290 g C m^{-2} year^{-1} for 1994, 1996, 1997 and 1998, respectively.

In our earlier discussion of the study of Argentinian pampas communities (see Figure 17.10) we noted that higher NPP was not only directly affected by precipitation and temperature but was partly determined by length of the growing season. Figure 17.13 shows that the start of the growing season was positively related to mean annual temperature (paralleling the boreal forest study above), whereas the end of the growing season was determined partly by temperature but also by precipitation (it ended earlier where temperatures were high and precipitation was low). Again we see a complex interaction between water availability and temperature.

17.3.5 Productivity may be low because mineral resources are deficient

the crucial importance of nutrient availability

No matter how brightly the sun shines and how often the rain falls, and no matter how equable the temperature is, productivity must be low if there is no soil in a terrestrial community, or if the soil is deficient in essential mineral nutrients. The geological conditions that determine slope and aspect also determine whether a soil forms, and they have a large, though not wholly dominant, influence on the mineral content of the soil. For this reason, a mosaic of different levels of community productivity develops within a particular climatic regime. Of all the mineral nutrients, the one that has the most pervasive influence on community productivity is fixed nitrogen (and this is invariably partly or mainly biological, not geological, in origin, as a result of nitrogen fixation by microorganisms). There is probably no agricultural system that does not respond to applied nitrogen by increased primary productivity, and this may well be true of natural vegetation as well. Nitrogen fertilizers added to forest soils almost always stimulate forest growth.

The deficiency of other elements can also hold the productivity of a community far below that of which it is theoretically capable. A classic example is deficiency of phosphate and zinc in South Australia, where the growth of commercial forest (Monterey pine, *Pinus radiata*) is made possible only when these nutrients are supplied artificially. In addition, many tropical systems are primarily limited by phosphorus.

17.3.6 Résumé of factors limiting terrestrial productivity

The ultimate limit on the productivity of a community is determined by the amount of incident radiation that it receives – without this, no photosynthesis can occur.

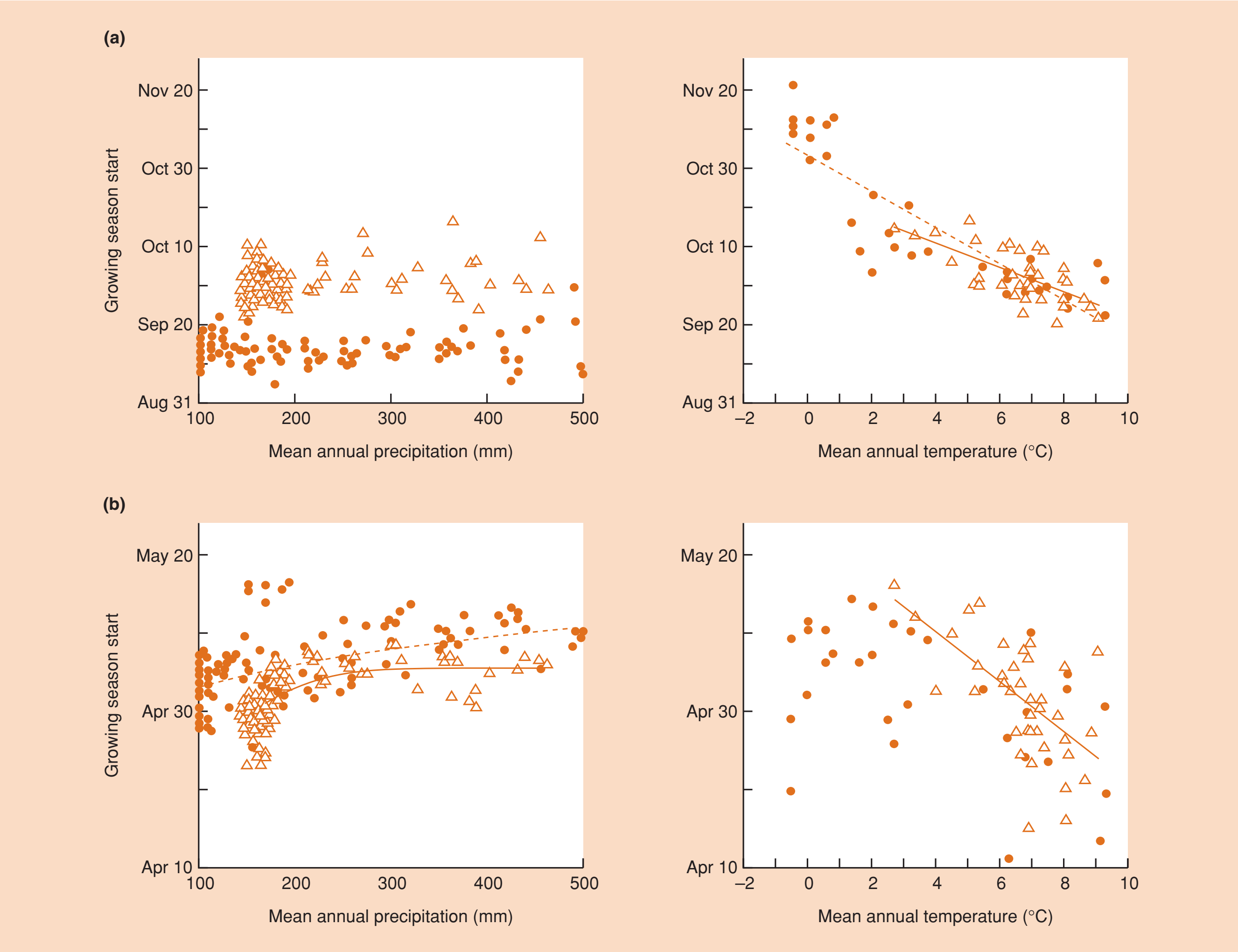


Figure 17.13 (a) Start and (b) end dates of the growing season for Argentinian pampas communities described in Section 17.3.2. Circles represent sites along the precipitation gradient in the mountainous region and triangles represent sites along the lowland gradient. (After Jobbagy *et al*., 2002.)

Incident radiation is used inefficiently by all communities. The causes of this inefficiency can be traced to: (i) shortage of water restricting the rate of photosynthesis; (ii) shortage of essential mineral nutrients, which slows down the rate of production of photosynthetic tissue and its effectiveness in photosynthesis; (iii) temperatures that are lethal or too low for growth; (iv) an insufficient depth of soil; (v) incomplete canopy cover, so that much of the incident radiation lands on the ground instead of on foliage (this may be because of seasonality in leaf production and leaf shedding *or* because of defoliation by grazing animals, pests and diseases); and (vi) the low efficiency with which leaves photosynthesize – under ideal conditions, efficiencies of more than 10% (of PAR) are hard to achieve even in the most productive agricultural systems. However, most of the variation in primary productivity of world vegetation is due to factors (i) to (v), and relatively little is accounted for by intrinsic differences between the photosynthetic efficiencies of the leaves of the different species.

In the course of a year, the productivity of a community may (and probably usually will) be limited by a succession of the factors (i) to (v). In a grassland community, for instance, the primary productivity may be far below the theoretical maximum because the winters are too cold and light intensity is low, the summers are too dry, the rate of nitrogen mobilization is too slow, and for periods grazing animals may reduce the standing crop to a level at which much incident light falls on bare ground.

17.4 Factors limiting primary productivity in aquatic communities

The factors that most frequently limit the primary productivity of aquatic environments are the availability of light and nutrients. The most commonly limiting nutrients are nitrogen (usually as nitrate) and phosphorus (phosphate), but iron can be important in open ocean environments.

17.4.1 Limitation by light and nutrients in streams

in small forest streams, light and nutrients interact to determine productivity

Streams flowing through deciduous forests undergo marked transitions in primary production by algae on the stream bed during the growing season as conditions shift from light-replete early in spring to severely light-limited when leaves develop on the overhanging trees. In a stream in Tennessee, leaf emergence reduced PAR reaching the stream bed from more than 1000 to less than 30 μmol m^{-2} s^{-1} (Hill *et al.*, 2001). The reduction in PAR was paralleled by an equally dramatic fall in stream GPP (Figure 17.14). This is despite a large increase in photosynthetic efficiency from less than 0.3 to 2%; the higher efficiencies arose both because existing taxa acclimated physiologically to low irradiances and because more efficient taxa became dominant later in the season. Intriguingly, as PAR levels fell, the concentration of both nitrate (Figure 17.14a) and phosphate rose. It seems that nutrients limited primary production when PAR was abundant early in spring, with uptake by the algae reducing the concentration in the water at this time. When light became limiting, however, the reduction in algal productivity meant that less of the available nutrients were removed from the supply in the flowing water.

17.4.2 Nutrients in lakes

productivity in lakes . . .

. . . shows a pervasive role for nutrients . . .

Like streams, lakes receive nutrients by the weathering of rocks and soils in their catchment areas, in the rainfall and as a result of human activity (fertilizers and sewage input). They vary considerably in nutrient availability. A study of 12 Canadian lakes shows a clear relationship between gross primary productivity (GPP) and phosphorus concentration and demonstrates the importance of nutrients in limiting lake productivity (Figure 17.15). Note that GPP easily exceeded ecosystem respiration in most lakes, emphasizing the overriding importance of autochthonous production in these lakes. The outlier in the top right corner of Figure 17.15b was atypical of the study sites because it received sewage effluent; here the allochthonous input of organic matter led to a higher consumption than production of organic carbon in the lake.

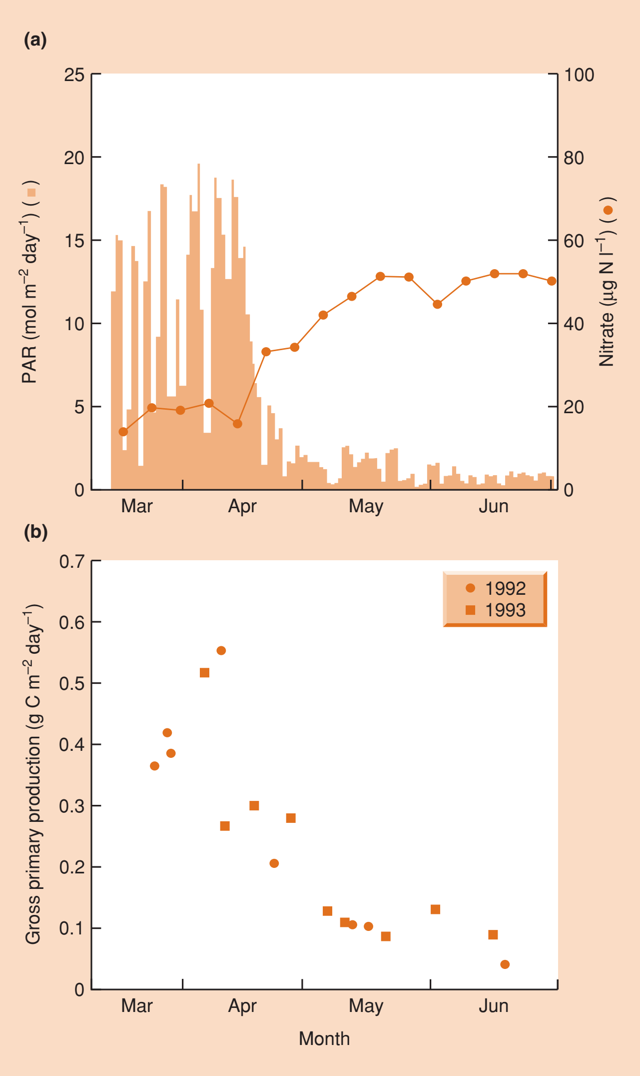


Figure 17.14 (a) Photosynthetically active radiation (PAR) reaching the bed of a Tennessee stream (bars) and stream water nitrate concentration (circles) during the spring of 1992 (the patterns were very similar in 1993). (b) Gross primary productivity in the stream during the spring in 1992 and 1993 (calculated on the basis of whole stream diurnal changes in oxygen concentration). (After Hill *et al.*, 2001.)

. . . whose availability may interact with radiant energy to affect algal 'stoichiometry' (C : N : P ratios)

It is worth noting that the balance of radiant energy relative to the availability of key nutrients can affect C : N : P ratios (stoichiometry) in the tissues of primary producers. Thus, Sterner *et al.* (1997b) found in some phosphorus-deficient Canadian lakes that the availability of PAR relative to total phosphorus (PAR : TP) affected the balance of carbon fixation and phosphorus uptake in algal communities and, thereby, caused variations in C : P ratios in

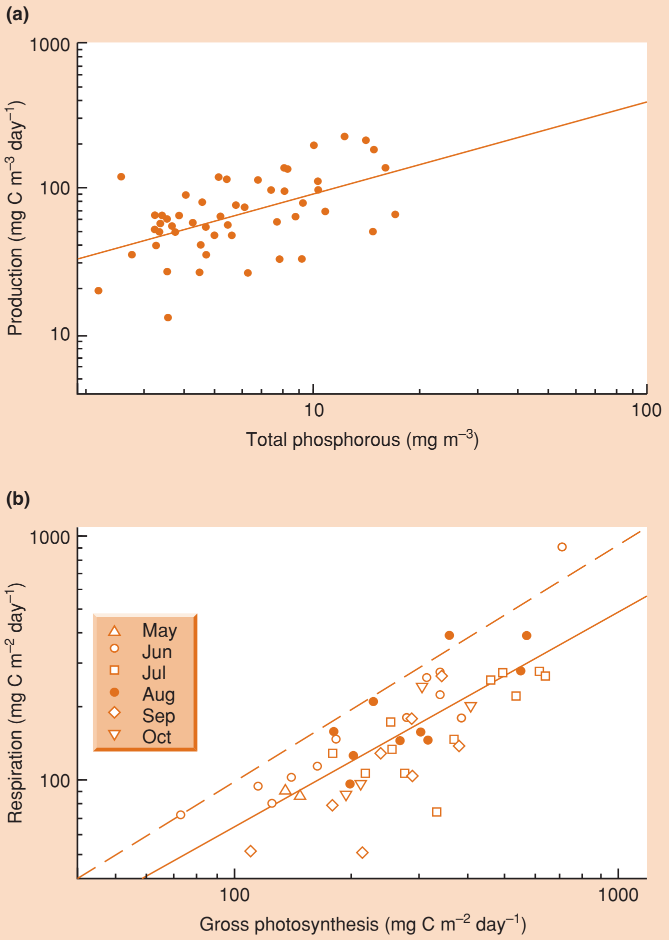


Figure 17.15 (a) Relationship between the gross primary productivity of phytoplankton (microscopic plants) in the open water of some Canadian lakes and phosphorus concentration. (b) The relationship between ecosystem respiration and gross photosynthesis measured on various dates in the study lakes. The dashed line shows where respiration equals GPP. The solid line shows the regression line for the relationship. Metabolic measurements were made in bottles in the laboratory at lake temperatures on depth-integrated water samples taken from the field. (After Carignan *et al*., 2000.)

living algal cells and algal detritus. The zooplankton that consume live algae and the decomposers and detritivores that depend on algal detritus each have specific nutrient requirements, and these are very different from the nutrient ratios in algae. Thus, the changes in algal stoichiometry noted by Sterner *et al*. have consequences for heterotrophic metabolism and productivity. We consider elsewhere how such imbalances between the stoichiometry of plant tissue and of its consumers affect food web interactions, decomposition and nutrient cycling (see Sections 11.2.4, 17.5.4 and 18.2.5).

17.4.3 Nutrients and the importance of upwellings in oceans

rich supplies of nutrients in marine environments . . .

. . . from estuaries . . .

In the oceans, locally high levels of primary productivity are associated with high nutrient inputs from two sources. First, nutrients may flow continuously into coastal shelf regions from estuaries. An example is provided in Figure 17.16. Productivity in the inner shelf region is particularly high both because of high nutrient concentrations and because the relatively clear water provides a reasonable depth within which net photosynthesis is positive (the *euphotic zone*). Closer to land, the water is richer in nutrients but is highly turbid and its productivity is less. The least productive zones are on the outer shelf (and open ocean) where it might be expected that primary productivity would be high because the water is clear and the euphotic zone is deep. Here, however, productivity is low because of the extremely low concentrations of nutrients.

. . . and upwellings

Ocean upwellings are a second source of high nutrient concentrations. These occur on continental shelves where the wind is consistently parallel to, or at a slight angle to, the coast. As a result, water moves offshore and is replaced by cooler, nutrient-rich water originating from the bottom, where nutrients have been accumulating by sedimentation. Strong upwellings can also occur adjacent to submarine ridges, as well as in areas of very strong currents. Where it reaches the surface,

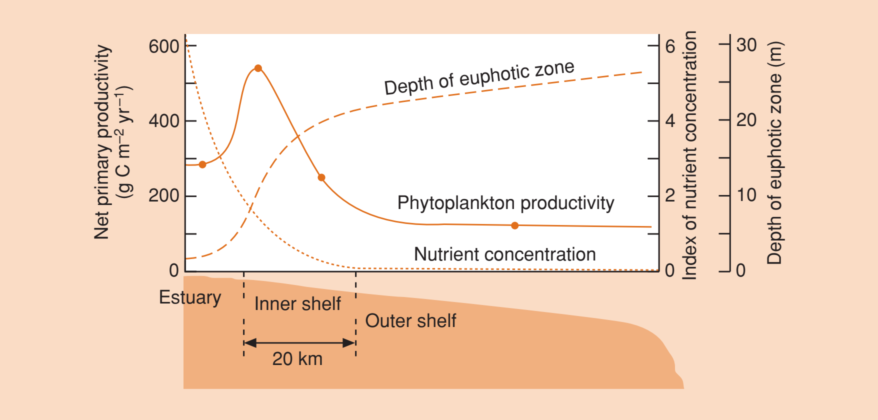


Figure 17.16 Variation in phytoplankton net primary productivity, nutrient concentration and euphotic depth on a transect from the coast of Georgia, USA, to the edge of the continental shelf. (After Haines, 1979.)

the nutrient-rich water sets off a bloom of phytoplankton production. A chain of heterotrophic organisms takes advantage of the abundant food, and the great fisheries of the world are located in these regions of high productivity.

iron as a limiting factor in oceans

Recently, iron has been identified as a limiting nutrient that potentially affects about one-third of the open ocean (Geider *et al.*, 2001). Iron, which is very insoluble in seawater, is ultimately derived from wind-blown particulate material, and large areas of ocean receive insufficient amounts. When iron is added experimentally to ocean areas, massive blooms of phytoplankton can result (Coale *et al.*, 1996); such blooms are also likely to occur when large storms supply land-derived iron to the oceans.

temperature and PAR also affect productivity

While nutrients are the most influential factors for local ocean productivity, temperature and PAR also play a role at a larger scale (Figure 17.17).

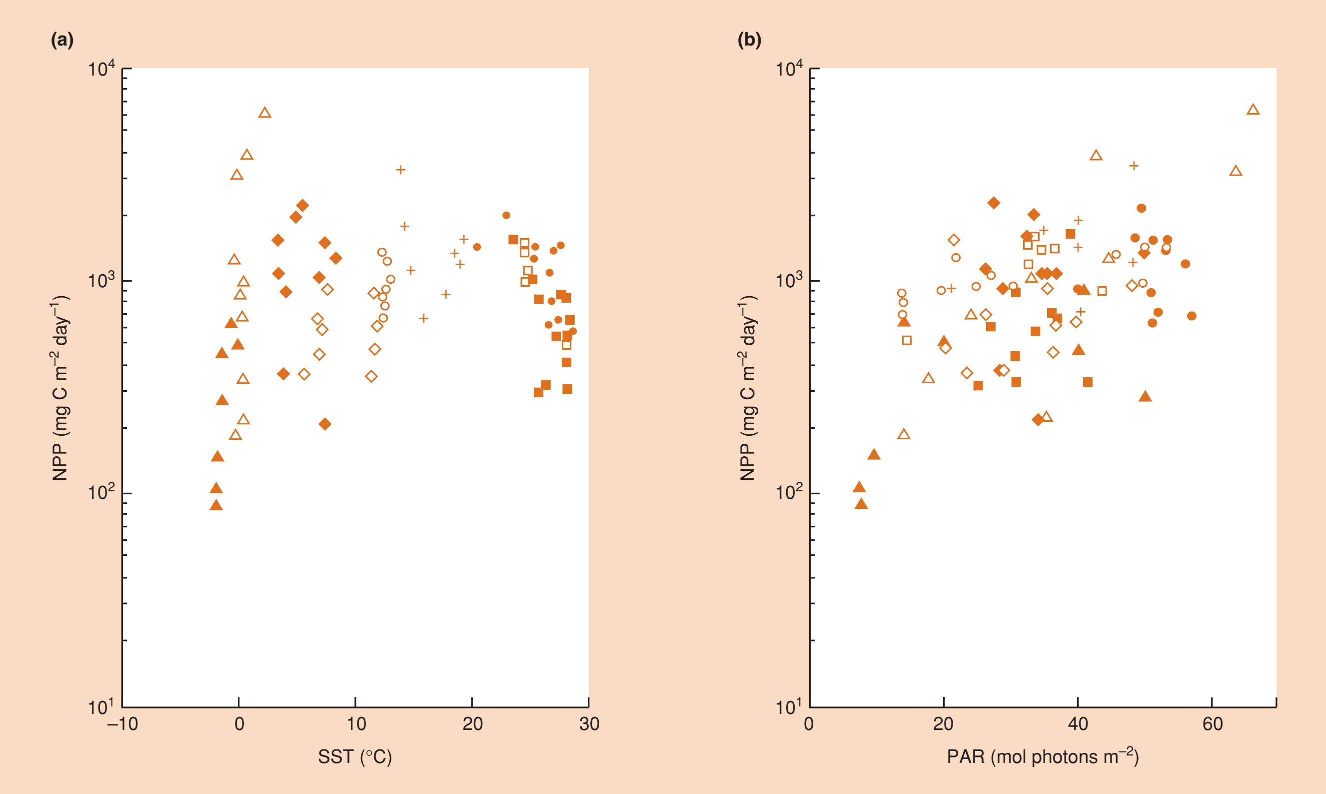


Figure 17.17 Relationships between daily depth-integrated estimates of net primary production (NPP) and: (a) sea surface temperature (SST), and (b) above-water daily photosynthetically available radiation (PAR). The different symbols relate to different data sets from various oceans. (After Campbell *et al.*, 2002.)

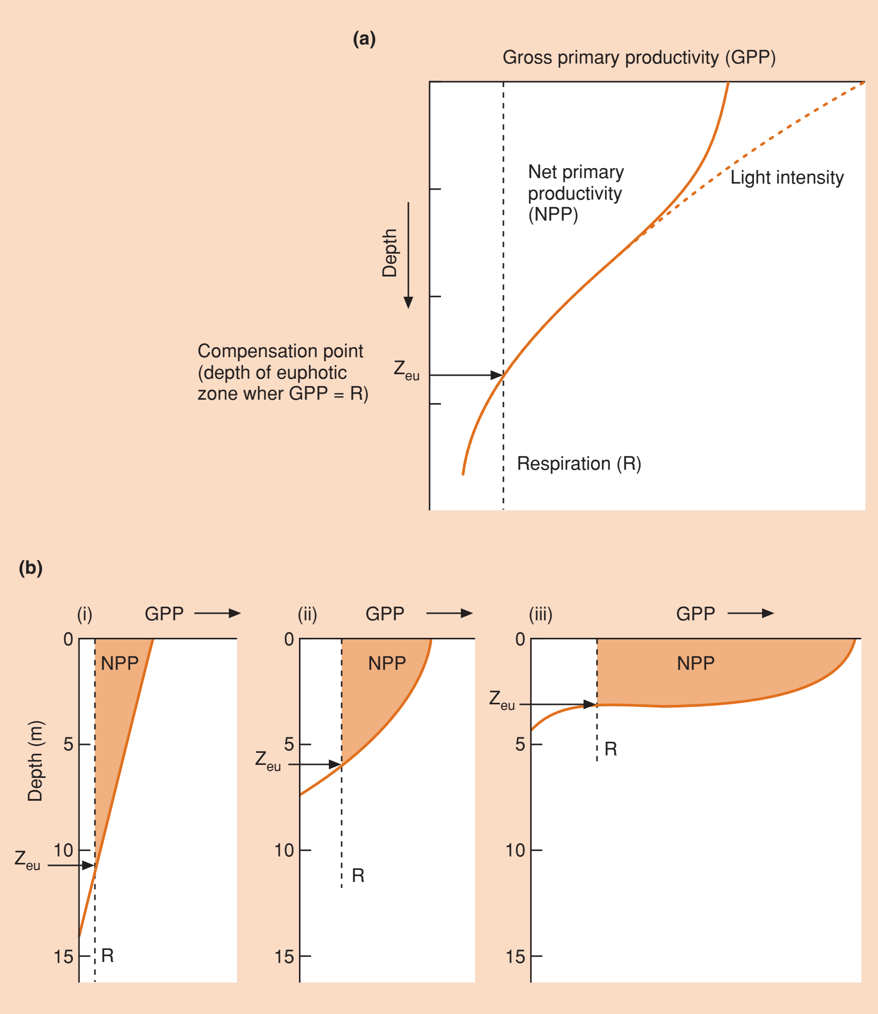


Figure 17.18 (a) The general relationship with depth, in a water body, of gross primary productivity (GPP), respiratory heat loss (R) and net primary productivity (NPP). The compensation point (or depth of the euphotic zone, eu) occurs at the depth (Z_{eu}) where GPP just balances R and NPP is zero. (b) Total NPP increases with nutrient concentration in the water (lake iii > ii > i). Increasing fertility itself is responsible for greater biomasses of phytoplankton and a consequent decrease in the depth of the euphotic zone.

This has significance for our ability to estimate ocean primary productivity because sea surface temperature and PAR (together with surface chlorophyll concentration, another factor correlated with NPP) can be measured using satellite telemetry.

17.4.4 Productivity varies with depth in aquatic communities

phytoplankton productivity varies with depth

Although the concentration of a limiting nutrient usually determines the productivity of aquatic communities on an areal basis, in any given water body there is also considerable variation with depth as a result of attenuation of light intensity. Figure 17.18a shows how GPP declines with depth. The depth at which GPP is just balanced by phytoplankton respiration, R, is known as the compensation point. Above this, NPP is positive. Light is absorbed by water molecules as well as by dissolved and particulate matter, and it declines exponentially with depth. Near the surface, light is superabundant, but at greater depths its supply is limited and light intensity ultimately determines the extent of the euphotic zone. Very close to the surface, particularly on sunny days, there may even be photoinhibition of photosynthesis. This seems to be due largely to radiation being absorbed by the photosynthetic pigments at such a rate that it cannot be used via the normal photosynthetic channels, and it overflows into destructive photo-oxidation reactions.

The more nutrient-rich a water body is, the shallower its euphotic zone is likely to be (Figure 17.18b). This is not really a paradox. Water bodies with higher nutrient concentrations usually possess a greater biomasses of phytoplankton that absorb light and reduce its availability at greater depth. (This is exactly analogous to the shading influence of the tree canopy in a forest, which may remove up to 98% of the radiant energy before it can reach the ground layer vegetation or, as we saw above, a stream bed.) Even quite shallow lakes, if sufficiently fertile, may be devoid of water weeds on the bottom because of shading by phytoplankton. The relationships shown in Figure 17.18a and b are derived from lakes but the pattern is qualitatively similar in ocean environments (Figure 17.19).

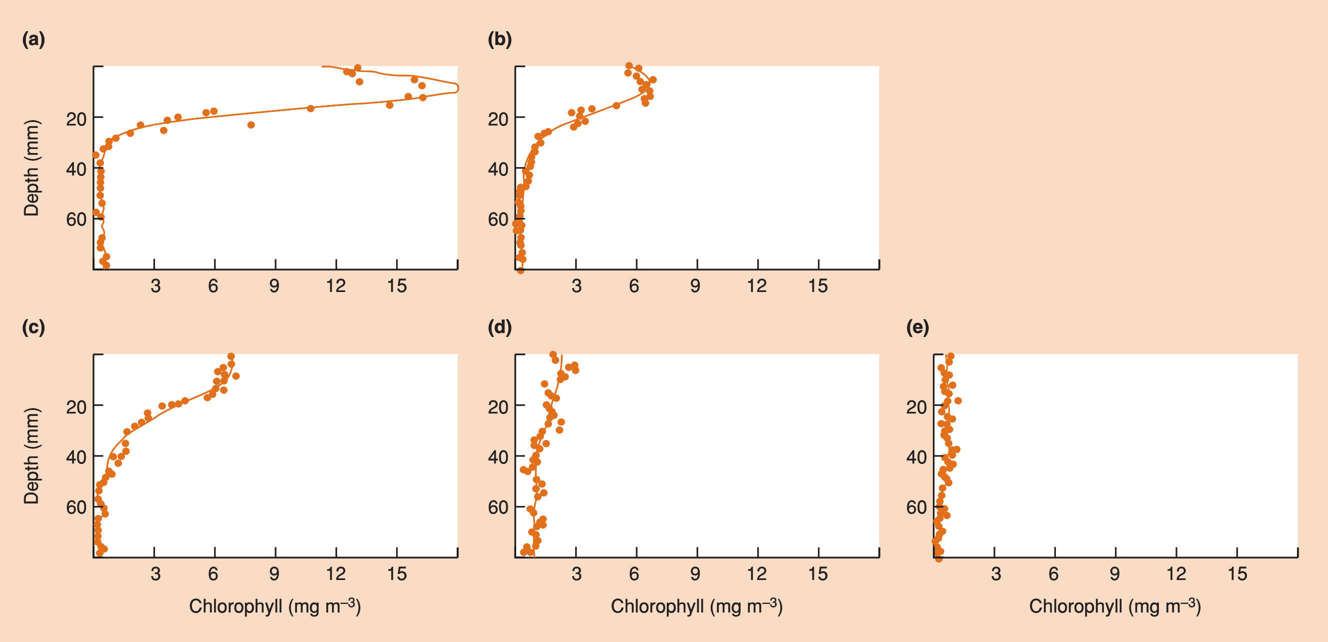


Figure 17.19 Examples of vertical chlorophyll profiles recorded in the ocean off the coast of Namibia. Example (a) is typical of locations associated with ocean upwelling: as cold upwelled water warms up, a surface phytoplankton bloom develops, reducing light penetration and thus productivity in deeper water. Example (b) illustrates how peak abundance can shift to deeper water as a surface bloom in an upwelling area depletes the nutrient concentrations there. The surface phytoplankton bloom in example (c) is less dramatic than in (a) (perhaps reflecting lower nutrient concentrations in the upwelling water); as a result, chlorophyll concentration remains relatively high to a greater depth. Examples (d) and (e) are for locations where nutrient concentrations are much lower. (After Silulwane *et al.*, 2001.)

17.5 The fate of energy in ecosystems

Secondary productivity is defined as the rate of production of new biomass by heterotrophic organisms. Unlike plants, heterotrophic bacteria, fungi and animals cannot manufacture from simple molecules the complex, energy-rich compounds they need. They derive their matter and energy either directly by consuming plant material or indirectly from plants by eating other heterotrophs. Plants, the primary producers, comprise the first trophic level in a community; primary consumers occur at the second trophic level; secondary consumers (carnivores) at the third, and so on.

17.5.1 Relationships between primary and secondary productivity

there is a general positive relationship between primary and secondary productivity

Since secondary productivity depends on primary productivity, we should expect a positive relationship between the two variables in communities. Turning again to the stream study described in Section 17.4.1, recall that primary productivity declined dramatically during the summer when a canopy of tree leaves above the stream shaded out most of the incident radiation. A principal grazer of the algal biomass is the snail *Elimia clavaeformis*. Figure 17.20a shows how the growth rate of individual snails in the stream was lowest in the summer; there was a statistically significant positive relationship between snail growth and monthly stream bed PAR (Hill *et al.*, 2001). Figure 17.20b–d illustrates the general relationship between primary and secondary productivity in aquatic and terrestrial examples. Secondary productivity by zooplankton, which principally consume phytoplankton cells, is positively related to phytoplankton productivity in a range of lakes in different parts of the world (Figure 17.20b). The productivity of heterotrophic bacteria in lakes and oceans also parallels that of phytoplankton (Figure 17.20c); they metabolize dissolved organic matter released from intact phytoplankton cells or produced as a result of ‘messy feeding’ by grazing animals. Figure 17.20d shows how the productivity of *Geospiza fortis* (one of Darwin’s finches), measured in terms of average brood size on an island in the Galápagos archipelago, is related to annual rainfall, itself an index of primary productivity.

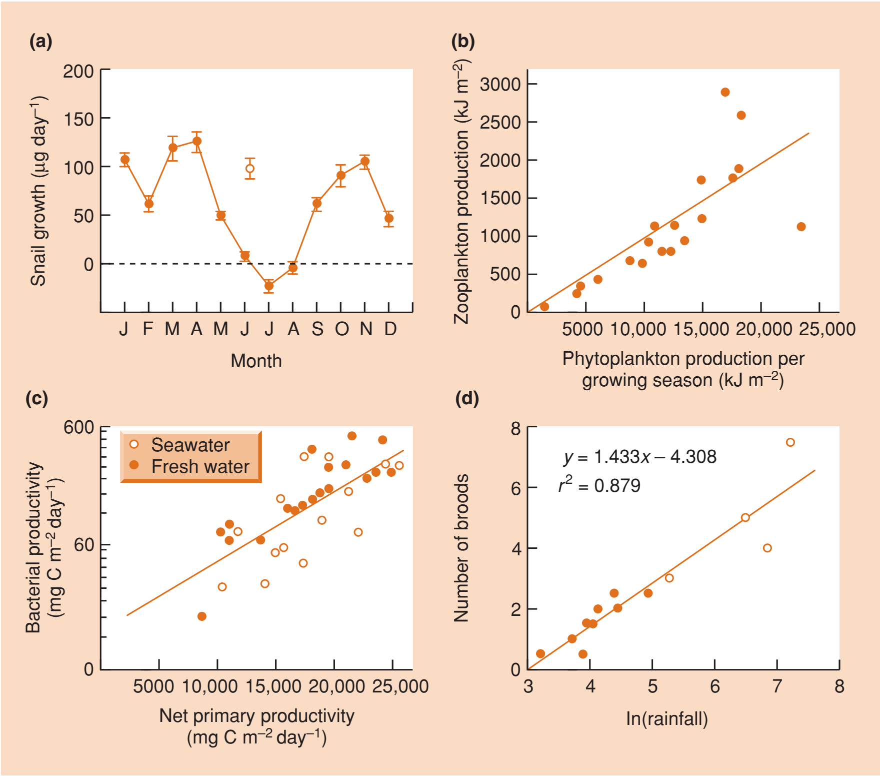


Figure 17.20 (a) Seasonal pattern of snail growth (mean increase in weight of individually marked snails during a month on the stream bed ± SE). The open circle represents growth at a nearby unshaded stream site in June. (After Hill *et al.*, 2001.) (b) Relationship between primary and secondary productivity for zooplankton in lakes. (After Brylinsky & Mann, 1973.) (c) Relationship between bacterial and phytoplankton productivity in fresh water and seawater. (After Cole *et al.* 1988.) (d) Mean clutch size of *Geospiza fortis* in relation to annual rainfall (positively related to primary productivity); the open circles are for particularly wet years when El Niño weather events occurred. (After Grant *et al.*, 2000.).

most primary productivity does not pass through the grazer system

A general rule in both aquatic and terrestrial ecosystems is that secondary productivity by herbivores is approximately an order of magnitude less than the primary productivity upon which it is based. This is a consistent feature of all grazer systems: that part of the trophic structure of a community that depends, at its base, on the consumption of *living* plant biomass (in the ecosystem context we use 'grazer' in a different sense to its definition in Chapter 9). It results in a pyramidal structure in which the productivity of plants provides a broad base upon which a smaller productivity of primary consumers depends, with a still smaller productivity of secondary consumers above that. Trophic levels may also have a pyramidal structure when expressed in terms of density or biomass. (Elton (1927) was the first to recognize this fundamental feature of community architecture and his ideas were later elaborated by Lindemann (1942).) But there are many exceptions. Food chains based on trees will certainly have larger numbers (but *not* biomass) of herbivores per unit area than of plants, while chains dependent on phytoplankton production may give inverted pyramids of biomass, with a highly productive but small biomass of short-lived algal cells maintaining a larger biomass of longer lived zooplankton.

The productivity of herbivores is invariably less than that of the plants on which they feed. Where has the missing energy gone? First, not all of the plant biomass produced is consumed alive by herbivores. Much dies without being grazed and supports the decomposer community (bacteria, fungi and detritivorous animals). Second, not all plant biomass eaten by herbivores (nor herbivore biomass eaten by carnivores) is assimilated and available for incorporation into consumer biomass. Some is lost in feces, and this also passes to the decomposers. Third, not all energy that has been assimilated is actually converted to biomass. A proportion is lost as respiratory heat. This occurs both because no energy conversion process is ever 100% efficient (some is lost as unusable random heat, consistent with the second law of thermodynamics) and also because animals do work that requires energy, again released as heat. These three energy pathways occur at all trophic levels and are illustrated in Figure 17.21.

17.5.2 Possible pathways of energy flow through a food web

alternative pathways that energy can trace through the community

Figure 17.22 provides a complete description of the trophic structure of a community. It consists of the grazer system pyramid of productivity, but with two additional elements of realism. Most importantly, it adds a *decomposer system* – this is invariably coupled to the grazer system in communities. Secondly, it recognizes that there are subcomponents of each trophic level in each

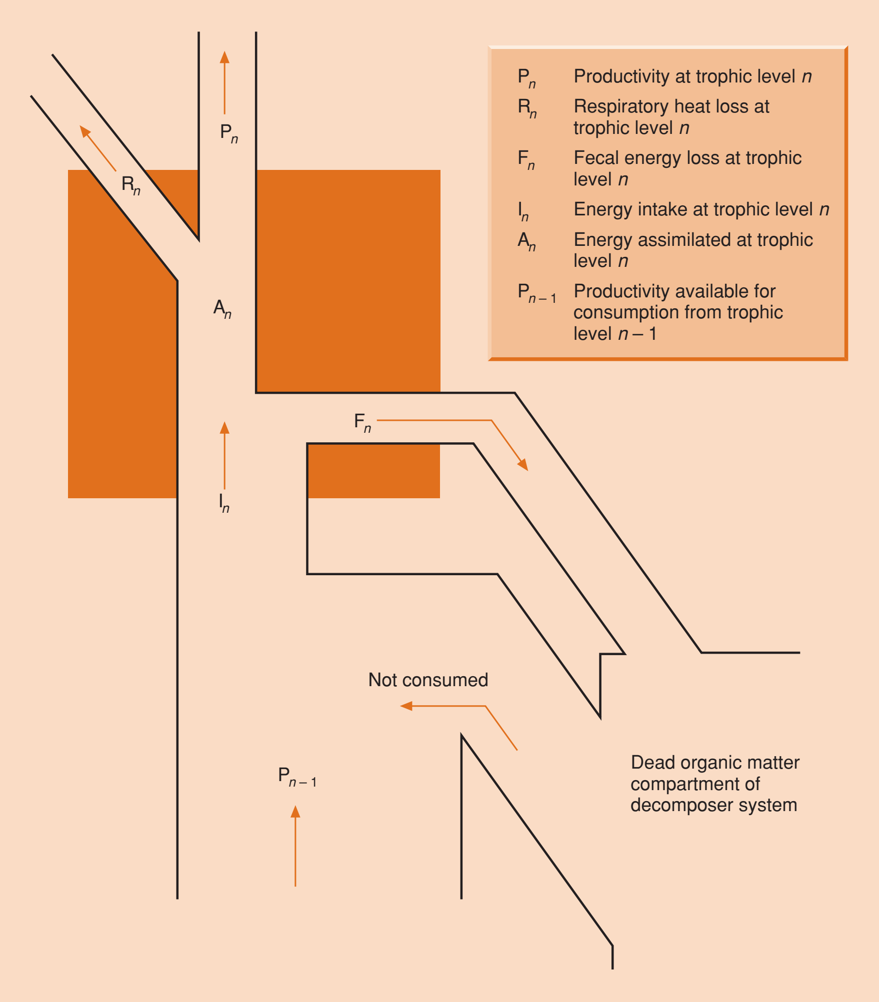


Figure 17.21 The pattern of energy flow through a trophic compartment.

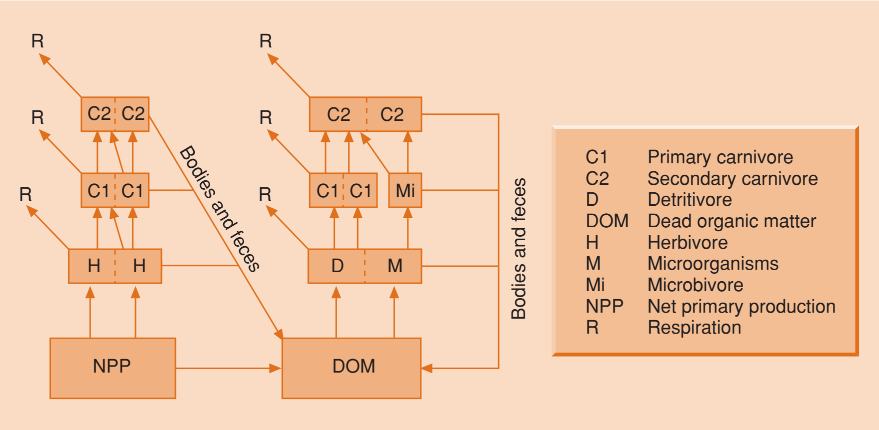


Figure 17.22 A generalized model of trophic structure and energy flow through a food web. (After Heal & MacLean, 1975.)

subsystem that operate in different ways. Thus a distinction is made between microbes and detritivores that occupy the same trophic level and utilize dead organic matter, and between consumers of microbes (microbivores) and of detritivores. Displayed in Figure 17.22 are the possible routes that a joule of energy, fixed in net primary production, can take as it is dissipated on its path through the community. A joule of energy may be consumed and assimilated by a herbivore that uses part of it to do work and loses it as respiratory heat. Or it might be consumed by a herbivore and later assimilated by a carnivore that dies and enters the dead organic matter compartment. Here, what remains of the joule may be assimilated by a fungal hypha and consumed by a soil mite, which uses it to do work, dissipating a further part of the joule as heat. At each consumption step, what remains of the joule may fail to be assimilated and may pass in the feces to be dead organic matter, or it may be assimilated and respired, or assimilated and incorporated into the growth of body tissue (or the production of offspring – as in the case of broods of the bird in Figure 17.20d). The body may die and what remains of the joule enter the dead organic matter compartment, or it may be captured alive by a consumer in the next trophic level where it meets a further set of possible branching pathways. Ultimately, each joule will have found its way out of the community, dissipated as respiratory heat at one or more of the transitions in its path along the food chain. Whereas a molecule or ion may cycle endlessly through the food chains of a community, energy passes through just once.

The possible pathways in the grazer and decomposer systems are the same, with one critical exception – feces and dead bodies are lost to the grazer system (and enter the decomposer system), but feces and dead bodies from the decomposer system are simply sent back to the dead organic matter compartment at its base. This has a fundamental significance. The energy available as dead organic matter may finally be completely metabolized – and all the energy lost as respiratory heat – even if this requires several circuits through the decomposer system. The exceptions to this are situations where: (i) matter is exported out of the local environment to be metabolized elsewhere, for example detritus washed out of a stream; and (ii) local abiotic conditions are very unfavorable to decomposition processes, leaving pockets of incompletely metabolized high-energy matter, otherwise known as oil, coal and peat.

17.5.3 The importance of transfer efficiencies in determining energy pathways

the relative importance of energy pathways depends on three transfer efficiencies: . . .

The proportions of net primary production that flow along each of the possible energy pathways depend on *transfer efficiencies* in the way energy is used and passed from one step to the next. A knowledge of the values of just three categories of transfer efficiency is all that is required to predict the pattern of energy flow. These are *consumption efficiency* (CE) *assimilation efficiency* (AE) and *production efficiency* (PE).

. . . consumption efficiency, . . .

consumption efficiency,

$$CE = I_n/P_{n-1} \times 100.$$

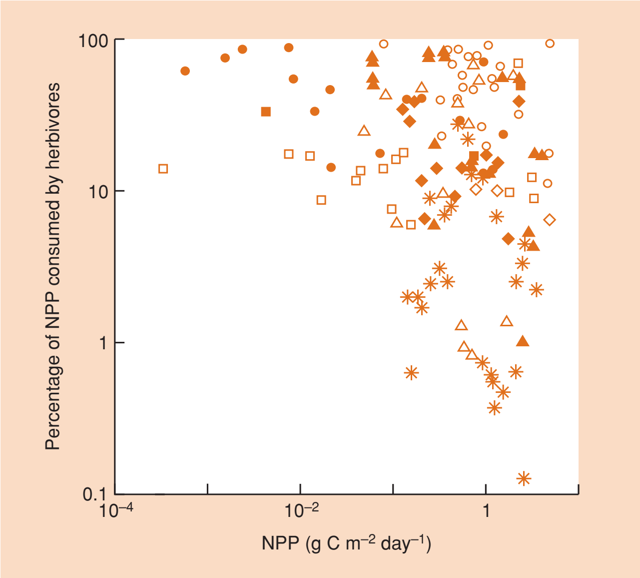


Figure 17.23 Relationship between the percentage of net primary production (NPP) consumed by herbivores and net primary productivity. ○, phytoplankton; ●, benthic microalgae; □, macroalgal beds; ◆, freshwater macrophyte meadows; ■, seagrass meadows; ▲, marshes; △, grasslands; ◇, mangroves; ✱, forests. (Data from a number of sources, compiled by Cebrian, 1999.)

Repeated in words, CE is the percentage of total productivity available at one trophic level (P_{n-1}) that is actually consumed ('ingested') by a trophic compartment 'one level up' (I_n). For primary consumers in the grazer system, CE is the percentage of joules produced per unit time as NPP that finds its way into the guts of herbivores. In the case of secondary consumers, it is the percentage of herbivore productivity eaten by carnivores. The remainder dies without being eaten and enters the decomposer chain.

Various reported values for the consumption efficiencies of herbivores are shown in Figure 17.23. Most of the estimates are remarkably low, usually reflecting the unattractiveness of much plant material because of its high proportion of structural support tissue, but sometimes also as a consequence of generally low herbivore densities (because of the action of their natural enemies). The consumers of microscopic plants (microalgae growing on beds or free-living phytoplankton) can achieve greater densities, have less structural tissue to deal with and account for a greater percentage of primary production. Median values for consumption efficiency are less than 5% in forests, around 25% in grasslands and more than 50% in phytoplankton-dominated communities. We know much less about the consumption efficiencies of carnivores feeding on their prey, and any estimates are speculative. Vertebrate predators may consume 50–100% of production from vertebrate prey but perhaps only 5% from invertebrate prey. Invertebrate predators consume perhaps 25% of available invertebrate prey production.

. . . assimilation efficiency . . .

assimilation efficiency,
$AE = A_n/I_n \times 100$.

Assimilation efficiency is the percentage of food energy taken into the guts of consumers in a trophic compartment (I_n) that is assimilated across the gut wall (A_n) and becomes available for incorporation into growth or to do work. The remainder is lost as feces and enters the base of the decomposer system. An 'assimilation efficiency' is much less easily ascribed to microorganisms. Food does not enter an invagination of the outside world passing through the microorganism's body (like the gut of a higher organism) and feces are not produced. In the sense that bacteria and fungi typically assimilate effectively 100% of the dead organic matter they digest externally and absorb, they are often said to have an 'assimilation efficiency' of 100%.

Assimilation efficiencies are typically low for herbivores, detritivores and microbivores (20–50%) and high for carnivores (around 80%). In general, animals are poorly equipped to deal with dead organic matter (mainly plant material) and living vegetation, no doubt partly because of the very widespread occurrence of physical and chemical plant defenses, but mainly as a result of the high proportion of complex structural chemicals such as cellulose and lignin in their make-up. As Chapter 11 describes, however, many animals contain a symbiotic gut microflora that produces cellulase and aids in the assimilation of plant organic matter. In one sense, these animals have harnessed their own personal decomposer system. The way that plants allocate production to roots, wood, leaves, seeds and fruits influences their usefulness to herbivores. Seeds and fruits may be assimilated with efficiencies as high as 60–70%, and leaves with about 50% efficiency, while the assimilation efficiency for wood may be as low as 15%. The animal food of carnivores (and detritivores such as vultures that consume animal carcasses) poses less of a problem for digestion and assimilation.

. . . and production efficiency . . .

production efficiency,
$PE = P_n/A_n \times 100$.

Production efficiency is the percentage of assimilated energy (A_n) that is incorporated into new biomass (P_n). The remainder is entirely lost to the community as respiratory heat. (Energy-rich secretory and excretory products, which have taken part in metabolic processes, may be viewed as production, P_n, and become available, like dead bodies, to the decomposers.)

Production efficiency varies mainly according to the taxonomic class of the organisms concerned. Invertebrates in general have high efficiencies (30–40%), losing relatively little energy in respiratory heat and converting more assimilate to production.

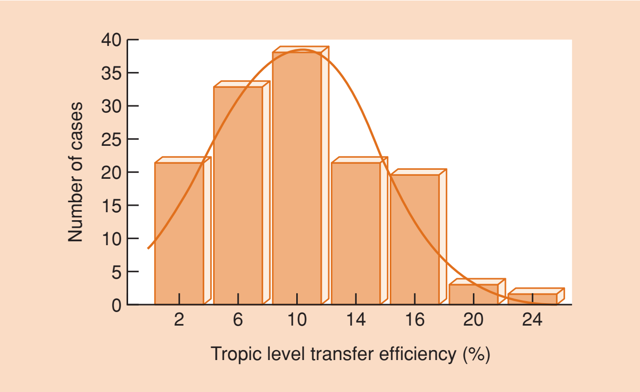


Figure 17.24 Frequency distribution of trophic-level transfer efficiencies in 48 trophic studies of aquatic communities. There is considerable variation among studies and among trophic levels. The mean is 10.13 % (SE = 0.49). (After Pauly & Christensen, 1995.)

Amongst the vertebrates, ectotherms (whose body temperature varies according to environmental temperature) have intermediate values for PE (around 10%), whilst endotherms, with their high energy expenditure associated with maintaining a constant temperature, convert only 1–2% of assimilated energy into production. The small-bodied endotherms have the lowest efficiencies, with the tiny insectivores (e.g. wrens and shrews) having the lowest production efficiencies of all. On the other hand, microorganisms, including protozoa, tend to have very high production efficiencies. They have short lives, small size and rapid population turnover. Unfortunately, available methods are not sensitive enough to detect population changes on scales of time and space relevant to microorganisms, especially in the soil. In general, efficiency of production increases with size in endotherms and decreases very markedly in ectotherms.

trophic level transfer efficiency,
$TLTE = P_n/P_{n-1} \times 100$.

. . . which combine to give trophic level transfer efficiency

The overall trophic transfer efficiency from one trophic level to the next is simply CE × AE × PE. In the period after Lindemann's (1942) pioneering work, it was generally assumed that trophic transfer efficiencies were around 10%; indeed some ecologists referred to a 10% 'law'. However, there is certainly no law of nature that results in precisely one-tenth of the energy that enters a trophic level transferring to the next. For example, a compilation of trophic studies from a wide range of freshwater and marine environments revealed that trophic level transfer efficiencies varied between about 2 and 24%, although the mean was 10.13% (Figure 17.24).

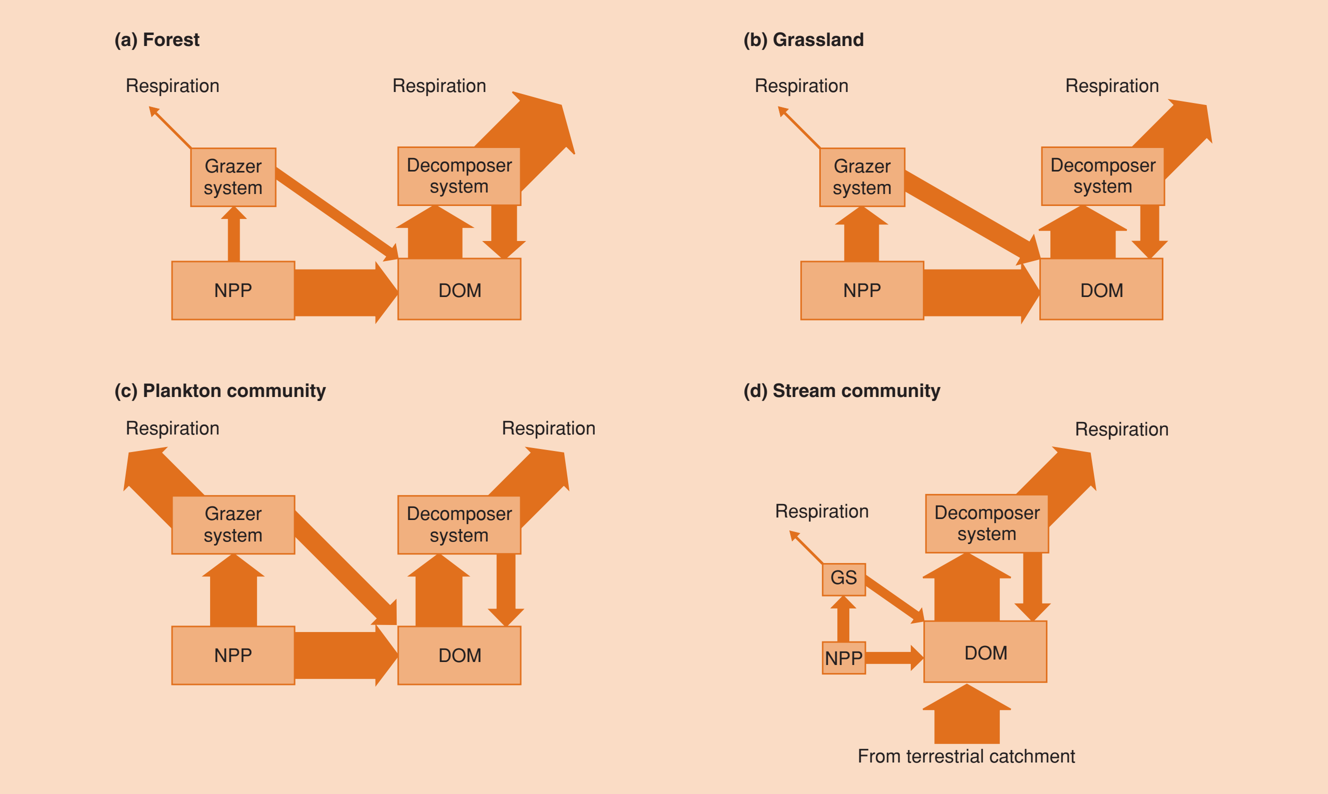


Figure 17.25 General patterns of energy flow for: (a) a forest, (b) a grassland, (c) a marine plankton community, and (d) the community of a stream or small pond. The relative sizes of the boxes and arrows are proportional to the relative magnitudes of compartments and flows. DOM, dead organic matter; NPP, net primary production.

17.5.4 Energy flow through contrasting communities

relative roles of grazer and decomposer systems in contrasting communities

Given accurate values for net primary productivity (NPP) in an ecosystem, and CE, AE and PE for the various trophic groupings shown in the model in Figure 17.22, it should be possible to predict and understand the relative importance of the different possible energy pathways. Perhaps not surprisingly, no study has incorporated all ecosystem compartments and all transfer efficiencies of the component species. However, some generalizations are possible when the gross features of contrasting systems are compared (Figure 17.25). Thus, the decomposer system is probably responsible for the majority of secondary production, and therefore respiratory heat loss, in every community in the world. The grazer system has its greatest role in plankton communities, where a large proportion of NPP is consumed alive and assimilated at quite a high efficiency. Even here, though, it is now clear that very high densities of heterotrophic bacteria in the plankton community subsist on dissolved organic molecules excreted by phytoplankton cells, perhaps consuming more than 50% of primary productivity as 'dead' organic matter in this way (Fenchel, 1987a). The grazer system holds little sway in terrestrial communities because of low herbivore consumption and assimilation efficiencies, and it is almost nonexistent in many small streams and ponds simply because primary productivity is so low. The latter depend for their energy base on dead organic matter produced in the terrestrial environment that falls or is washed or blown into the water. The deep-ocean benthic community has a trophic structure very similar to that of streams and ponds (all can be described as heterotrophic communities). In this case, the community lives in water too deep for photosynthesis to be appreciable or even to take place at all, but it derives its energy base from dead phytoplankton, bacteria, animals and feces that sink from the autotrophic community in the euphotic zone above. From a different perspective, the ocean bed is equivalent to a forest floor beneath an impenetrable forest canopy.

grazer consumption efficiencies are highest where plants have low C : N and C : P ratios

We can move from the relatively gross generalizations above to consider in Figure 17.26 a greater range of terrestrial and aquatic ecosystems (data compiled from over 200 published reports by Cebrian, 1999). Figure 17.26a first shows the range of values for NPP

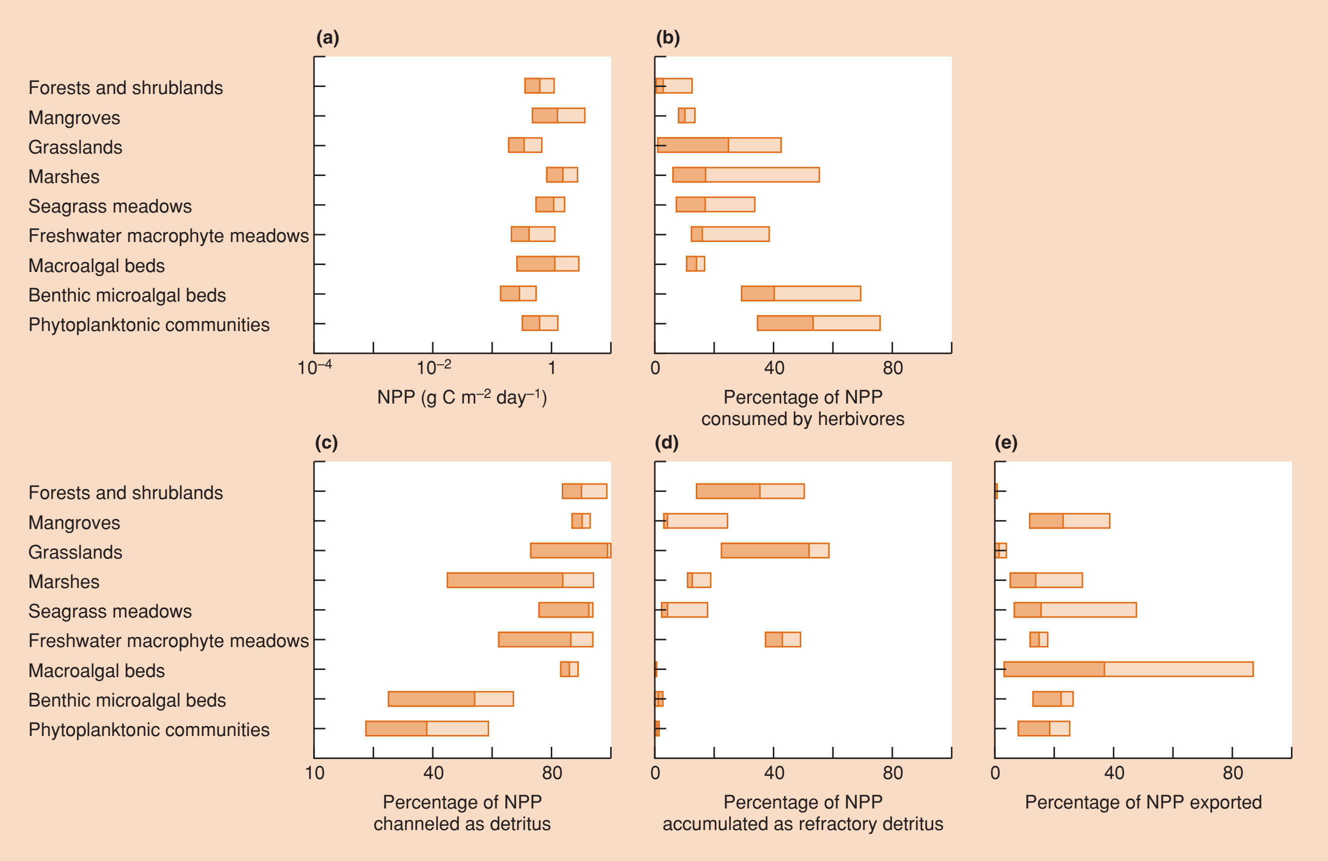


Figure 17.26 Box plots showing for a range of ecosystem types: (a) net primary productivity (NPP), (b) percentage of NPP consumed by detritivores, (c) percentage of NPP channeled as detritus, (d) percentage of NPP accumulated as refractory detritus, and (e) percentage of NPP exported. Boxes encompass 25 and 75% quartiles and the central lines represents the median of a number of studies. (After Cebrian, 1999.)

in a variety of terrestrial and aquatic ecosystems. Figure 17.26b re-emphasizes how consumption efficiency by grazers is particularly low in ecosystems where plant biomass contains considerable support tissue and relatively low amounts of nitrogen and phosphorus (i.e. forests, shrublands and mangroves). Plant biomass not consumed by herbivores becomes detritus and contributes by far the largest proportion to the dead organic matter (DOM) box in Figure 17.25. Not surprisingly, the percentage of NPP destined to be detritus is highest in forests and lowest in phytoplankton and benthic microalgal communities (Figure 17.26c). Plant biomass from terrestrial communities is not only unpalatable to herbivores, it is also relatively more difficult for decomposers and detritivores to deal with. Thus, Figure 17.26d shows that a greater proportion of primary production accumulates as refractory detritus (persisting for more than a year) in forests, shrublands, grasslands and freshwater macrophyte meadows. Finally, Figure 17.26e shows the percentage of NPP that is exported out of the systems. The values are generally modest (medians of 20% or less) indicating that, in most cases, the majority of biomass produced in an ecosystem is consumed or decomposed there. The most obvious exceptions are mangroves and, in particular, macroalgal beds (which often inhabit rocky shores), where relatively large proportions of plant biomass are displaced and moved away by storm and tidal action.

In general then, communities composed of plants whose stoichiometry represents a higher nutritional status (higher nitrogen and phosphorus concentrations, i.e. lower C : N and C : P) lose a higher percentage to herbivores, produce a smaller proportion of detritus, experience faster decomposition rates and, in consequence, accumulate less refractory detritus and have smaller stores of dead organic carbon (Cebrian, 1999).

temporal patterns in the balance between production and consumption of organic matter

The presentation of information in Figure 17.26 emphasizes spatial patterns in the way energy moves through the world's ecosystems. However, we should not lose sight of the temporal patterns that exist in the balance between production and consumption

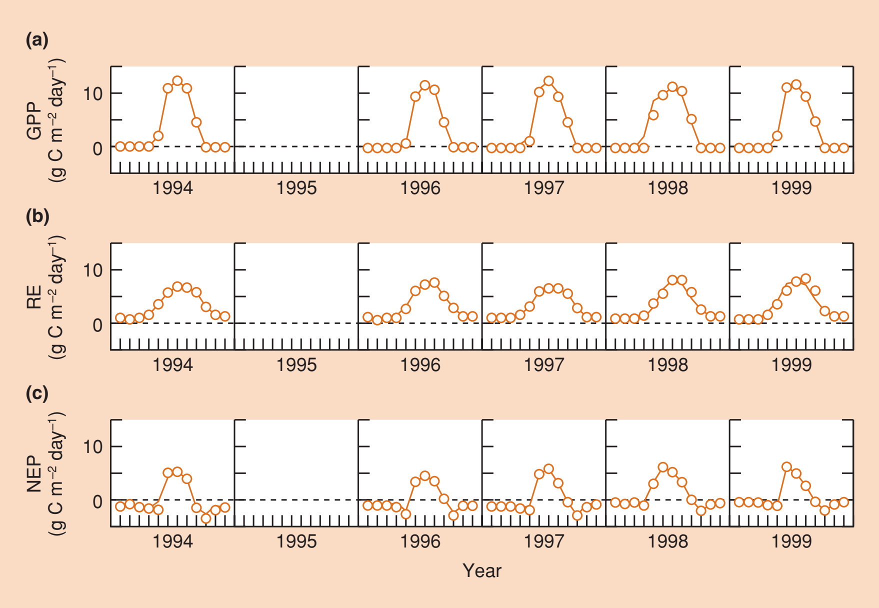


Figure 17.27 Monthly mean values for: (a) gross primary productivity (GPP), (b) ecosystem respiration (RE), and (c) net ecosystem productivity (NEP) in a Canadian aspen forest. (After Arain *et al.*, 2002.)

of organic matter. Figure 17.27 shows how GPP, RE (the sum of autotrophic and heterotrophic respiration) and net ecosystem productivity (NEP) varied seasonally during 5 years of study of a boreal aspen (*Populus tremuloides*) forest in Canada. Total annual GPP (the area under the GPP curves in Figure 17.27a) was highest in 1998 when the temperature was high (probably the result of an El Niño event – see below) and lowest in 1996 when the temperature was particularly low. Annual variations in GPP (e.g. 1419 g C m^{-2} in 1998, 1187 g C m^{-2} in 1996) were large compared to variations in RE (1132 g C m^{-2} and 1106 g C m^{-2}, respectively) because the occurrence of warm springs caused photosynthesis to increase faster than respiration. This led overall to higher values of NEP in warmer years (290 g C m^{-2} in 1998, 80 g C m^{-2} in 1996). Note how NEP is negative (RE exceeds GPP and carbon stores are being used by the community) except in the summer months when GPP consistently exceeds RE. At this site, the cumulative annual values for NEP were always positive, indicating that more carbon is fixed than is respired each year and the forest is a carbon sink. However, this is not true for all ecosystems every year (Falge *et al.*, 2002).

consequences of the ENSO for ecosystem energetics

The aspen forest discussed above is by no means the only ecosystem where annual variations in energy flux may be due to climatic cycles such as the El Niño–Southern Oscillation (ENSO; see also Section 2.4.1). ENSO events occur sporadically but typically occur every 3–6 years. During such events, the temperature may be significantly higher in some locations and lower in others and, just as significantly, rainfall can be 4–10 times higher in some areas (Holmgren *et al.*, 2001). The El Niño has been correlated with dramatic changes in aquatic ecosystems (even leading to the collapse of fisheries; Jordan, 1991). More recently, it has become obvious that the El Niño can cause major changes on land too. Figure 17.28 shows the annual variation in caterpillar numbers on the Galápagos Islands in a standard census conducted in various years since 1977, plotted on the same graph as annual rainfall. The remarkably strong correlation comes about because of the dependence of caterpillar numbers on primary productivity, which itself is considerably higher in wet years. We saw in Figure 17.20d how the total number of broods of the finch *Geospiza fortis* was much greater in the four ENSO years (open circles in that figure). This reflects the much greater production in very wet years of the seeds, fruits and caterpillars that they feed on. Not only do the finches increase the number of broods, but also the size of their clutches and the probability of successful rearing to the fledging stage.

Our growing knowledge of the impact of ENSO events on energy flux through ecosystems suggests that the predicted changes in extreme weather events expected as a result of human-induced global climate change will profoundly alter ecosystem processes in many parts of the world, a topic to which we will return in Chapter 22.

But next we turn to the flux of matter through ecosystems, recognizing that the rate at which resources are supplied and used by autotrophs and heterotrophs depends fundamentally on the supply of nutrients (Chapter 18). We shall see later how ecosystem productivity helps determine the consequences of competitive and predator–prey interactions for community composition (Chapter 19), food web ecology (Chapter 20) and species richness (Chapter 21).

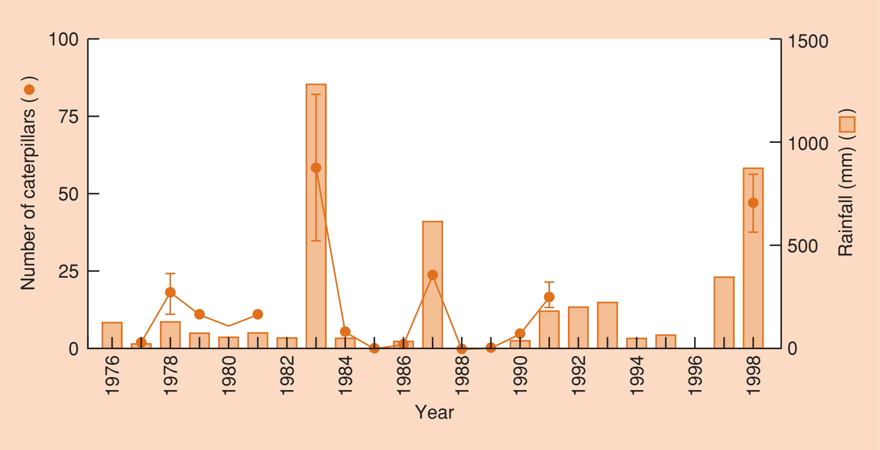


Figure 17.28 Annual variation in mean caterpillar numbers (± SE; ●) in a standard census against a histogram of annual rainfall on the Galápagos island of Daphne Major. (After Grant *et al*., 2000.)

Summary

The term ecosystem is used to denote the biological community (primary producers, decomposers, detritivores, herbivores, etc.) together with the abiotic environment in which it is set. Lindemann laid the foundations of a science of ecological energetics by considering the efficiency of transfer between trophic levels – from incident radiation received by a community through its capture by green plants in photosynthesis to its subsequent use by heterotrophs. This is the topic of the present chapter.

The bodies of the living organisms within a unit area constitute a standing crop of biomass. Primary productivity is the rate at which biomass is produced per unit area by plants. The total fixation of energy by photosynthesis is gross primary productivity (GPP), a proportion of which is respired by the plants as autotrophic respiration (RA). The difference between GPP and RA is net primary productivity (NPP) and represents the actual rate of production of new biomass that is available for consumption by heterotrophic organisms. The rate of production of biomass by heterotrophs is secondary productivity, and their respiration is heterotrophic respiration (HE). Net ecosystem productivity (NEP) is GPP minus total respiration (RA + RH).

We discuss the broad patterns in primary productivity across the face of the globe and in relation to seasonal and annual variations in conditions, and note that primary productivity : biomass ratios are higher in aquatic than terrestrial communities. The factors that limit terrestrial primary productivity are solar energy (and particularly its inefficient use by plants), water and temperature (and their complex interactions), soil texture and drainage, and mineral nutrient availability. The length of the growing season is particularly influential. In aquatic environments, primary productivity depends in particular on the availability of solar radiation (with strong patterns related to water depth) and nutrients (especially important are human inputs to lakes, estuarine inputs to oceans and ocean upwelling zones).

Unlike plants, heterotrophic bacteria, fungi and animals cannot manufacture from simple molecules the complex, energy-rich compounds they need. They derive their matter and energy either directly by consuming plant material or indirectly from plants by eating other heterotrophs. There is a general positive relationship between primary and secondary productivity in ecosystems, but most primary production passes, when dead, through the detritus system rather than as living material through the grazing system. The pathways traced by energy through communities are determined by three energy transfer efficiencies (consumption, assimilation and production efficiencies). Grazer consumption efficiencies are highest where plants have little structural support tissue and low C : N and C : P ratios. We discuss temporal patterns in the balance between primary productivity and its consumption by heterotrophs, and show that broad climatic patterns (such as El Niño) can profoundly influence ecosystem energetics.

Chapter 18

The Flux of Matter through Ecosystems

18.1 Introduction

Chemical elements and compounds are vital for the processes of life. Living organisms expend energy to extract chemicals from their environment, they hold on to them and use them for a period, then lose them again. Thus, the activities of organisms profoundly influence the patterns of flux of chemical matter in the biosphere. Physiological ecologists focus their attention on how individual organisms obtain and use the chemicals they need (see Chapter 3). However, in this chapter, as in the last, we change the emphasis and consider the ways in which the biota on an area of land, or within a volume of water, accumulates, transforms and moves matter between the various components of the ecosystem. The area that we choose may be that of the whole globe, a continent, a river catchment or simply a square meter.

18.1.1 Relationships between energy flux and nutrient cycling

The great bulk of living matter in any community is water. The rest is made up mainly of carbon compounds (95% or more) and this is the form in which energy is accumulated and stored. The energy is ultimately dissipated when the carbon compounds are oxidized to carbon dioxide (CO_2) by the metabolism of living tissue or of its decomposers. Although we consider the fluxes of energy and carbon in different chapters, the two are intimately bound together in all biological systems.

Carbon enters the trophic structure of a community when a simple molecule, CO_2, is taken up in photosynthesis. If it becomes incorporated in net primary productivity, it is available for consumption as part of a molecule of sugar, fat, protein or, very often, cellulose. It follows exactly the same route as energy, being successively consumed, defecated, assimilated and perhaps incorporated into secondary productivity somewhere within one of the trophic compartments. When the high-energy molecule in which the carbon is resident is finally used to provide energy for work, the energy is dissipated as heat (as we have discussed in Chapter 17) and the carbon is released again to the atmosphere as CO_2. Here, the tight link between energy and carbon ends.

energy cannot be cycled and reused; matter can . . .

Once energy is transformed into heat, it can no longer be used by living organisms to do work or to fuel the synthesis of biomass. (Its only possible role is momentary, in helping to maintain a high body temperature.) The heat is eventually lost to the atmosphere and can never be recycled. In contrast, the carbon in CO_2 can be used again in photosynthesis. Carbon, and all other nutrient elements (e.g. nitrogen, phosphorus, etc.) are available to plants as simple inorganic molecules or ions in the atmosphere (CO_2), or as dissolved ions in water (nitrate, phosphate, potassium, etc.). Each can be incorporated into complex organic carbon compounds in biomass. Ultimately, however, when the carbon compounds are metabolized to CO_2, the mineral nutrients are released again in simple inorganic form. Another plant may then absorb them, and so an individual atom of a nutrient element may pass repeatedly through one food chain after another. The relationship between energy flow and nutrient cycling is illustrated in Figure 18.1.

By its very nature, then, each joule of energy can be *used* only once, whereas chemical nutrients, the building blocks of biomass, simply change the form of molecule of which they are part (e.g. nitrate-N to protein-N to nitrate-N). They can be used again, and repeatedly recycled. Unlike the energy of solar radiation, nutrients are not in unalterable supply, and the process of locking some up into living biomass reduces the supply remaining to the rest of the community. If plants, and their consumers, were not eventually decomposed, the supply of nutrients would become exhausted and life on the planet would cease. The activity of heterotrophic organisms is crucial in bringing about nutrient

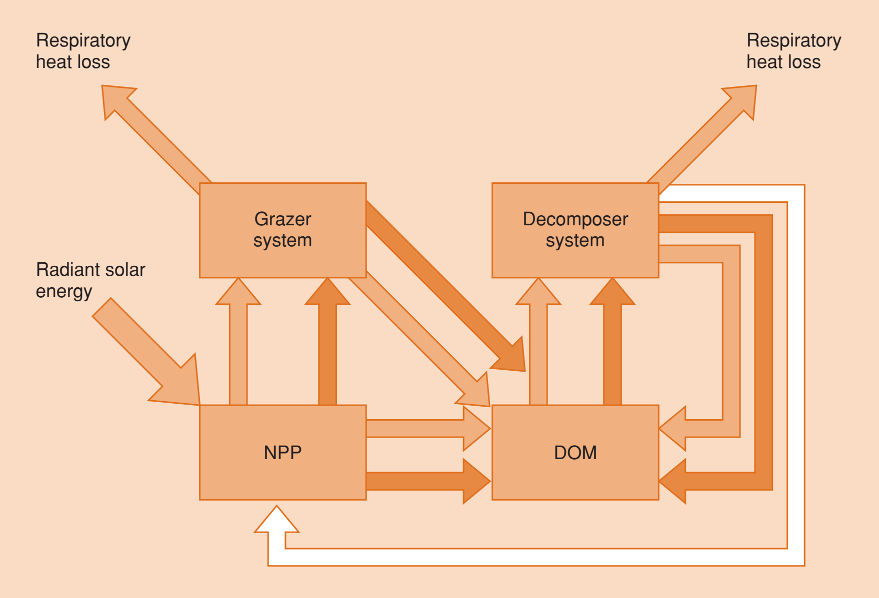


Figure 18.1 Diagram to show the relationship between energy flow (pale arrows) and nutrient cycling. Nutrients locked in organic matter (dark arrows) are distinguished from the free inorganic state (white arrow). DOM, dead organic matter; NPP, net primary production.

cycling and maintaining productivity. Figure 18.1 shows the release of nutrients in their simple inorganic form as occurring only from the decomposer system. In fact, some is also released from the grazer system. However, the decomposer system plays a role of overwhelming importance in nutrient cycling.

. . . but nutrient cycling is never perfect

The picture described in Figure 18.1 is an oversimplification in one important respect. Not all nutrients released during decomposition are necessarily taken up again by plants. Nutrient recycling is never perfect and some nutrients are exported from land by runoff into streams (ultimately to the ocean) and others, such as nitrogen and sulfur, that have gaseous phases, can be lost to the atmosphere. Moreover, a community receives additional supplies of nutrients that do not depend directly on inputs from recently decomposed matter – minerals dissolved in rain, for example, or derived from weathered rock.

18.1.2 Biogeochemistry and biogeochemical cycles

the 'bio' in biogeochemistry

We can conceive of pools of chemical elements existing in compartments. Some compartments occur in the *atmosphere* (carbon in CO_2, nitrogen as gaseous nitrogen, etc.), some in the rocks of the *lithosphere* (calcium as a constituent of calcium carbonate, potassium in feldspar) and others in the *hydrosphere* – the water in soil, streams, lakes or oceans (nitrogen in dissolved nitrate, phosphorus in phosphate, carbon in carbonic acid, etc.). In all these cases the elements exist in an inorganic form. In contrast, living organisms (the biota) and dead and decaying bodies can be viewed as compartments containing elements in an organic form (carbon in cellulose or fat, nitrogen in protein, phosphorus in adenosine triphosphate, etc.). Studies of the chemical processes occurring within these compartments and, more particularly, of the fluxes of elements between them, comprise the science of biogeochemistry.

Many geochemical fluxes would occur in the absence of life, if only because all geological formations above sea level are eroding and degrading. Volcanoes release sulfur into the atmosphere whether there are organisms present or not. On the other hand, organisms alter the rate of flux and the differential flux of the elements by extracting and recycling some chemicals from the underlying geochemical flow (Waring & Schlesinger, 1985). The term biogeochemistry is apt.

biogeochemistry can be studied at different scales

The flux of matter can be investigated at a variety of spatial and temporal scales. Ecologists interested in the gains, uses and losses of nutrients by the community of a small pond or a hectare of grassland can focus on local pools of chemicals. They need not concern themselves with the contribution to the nutrient budget made by volcanoes or the possible fate of nutrients leached from land to eventually be deposited on the ocean floor. At a larger scale, we find that the chemistry of streamwater is profoundly influenced by the biota of the area of land it drains (its catchment area; see Section 18.2.4) and, in turn, influences the chemistry and biota of the lake, estuary or sea into which it flows. We deal with the details of nutrient fluxes through terrestrial and aquatic ecosystems in Sections 18.2 and 18.3. Other investigators are interested in the global scale. With their broad brush they paint a picture of the contents and fluxes of the largest conceivable compartments – the entire

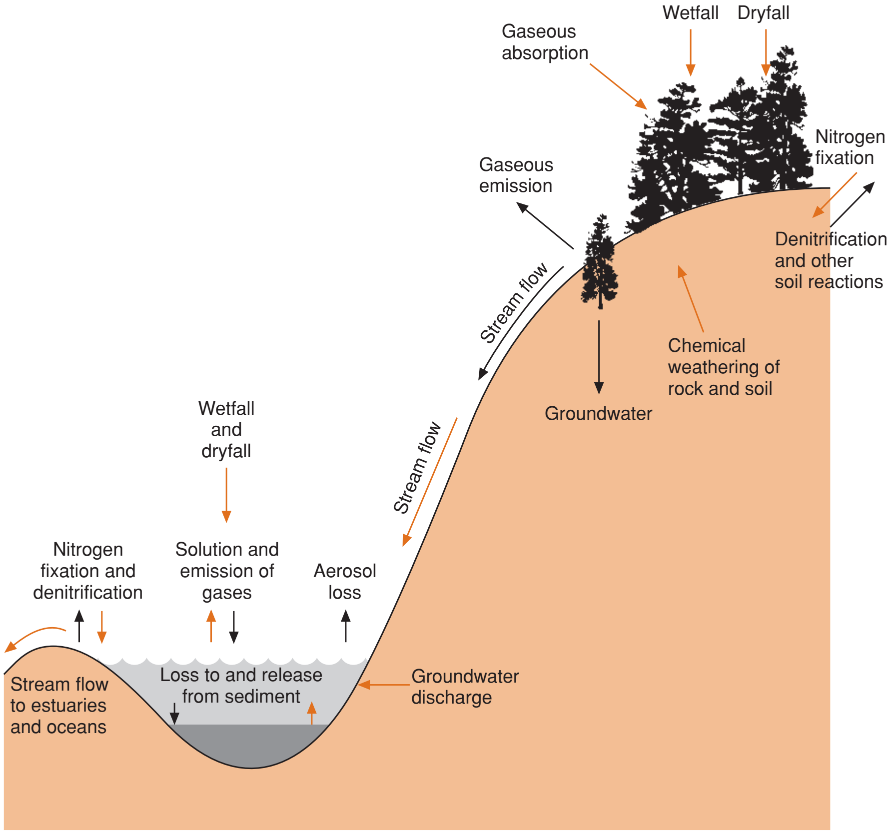


Figure 18.2 Components of the nutrient budgets of a terrestrial and an aquatic system. Note how the two communities are linked by stream flow, which is a major output from the terrestrial system and a major input to the aquatic one. Inputs are shown in color and outputs in black.

atmosphere, the oceans as a whole, and so on. Global biogeochemical cycles will be discussed in Section 18.4.

18.1.3 Nutrient budgets

Nutrients are gained and lost by ecosystems in a variety of ways (Figure 18.2). We can construct a nutrient budget by identifying and measuring all the processes on the credit and debit sides of the equation. For some nutrients, in some ecosystems, the budget may be more or less in balance.

inputs sometimes balance outputs . . . but not always

In other cases, the inputs exceed the outputs and nutrients accumulate in the compartments of living biomass and dead organic matter. This is especially obvious during community succession (see Section 17.4).

Finally, outputs may exceed inputs if the biota is disturbed by an event such as fire, massive defoliation (such as that caused by a plague of locusts) or large-scale deforestation or crop harvesting by people. Another important source of loss in terrestrial systems occurs where mineral export (e.g. of base cations due to acid rain) exceeds replenishment from weathering.

The components of nutrient budgets are discussed below.

18.2 Nutrient budgets in terrestrial communities

18.2.1 Inputs to terrestrial communities

nutrient inputs . . . . . . from the weathering of rock and soil, . . .

Weathering of parent bedrock and soil is generally the dominant source of nutrients such as calcium, iron, magnesium, phosphorus and potassium, which may then be taken up via the roots of plants. Mechanical weathering is caused by processes such as freezing of water and the growth of roots in crevices. However, much more important to the release of plant nutrients are chemical weathering processes. Of particular significance is carbonation, in which carbonic acid (H_2CO_3) reacts with minerals to release ions, such as calcium and potassium. Simple dissolution of minerals in water also makes nutrients available from rock and soil, and so do hydrolytic reactions involving organic acids released by the ectomycorrhizal fungi (see Section 13.8.1) associated with plant roots (Figure 18.3).

. . . from the atmosphere, . . .

Atmospheric CO_2 is the source of the carbon content of terrestrial communities. Similarly, gaseous nitrogen from the atmosphere provides most of the nitrogen content of communities. Several types of bacteria and blue-green algae possess

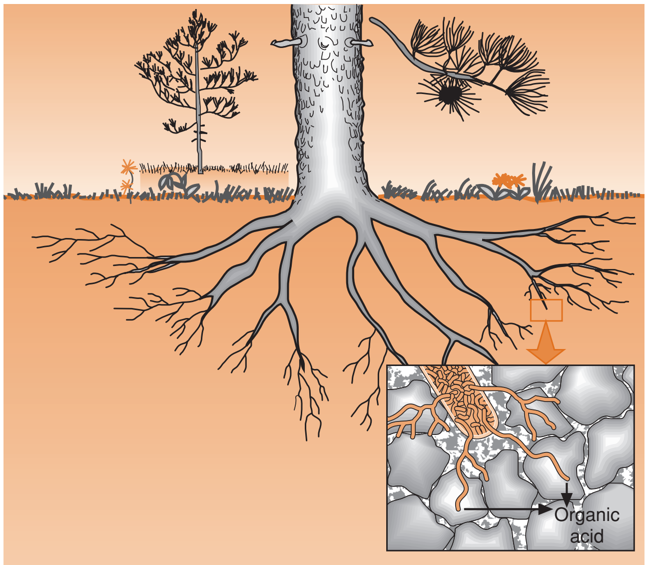


Figure 18.3 Ectomycorrhizal fungi associated with tree roots can mobilize phosphorus, potassium, calcium and magnesium from solid mineral substrates through organic acid secretion, and these nutrients then become available to the host plant via the fungal mycelium. (After Landeweert *et al.*, 2001.)

the enzyme nitrogenase and convert atmospheric nitrogen to soluble ammonium (NH_4^+) ions, which can then be taken up through the roots and used by plants. All terrestrial ecosystems receive some available nitrogen through the activity of free-living bacteria, but communities containing plants such as legumes and alder trees (*Alnus* spp.), with their root nodules containing symbiotic nitrogen-fixing bacteria (see Section 13.10), may receive a very substantial proportion of their nitrogen in this way. More than 80 kg ha^{-1} year^{-1} of nitrogen was supplied to a stand of alder by biological nitrogen fixation, for example, compared with 1–2 kg ha^{-1} year^{-1} from rainfall (Bormann & Gordon, 1984); and nitrogen fixation by legumes can be even more dramatic: values in the range 100–300 kg ha^{-1} year^{-1} are not unusual.

. . . as wetfall and dryfall, . . .

Other nutrients from the atmosphere become available to communities as *wetfall* (in rain, snow and fog) or *dryfall* (settling of particles during periods without rain, and gaseous uptake). Rain is not pure water but contains chemicals derived from a number of sources: (i) trace gases, such as oxides of sulfur and nitrogen; (ii) aerosols produced when tiny water droplets from the oceans evaporate in the atmosphere and leave behind particles rich in sodium, magnesium, chloride and sulfate; and (iii) dust particles from fires, volcanoes and windstorms, often rich in calcium, potassium and sulfate. The constituents of rainfall that serve as nuclei for raindrop formation make up the *rainout* component, whereas other constituents, both particulate and gaseous, are cleansed from the atmosphere as the rain falls – these are the *washout* component (Waring & Schlesinger, 1985). The nutrient concentrations in rain are highest early in a rainstorm, but fall subsequently as the atmosphere is progressively cleansed. Snow scavenges chemicals from the atmosphere less effectively than rain, but tiny fog droplets have particularly high ionic concentrations. Nutrients dissolved in precipitation mostly become available to plants when the water reaches the soil and can be taken up by the plant roots. However, some are absorbed by leaves directly.

Dryfall can be a particularly important process in communities with a long dry season. In four Spanish oak forests (*Quercus pyrenaica*) situated along a rainfall gradient, for example, dryfall sometimes accounted for more than half of the atmospheric input to the tree canopy of magnesium, manganese, iron, phosphorus, potassium, zinc and copper (Figure 18.4). For most elements, the importance of dryfall was more marked in forests in drier environments. However, dryfall was not insignificant for forests in wetter locations. Figure 18.4 also plots for each nutrient the annual forest demand (annual increase in above-ground biomass multiplied by the mineral concentration in the biomass). Annual deposition of many elements in wetfall and dryfall was much greater than needed to satisfy demand (e.g. Cl, S, Na, Zn). But for other elements, and especially for forests in dryer environments, annual atmospheric inputs more or less matched demand (e.g. P, K, Mn, Mg) or were inadequate (N, Ca). Of course element deficits would be greater if root productivity had been taken into account, and other sources of nutrient input must be particularly significant for a number of these elements.

While we may conceive of wetfall and dryfall inputs arriving vertically, part of the pattern of nutrient income to a forest depends on its ability to intercept horizontally driven air-borne nutrients. This was demonstrated for mixed deciduous forests in New York State when the aptly named Weathers *et al.* (2001) showed that inputs of sulfur, nitrogen and calcium at the forest edge were 17–56% greater than in its interior. The widespread tendency for forests to become fragmented as a result of human activities is likely to have had unexpected consequences for their nutrient budgets because more fragmented forests have a greater proportion of edge habitat.

. . . from hydrological inputs . . .

Streamwater plays a major role in the output of nutrients from terrestrial ecosystems (see Section 18.3). However, in a few cases, stream flow can provide a significant input to terrestrial communities when, after flooding, material is deposited in floodplains.

. . . and from human activities

Last, and by no means least, human activities contribute significant inputs of nutrients to many communities. For example, the amounts of CO_2 and oxides of nitrogen and sulfur in the atmosphere have been increased by the burning of fossil fuels, and the concentrations of nitrate and phosphate in streamwater have been raised by agricultural practices and sewage disposal. These changes have far-reaching consequences, which will be discussed later.

Figure 18.4 Annual atmospheric deposition as wetfall (WF) and dryfall (DF) compared to annual nutrient demand (ND; to account for above-ground tree growth) for four oak forests along a rainfall gradient (S1 wettest, S4 driest) in Spain. (After Marcos & Lancho, 2002.)

18.2.2 Outputs from terrestrial communities

nutrients can be lost . . .

A particular nutrient atom may be taken up by a plant that is then eaten by a herbivore which then dies and is decomposed, releasing the atom back to the soil from where it is taken up through the roots of another plant. In this manner, nutrients may circulate within the community for many years. Alternatively, the atom may pass through the system in a matter of minutes, perhaps without interacting with the biota at all. Whatever the case, the atom will eventually be lost through one of the variety of processes that remove nutrients from the system (see Figure 18.2). These processes constitute the debit side of the nutrient budget equation.

. . . to the atmosphere . . .

Release to the atmosphere is one pathway of nutrient loss. In many communities there is an approximate annual balance in the carbon budget; the carbon fixed by photosynthesizing plants is balanced by the carbon released to the atmosphere as CO_2 from the respiration of plants, microorganisms and animals. Other gases are released through the activities of anaerobic bacteria. Methane is a well-known product of the soils of bogs, swamps and floodplain forests, produced by bacteria in the waterlogged, anoxic zone of wetland soils. However, its net flux to the atmosphere depends on the rate at which it is produced in relation to its rate of consumption by aerobic bacteria in the shallower, unsaturated soil horizons, with as much as 90% consumed before it reaches the atmosphere (Bubier & Moore, 1994). Methane may be of some importance in drier locations too. It is produced by fermentation in the anaerobic stomachs of grazing animals, and even in upland forests, periods of heavy rainfall may produce anaerobic conditions that can persist for some time within microsites in the organic layer of the soil (Sexstone *et al.*, 1985). In such locations, bacteria such as *Pseudomonas* reduce nitrate to gaseous nitrogen or N_2O in the process of denitrification. Plants themselves may be direct sources of gaseous and particulate release. For example, forest canopies produce volatile hydrocarbons (e.g. terpenes) and tropical forest trees emit aerosols containing phosphorus, potassium and sulfur (Waring & Schlesinger, 1985). Finally, ammonia gas is released during the decomposition of vertebrate excreta and has been shown to be a significant component in the nutrient budget of many systems (Sutton *et al.*, 1993).

Other pathways of nutrient loss are important in particular instances. For example, fire can turn a very large proportion of a community's carbon into CO_2 in a very short time. The loss of nitrogen as volatile gas can be equally dramatic: during an intense wild fire in a conifer forest in northwest USA, 855 kg ha^{-1} (equal to 39% of the pool of organic nitrogen) was lost in this way (Grier, 1975). Substantial losses of nutrients also occur when foresters or farmers harvest and remove their trees and crops.

. . . and to groundwater and streams

For many elements, the most important pathway of loss is in stream flow. The water that drains from the soil of a terrestrial community, via the groundwater, into a stream carries a load of nutrients that is partly dissolved and partly particulate. With the exception of iron and phosphorus, which are not mobile in soils, the loss of plant nutrients is predominantly in solution. Particulate matter in stream flow occurs both as dead organic matter (mainly tree leaves) and as inorganic particles. After rainfall or snowmelt the water draining into streams is generally more dilute than during dry periods, when the concentrated waters of soil solution make a greater contribution. However, the effect of high volume more than compensates for lower concentrations in wet periods. Thus, total loss of nutrients is usually greatest in years when rainfall and stream discharge are high. In regions where the bedrock is permeable, losses occur not only in stream flow but also in water that drains deep into the groundwater. This may discharge into a stream or lake after a considerable delay and at some distance from the terrestrial community.

18.2.3 Carbon inputs and outputs may vary with forest age

Law *et al.* (2001) compared patterns of carbon storage and flux in a young (clear cut 22 years previously) and an old forest (not previously logged, trees from 50 to 250 years old) of ponderosa pine (*Pinus ponderosa*) in Oregon, USA. Their results are summarized in Figure 18.5.

an old forest is a net sink for carbon (input greater than output) . . .

Total ecosystem carbon content (vegetation, detritus and soil) of the old forest was about twice that of its young counterpart. There were notable differences in percentage carbon stored in living biomass (61% in old, 15% in young) and in dead wood on the forest floor (6% in old, 26% in young). These differences reflect the influence of soil organic matter and woody debris in the young forest derived from the prelogged period of its history. As far as living biomass is concerned, the old forest contained more than 10 times as much as the young forest, with the biggest difference in the wood component of tree biomass.

Below-ground primary productivity differed little between the two forests but because of a much lower above-ground net primary productivity (ANPP) in the young forest, total net primary productivity (NPP) was 25% higher in the old forest. Shrubs accounted for 27% of ANPP in the young forest, but only 10% in the old forest. Heterotrophic respiration (decomposers, detritivores and other animals) was somewhat lower in the old forest than NPP, indicating that this forest is a net sink for carbon. In the young forest, however, heterotrophic respiration exceeded NPP making this site a net source of CO_2 to the atmosphere. In

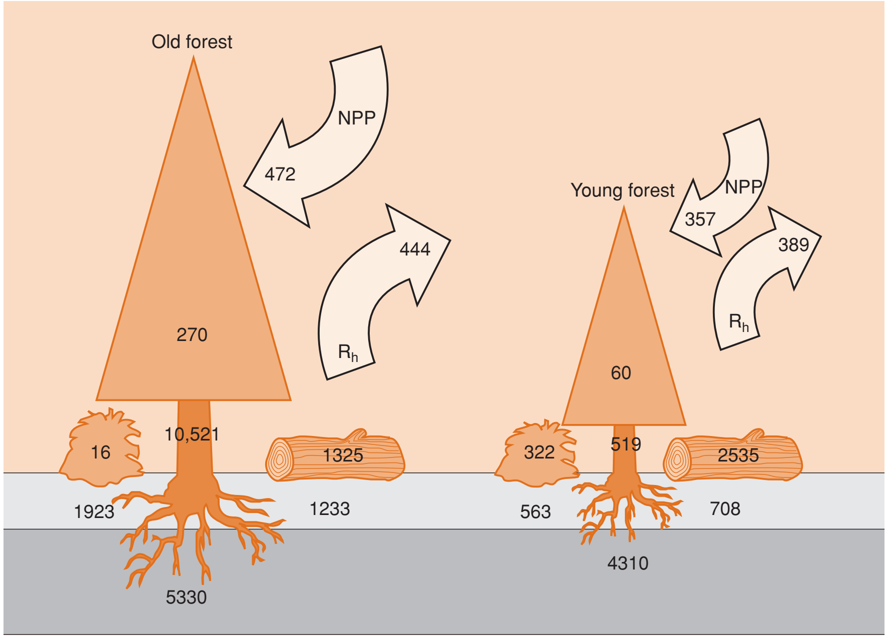


Figure 18.5 Annual carbon budgets for an old and a young ponderosa pine forest. Carbon storage figures are in g C m^{-2} while net primary productivity (NPP) and heterotrophic respiration (R_h) are in g C m^{-2} $year^{-1}$ (arrows). The numbers above ground represent carbon storage in tree foliage, in the remainder of forest biomass, in understory plants, and in dead wood on the forest floor. The numbers just below the ground surface are for tree roots and litter. The lowest numbers are for soil carbon. (After Law *et al.*, 2001.)

. . . whereas a young forest is a net carbon source (output greater than input)

both forests, respiration from the soil community accounted for 77% of total heterotrophic respiration.

These results provide a good illustration of the pathways, stores and fluxes of carbon in forest communities. They also serve to emphasize that nutrient inputs and outputs are by no means always in balance in ecosystems.

Table 18.1 Annual nutrient budgets for forested catchments at Hubbard Brook (kg ha^{-1} $year^{-1}$). Inputs are for dissolved materials in precipitation or as dryfall. Outputs are losses in streamwater as dissolved material plus particulate organic matter. (After Likens *et al.*, 1971.)

	NH_4^+	NO_3^-	K^+	Ca^{2+}	Mg^{2+}	Na^+
Input	2.7	16.3	1.1	2.6	0.7	1.5
Output	0.4	8.7	1.7	11.8	2.9	6.9
Net change*	+2.3	+7.6	−0.6	−9.2	−2.2	−5.4

* Net change is positive when the catchment gains matter and negative when it loses it.

18.2.4 Importance of nutrient cycling in relation to inputs and outputs

the movement of water links terrestrial and aquatic communities

Because many nutrient losses from terrestrial communities are channeled through streams, a comparison of the chemistry of streamwater with that of incoming precipitation can reveal a lot about the differential uptake and cycling of chemical elements by the terrestrial biota. Just how important is nutrient cycling in relation to the through-put of nutrients? Is the amount of nutrients cycled per year small or large in comparison with external supplies and losses? The most thorough study of this question has been carried out by Likens and his associates in the Hubbard Brook Experimental Forest, an area of temperate deciduous forest drained by small streams in the White Mountains of New Hampshire, USA. The catchment area – the extent of terrestrial environment drained by a particular stream – was taken as the unit of study because of the role that streams play in nutrient export. Six small catchments were defined and their outflows were monitored. A network of precipitation gauges recorded the incoming amounts of rain, sleet and snow. Chemical analyses of precipitation and streamwater made it possible to calculate the amounts of various nutrients entering and leaving the system, and these are shown in Table 18.1. A similar pattern is found each year. In most cases, the output of chemical nutrients in stream flow is greater than their input from rain, sleet and snow. The source of the excess chemicals is parent rock and soil, which are weathered and leached at a rate of about 70 g m^{-2} $year^{-1}$.

Hubbard Brook – forest inputs and outputs are small compared to internal cycling

In almost every case, the inputs and outputs of nutrients are small in comparison with the amounts held in biomass and recycled within the system. Nitrogen, for example, was added to the system not only in precipitation

(6.5 kg ha^{-1} year^{-1}) but also through atmospheric nitrogen fixation by microorganisms (14 kg ha^{-1} year^{-1}). (Note that denitrification by other microorganisms, releasing nitrogen to the atmosphere, will also have been occurring but was not measured.) The export in streams of only 4 kg ha^{-1} year^{-1} emphasizes how securely nitrogen is held and cycled within the forest biomass. Stream output represents only 0.1% of the total nitrogen standing crop held in living and dead forest organic matter. Nitrogen was unusual in that its net loss in stream runoff was less than its input in precipitation, reflecting the complexity of inputs and outputs and the efficiency of its cycling. However, despite the net loss to the forest of other nutrients, their export was still low in relation to the amounts bound in biomass. In other words, relatively efficient recycling is the norm.

deforestation uncouples cycling and leads to a loss of nutrients

In a large-scale experiment, all the trees were felled in one of the Hubbard Brook catchments and herbicides were applied to prevent regrowth. The overall export of dissolved inorganic nutrients from the disturbed catchment then rose to 13 times the normal rate (Figure 18.6). Two phenomena were responsible. First, the enormous reduction in transpiring surfaces (leaves) led to 40% more precipitation passing through the groundwater to be discharged to the streams, and this increased outflow caused greater rates of leaching of chemicals and weathering of rock and soil. Second, and more significantly, deforestation effectively broke the within-system nutrient cycling by uncoupling the decomposition process from the plant uptake process. In the absence of nutrient uptake in the spring, when the deciduous trees would have started production, the inorganic nutrients released by decomposer activity were available to be leached in the drainage water.

The main effect of deforestation was on nitrate-N, emphasizing the normally efficient cycling to which inorganic nitrogen is subject. The output of nitrate in streams increased 60-fold after the disturbance. Other biologically important ions were also leached faster as a result of the uncoupling of nutrient cycling mechanisms (potassium: 14-fold increase; calcium: sevenfold increase; magnesium: fivefold increase). However, the loss of sodium, an element of lower biological significance, showed a much less dramatic change following deforestation (2.5-fold increase). Presumably it is cycled less efficiently in the forest and so uncoupling had less effect.

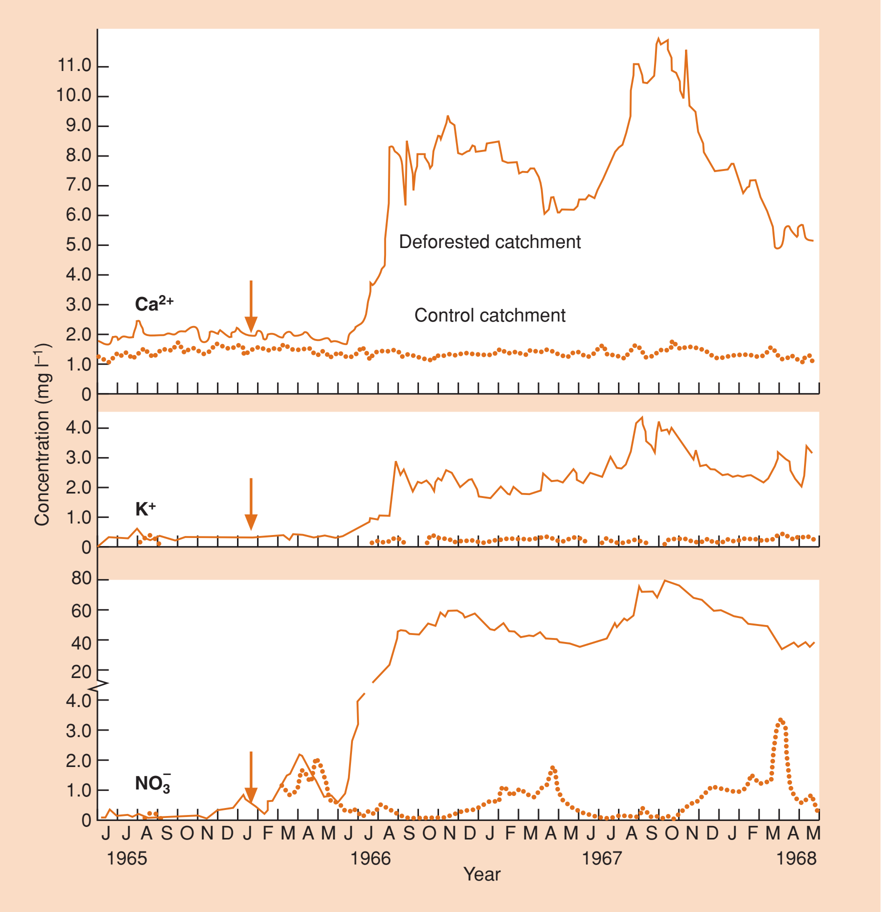


Figure 18.6 Concentrations of ions in streamwater from the experimentally deforested catchment and a control catchment at Hubbard Brook. The timing of deforestation is indicated by arrows. Note that the 'nitrate' axis has a break in it. (After Likens & Borman, 1975.)

18.2.5 Some key points about nutrient budgets in terrestrial ecosystems

diversity of patterns of nutrient input and output

The examples discussed above have illustrated that ecosystems do not generally have balanced inputs and outputs of nutrients. However, in many cases (as in the Hubbard Brook Forest) nutrients such as nitrogen are cycled quite tightly, and inputs and outputs are small compared to stored pools. For carbon too, fluxes may be small compared to storage, but note that tight cycling is not the rule in this case; the carbon molecules in respired CO_2 will rarely be the same ones taken up by photosynthesis (because of the huge pool of CO_2 involved).

We have also seen that nutrient budgets of a single category of ecosystem can differ dramatically, either because of internal properties (the age of trees in the pine forests in Section 18.2.3) or external factors (the dryness of the climate in the oak forests in Figure 18.4). Similarly, in a semiarid grassland in Colorado, nitrogen availability to grass plants adjacent to actively growing roots was greater in months when there was more rainfall (Figure 18.7).

decomposition and nutrient flux . . .

. . . influenced by stoichiometry . . .

Many other factors influence nutrient flux rates and stores. For example, the stoichiometry of elements in foliage (and thus in detritus when the leaves die) can influence decomposition rates and nutrient flux (see Section 11.2.4). There is a theoretical critical detritus C : N ratio of 30 : 1 above which bacteria and fungi are nitrogen-limited, when they then take up exogenous ammonium and nitrate ions from the soil, competing with plants for these resources (Daufresne & Loreau, 2001). When the C : N ratio is below 30 : 1, the microbes are carbon-limited and decomposition increases soil inorganic nitrogen, which may in turn increase plant nitrogen uptake (Kaye & Hart, 1997). In general, plants are most often nitrogen-limited and microbes carbon-limited, and whilst microbes are more significant in the control of nitrogen cycling, it is the plants that regulate carbon inputs which control microbial activity (Knops *et al.*, 2002).

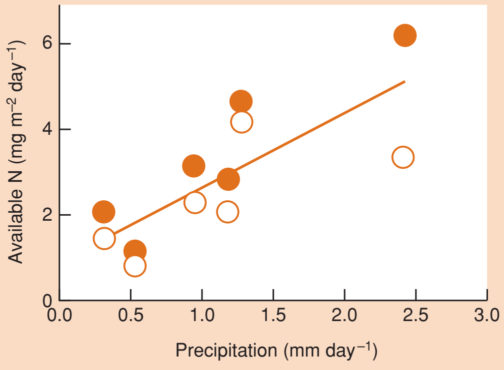


Figure 18.7 Nitrogen available to actively growing roots of the bunchgrass *Bouteloua gracilis* in shortgrass steppe ecosystems in relation to precipitation in the study period. The values for the six sampling periods are the averages of eight replicate plots. ●, downslope plots; ○, upslope plots (up to 11 m further up the same hillslope). (After Hook & Burke, 2000.)

. . . and plant defense chemicals

A quite different chemical property of foliage may have an equally dramatic effect. Polyphenols are a very widely distributed class of secondary metabolites in plants that often provide protection against attack; their evolution is usually interpreted in terms of defense against herbivores. However, the polyphenols in detritus can also influence the flux of soil nutrients (Hattenschwiler & Vitousek, 2000). Different classes of polyphenols have been found to affect fungal spore germination and hyphal growth. They have also been shown to inhibit nitrifying bacteria and to suppress or, in some cases, stimulate symbiotic nitrogen-fixing bacteria. Finally, polyphenols may restrict the activity and abundance of soil detritivores. Overall, polyphenols may tend to reduce decomposition rates (as they decrease herbivory rates) with important consequences for nutrient fluxes, but more work is needed on this topic (Hattenschwiler & Vitousek, 2000).

18.3 Nutrient budgets in aquatic communities

When attention is switched from terrestrial to aquatic communities, there are several important distinctions to be made. In particular, aquatic systems receive the bulk of their supply of nutrients from stream inflow (see Figure 18.2). In stream and river communities, and also in lakes with a stream outflow, export in outgoing stream water is a major factor. By contrast, in lakes without an outflow (or where this is small relative to the volume of the lake), and also in oceans, nutrient accumulation in permanent sediments is often the major export pathway.

18.3.1 Streams

nutrient ‘spiraling’ in streams

We noted, in the case of Hubbard Brook, that nutrient cycling within the forest was great in comparison to nutrient exchange through import and export. By contrast, only a small fraction of available nutrients take part in biological interactions in stream and river communities (Winterbourn & Townsend, 1991). The majority flows on, as particles or dissolved in the water, to be discharged into a lake or the sea. Nevertheless, some nutrients do cycle from an inorganic form in streamwater to an organic form in biota to an inorganic form in streamwater, and so on. But because of the inexorable transport downstream,

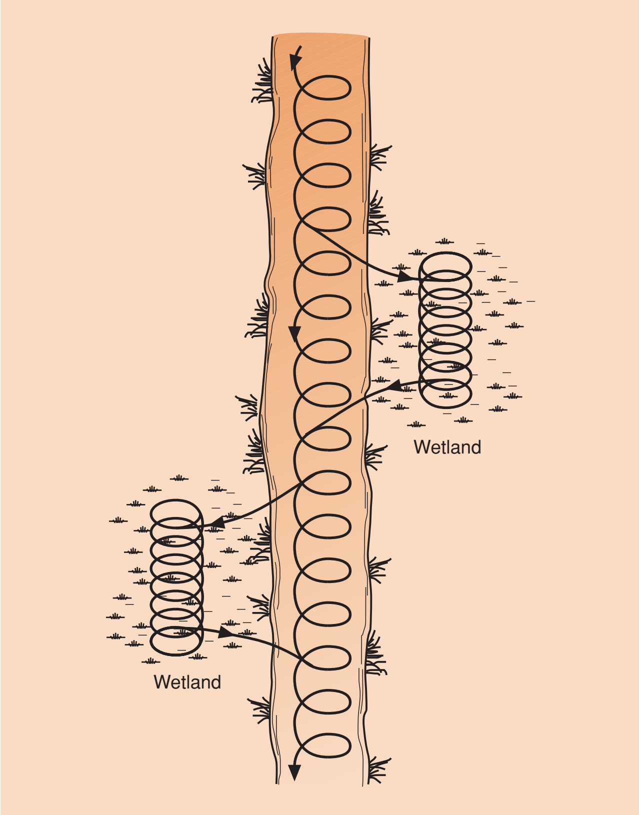


Figure 18.8 Nutrient spiraling in a river channel and adjacent wetland areas. (After Ward, 1988.)

the displacement of nutrients is better represented as a spiral (Elwood *et al.*, 1983), where fast phases of inorganic nutrient displacement alternate with periods when the nutrient is locked in biomass at successive locations downstream (Figure 18.8). Bacteria, fungi and microscopic algae, growing on the substratum of the stream bed, are mainly responsible for the uptake of inorganic nutrients from streamwater in the biotic phase of spiraling. Nutrients, in organic form, pass on through the food web via invertebrates that graze and scrape microbes from the substratum (grazer–scrapers – see Figure 11.5). Ultimately, decomposition of the biota releases inorganic nutrient molecules and the spiral continues. The concept of nutrient spiraling is equally applicable to 'wetlands', such as backwaters, marshes and alluvial forests, which occur in the floodplains of rivers. However, in these cases spiraling can be expected to be much tighter because of reduced water velocity (Prior & Johnes, 2002).

A dramatic example of spiraling occurs when the larvae of blackflies (collector–filterers; see Figure 11.5) use their modified mouthparts to filter out and consume fine particulate organic matter which otherwise would be carried downstream. Because of very high densities (sometimes as many as 600,000 blackfly larvae per square meter of river bed) a massive quantity of fine particulate matter may be converted by the larvae into fecal pellets (estimated at 429 t dry mass of fecal pellets per day in a Swedish river; Malmqvist *et al.*, 2001). Fecal pellets are much larger than the particulate food of the larvae and so are much more likely to settle out on the river bed, especially in slower flowing sections of river (Figure 18.9). Here they provide organic matter as food for many other detritivorous species.

18.3.2 Lakes

nutrient flux in lakes: important roles for plankton and lake position

In lakes, it is usually the phytoplankton and their consumers, the zooplankton, which play the key roles in nutrient cycling. However, most lakes are interconnected with each other by rivers, and standing stocks of nutrients are determined only partly by processes within the lakes. Their position with respect to other water bodies in the landscape can also have a marked effect on nutrient status. This is well illustrated for a series of lakes connected by a river that ultimately flows into Toolik Lake in arctic Alaska (Figure 18.10a).

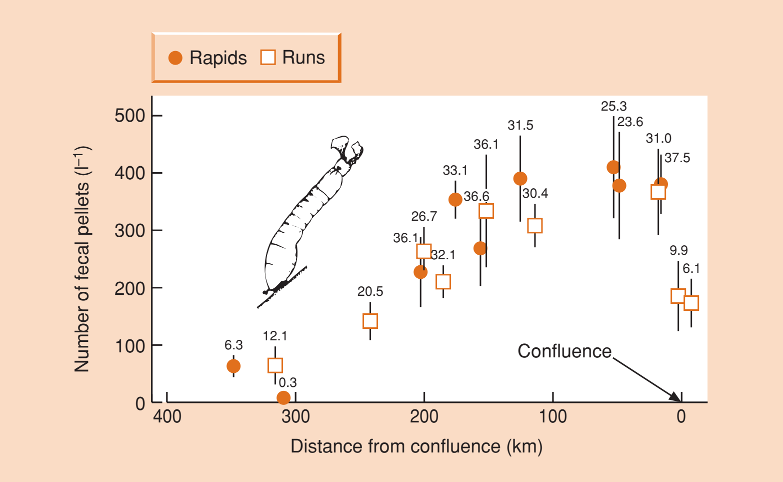


Figure 18.9 Downstream trends in the Vindel River in Sweden (shown as distance from the confluence with the larger Ume River) in the concentration of fecal pellets (number of fecal pellets per liter ± SE) of blackfly larvae (family Simuliidae). The generally lower concentrations in the 'runs' reflect the higher probability of pellets settling to the river bed in these sections compared to the 'rapids' sections. The numbers above the error bars are percentages of the mass of total organic matter in the flowing water (seston) made up of fecal pellets. (After Malmqvist *et al.*, 2001.)

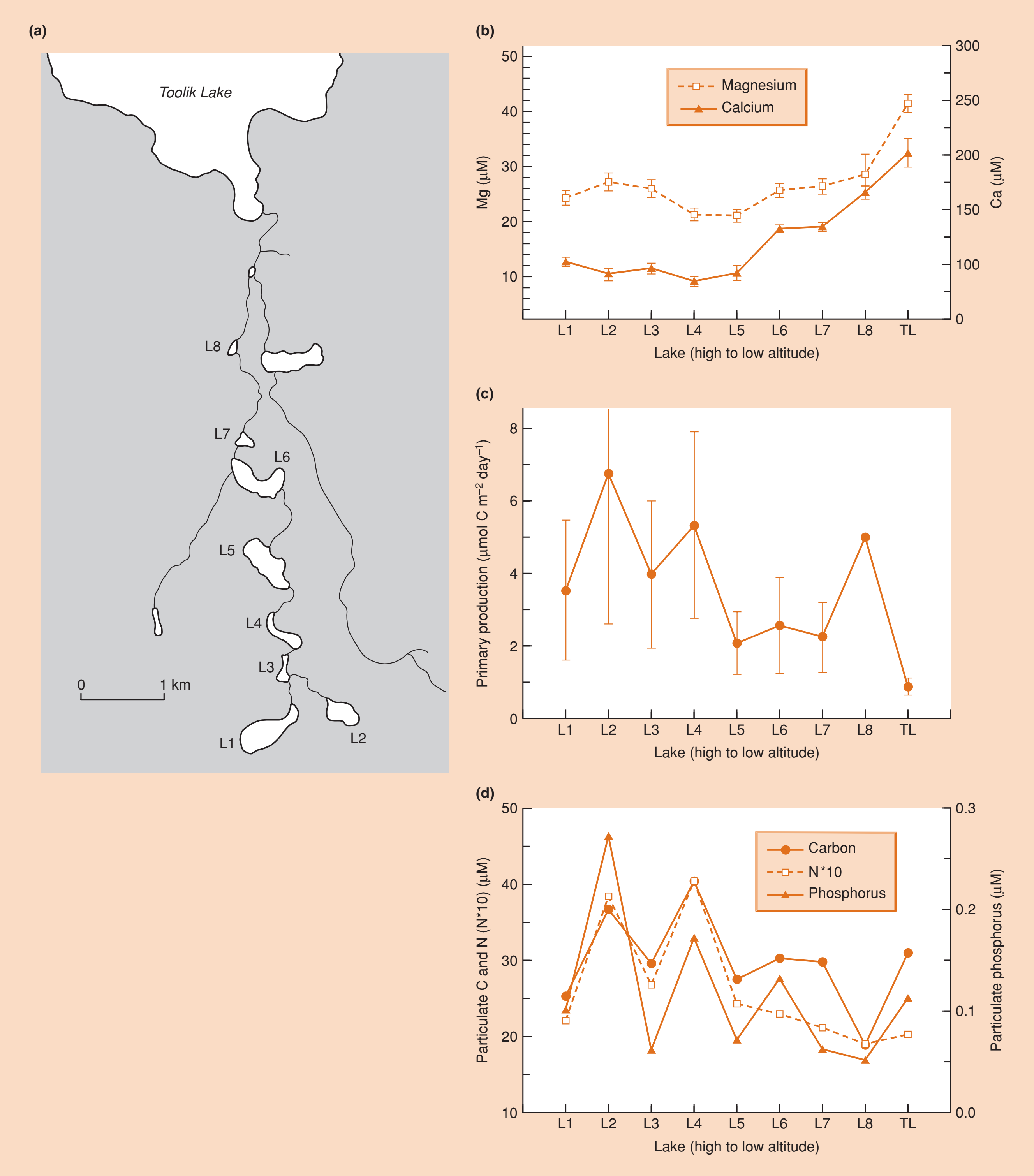


Figure 18.10 (a) Spatial arrangement of eight small lakes (L1–L8) interconnected by a river that flows into Toolik Lake (TL) in arctic Alaska. (b) Mean values, averaged over all sampling occasions during 1991–97 (±SE), for magnesium (Mg) and calcium (Ca) concentrations in the study lakes. (c) Pattern in primary productivity down the lake chain. (d) Mean values for carbon (C), nitrogen (N) and phosphorus in particulate form. (After Kling *et al.*, 2000.)

The main reason for the downstream increase in magnesium and calcium was increased weathering (Figure 18.10b). This comes about because a greater proportion of the water entering downstream lakes has been in intimate contact with the parent rock for longer; put another way, the higher concentrations reflect the larger catchment areas that feed the downstream lakes. The pattern for calcium and magnesium may also partly reflect progressive evaporative concentration with longer residence times of water in the system as well as material processing by the biota in streams and lakes as the water moves downstream. The nutrients that generally limit production in lakes, nitrogen and phosphorus, were in very low concentrations and could not be reliably measured. However, the downstream decrease in productivity that was observed (Figure 18.10c) suggests that the available nutrients were consumed by the plankton in each lake and this consumption was sufficient to lower the nutrient availability in successive lakes downstream. The downstream decrease of nitrogen, phosphorus and carbon in particulate matter (Figure 18.10d) simply reflects the lower downstream rates of primary productivity. Note that it is unusual to have a downstream decline in productivity. In less pristine conditions, productivity is more likely to increase in a downstream direction (e.g. Kratz *et al.*, 1997), partly because of the addition of more nutrients from larger catchment areas but also because of increasing human inputs in lowland areas through fertilizer application and sewage.

saline lakes lose water only by evaporation, and have high nutrient concentrations

Many lakes in arid regions, lacking a stream outflow, lose water only by evaporation. The waters of these endorheic lakes (internal flow) are thus more concentrated than their freshwater counterparts, being particularly rich in sodium (with values up to 30,000 mg l^{-1} or more) but also in other nutrients such as phosphorus (up to 7000 μg l^{-1} or more). Saline lakes should not be considered as oddities; globally, they are just as abundant in terms of numbers and volume as freshwater lakes (Williams, 1988). They are usually very fertile and have dense populations of blue-green algae (for example, *Spirulina platensis*), and some, such as Lake Nakuru in Kenya, support huge aggregations of plankton-filtering flamingoes (*Phoeniconaias minor*). No doubt, the high level of phosphorus is due in part to the concentrating effect of evaporation. In addition, there may be a tight nutrient cycle in lakes such as Nakuru in which continuous flamingo feeding and the supply of their excreta to the sediment creates circumstances where phosphorus

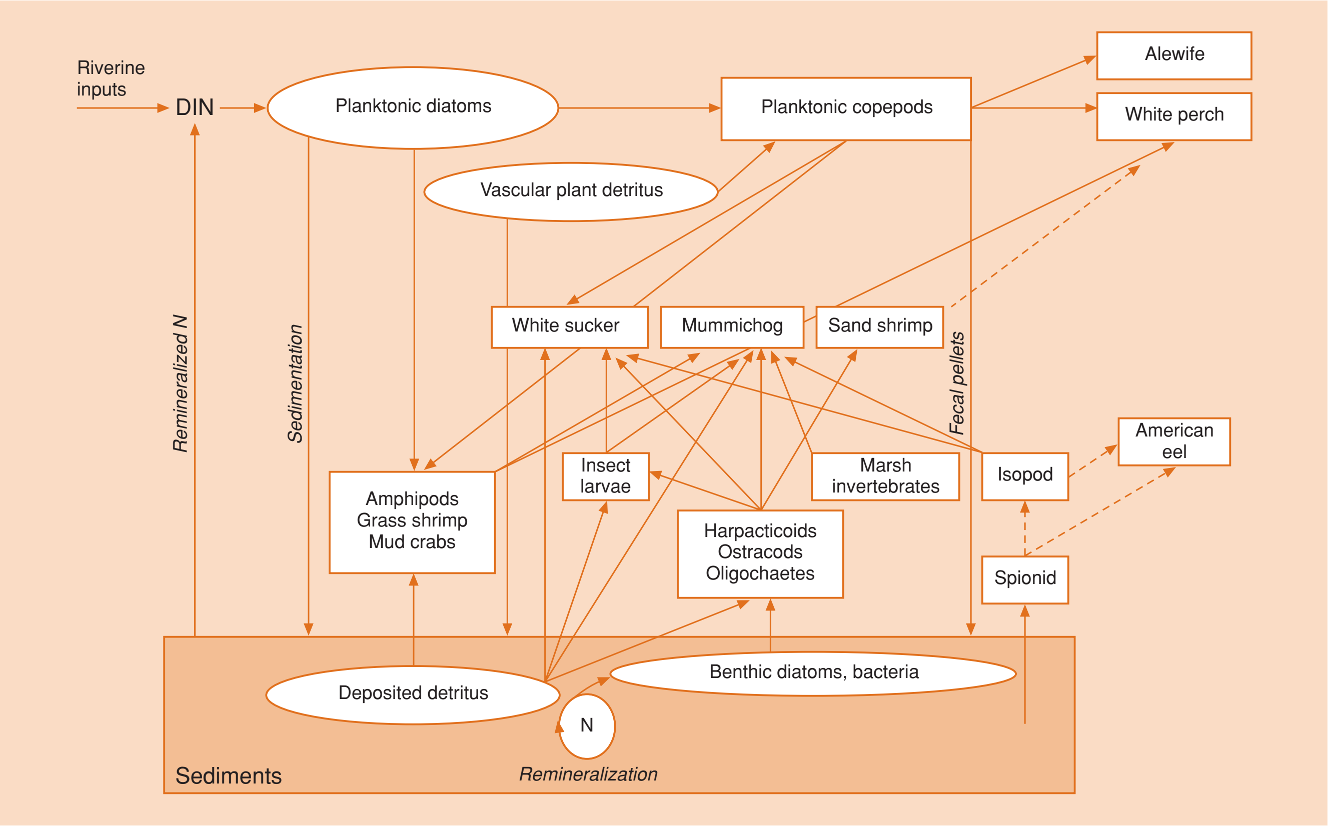


Figure 18.11 Conceptual model of nitrogen (N) flux through the food web of the upper Parker River estuary, Massachusetts, USA. Dashed arrows indicate suspected pathways. DIN, dissolved inorganic nitrogen. (After Hughes *et al.*, 2000.)

is continuously regenerated from the sediment to be taken up again by phytoplankton (Moss, 1989).

18.3.3 Estuaries

nutrient flux in estuaries: roles for planktonic and benthic organisms . . .

In estuaries, both planktonic organisms (as in lakes) and benthic organisms (as in rivers) are significant in nutrient flux. Hughes *et al.* (2000) introduced tracer levels of a rare isotope of nitrogen (as nitrate-containing ^{15}N) into the water of an estuary in Massachusetts, USA, to study how nitrogen derived from the catchment area is used and transformed in the estuarine food web. They focused their study on the upper, low salinity part of the estuary where water derived from the river catchment first meets the saline influence of tidal seawater. The planktonic centric diatom *Actinocyclus normanii* turned out to be the primary vector of nitrogen to some benthic organisms (large crustaceans) and particularly pelagic organisms (planktonic copepods and juvenile fishes). Certain components of the sedimentary biota received a small proportion of their nitrogen via the centric diatom (10–30%; e.g. pennate diatoms, harpacticoid copepods, oligochaete worms, bottom-feeding fishes such as mummichog, *Fundulus heteroclitus*, and sand shrimps). But many others obtained almost all their nitrogen from a pathway based on plant detritus. The patterns of nitrogen flow through this estuarine food web are shown in Figure 18.11. The relative importance of nutrient fluxes through the grazer and decomposer systems can be expected to vary from estuary to estuary.

. . . and human activities

The chemistry of estuarine (and coastal marine) water is strongly influenced by features of the catchment area through which the rivers have been flowing, and human activities play a major role in determining the nature of the water supplied. In a revealing comparison, van Breeman (2002) describes the forms of nitrogen in water at the mouths of rivers in North and South America. In the North American case, where the river flows through a largely forested region but has been subject to considerable human impact (fertilizer input, logging, acid precipitation, etc.), nitrogen was almost exclusively exported to estuaries and the sea in inorganic form (only 2% organic). In contrast, a pristine South American river, subject to very little human impact, exported 70% of its nitrogen in organic form. In Australian rivers too, pristine forested catchments export little nitrogen or phosphorus, and the predominant form of nitrogen is organic. As human population density increases (greater agricultural runoff and sewage) and forests are cleared (less tight retention of nutrients), however, the export to river mouths of both nitrogen and phosphorus increases and the predominant form of nitrogen changes to inorganic (Figure 18.12).

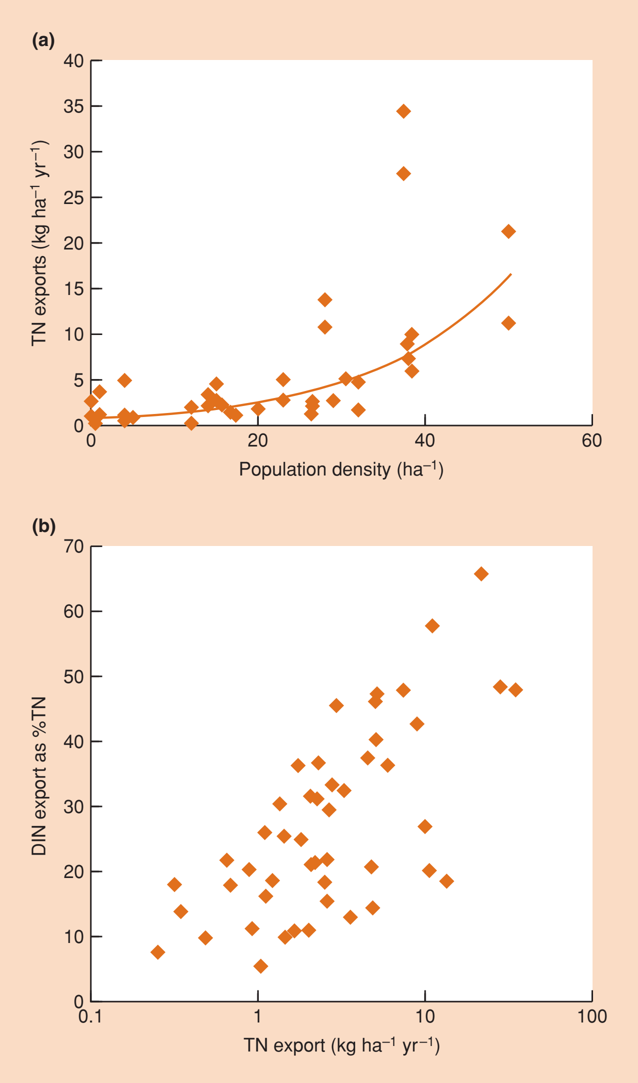


Figure 18.12 (a) Export of total nitrogen (TN) in relation to population density in 24 catchment areas near Sydney, Australia. (b) Rivers with low TN export rates (more pristine) contain nitrogen predominantly in organic form and the percentage of TN that is inorganic increases with TN. DIN, dissolved inorganic nitrogen. (After Harris, 2001.)

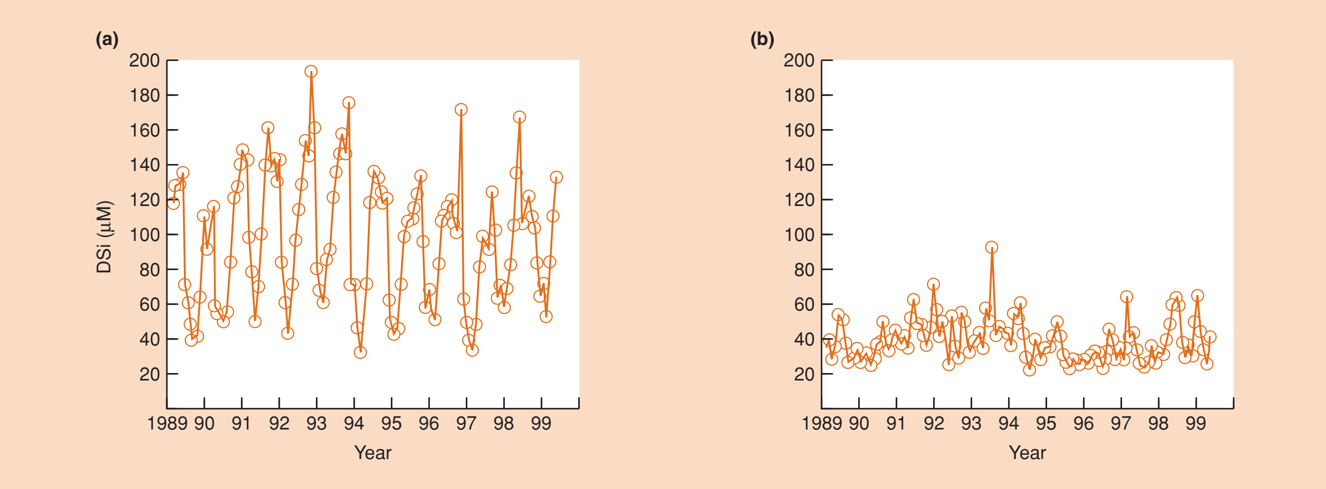


Figure 18.13 Dissolved silicate (DSi) concentrations at the river mouths of (a) the nondammed River Kalixalven and (b) the dammed River Lulealven. (Humborg *et al.*, 2002).

18.3.4 Continental shelf regions of the oceans

coastal regions of oceans are influenced by their terrestrial catchment areas . . .

The nutrient budgets of coastal regions of oceans, like estuaries, are strongly influenced by the nature of catchment areas that supply the water, via rivers, to the sea. Concentrations of nitrogen or phosphorus may limit productivity in these areas as in other water bodies, but a further human-induced effect on the chemistry of riverwater has special significance for planktonic communities in the oceans. Today, more than 25% of the world's rivers have been dammed or diverted (for hydroelectric generation, irrigation and human water supply). Associated with damming is the loss of upper soils and vegetation through inundation, loss of soil through shoreline erosion, and underground channeling of water through tunnels. These effects reduce the contact of water with vegetated soil and, therefore, reduce weathering. Figure 18.13 illustrates the patterns of export of dissolved silicate, an essential component of the cells of planktonic diatoms in the sea, for a dammed river and a freely flowing river in Sweden. The export of silicate was dramatically lower in the dammed case. The possible ecological effects of silicate reduction to nutrient fluxes and productivity in the sea may become particularly significant in East Asia, where major rivers are being dammed at accelerating rates (Milliman, 1997).

. . . and local upwelling

Another important mechanism of nutrient enrichment in coastal regions is local upwelling, bringing high nutrient concentrations from deep to shallow water where they fuel primary productivity, often producing phytoplankton blooms. Three categories of upwelling have been described and studied off the east coast of Australia: (i) wind-driven upwellings in response to seasonal north and northeasterly breezes; (ii) upwelling driven by the encroachment of the East Australian Current (EAC) onto the continental shelf; and (iii) upwelling caused by the separation of the EAC from the coast. Figure 18.14 provides examples of the distribution of nitrate concentrations associated with each mechanism. Wind-driven upwellings (generally considered to be the dominant mechanism globally) are not persistent or massive in scale. The highest nitrate concentrations are generally associated with encroachment upwellings, whilst separation upwellings are the most widespread along the coast of New South Wales.

18.3.5 Open oceans

We can view the open ocean as the largest of all endorheic 'lakes' – a huge basin of water supplied by the world's rivers and losing water only by evaporation. Its great size, in comparison to the input from rain and rivers, leads to a remarkably constant chemical composition.

the open ocean: an important role for plankton . . .

We considered biologically mediated transformations of carbon in terrestrial ecosystems in Section 18.2.3. Figure 18.15 illustrates the same thing but for the open ocean. The main transformers of dissolved inorganic carbon (essentially CO_2) are the small phytoplankton, which recycle CO_2 in the euphotic zone, and the larger plankton, which generate the majority of the carbon flux in particulate and dissolved organic form to the deep ocean floor. Figure 18.16 shows that, in general, only a small proportion of carbon fixed near the

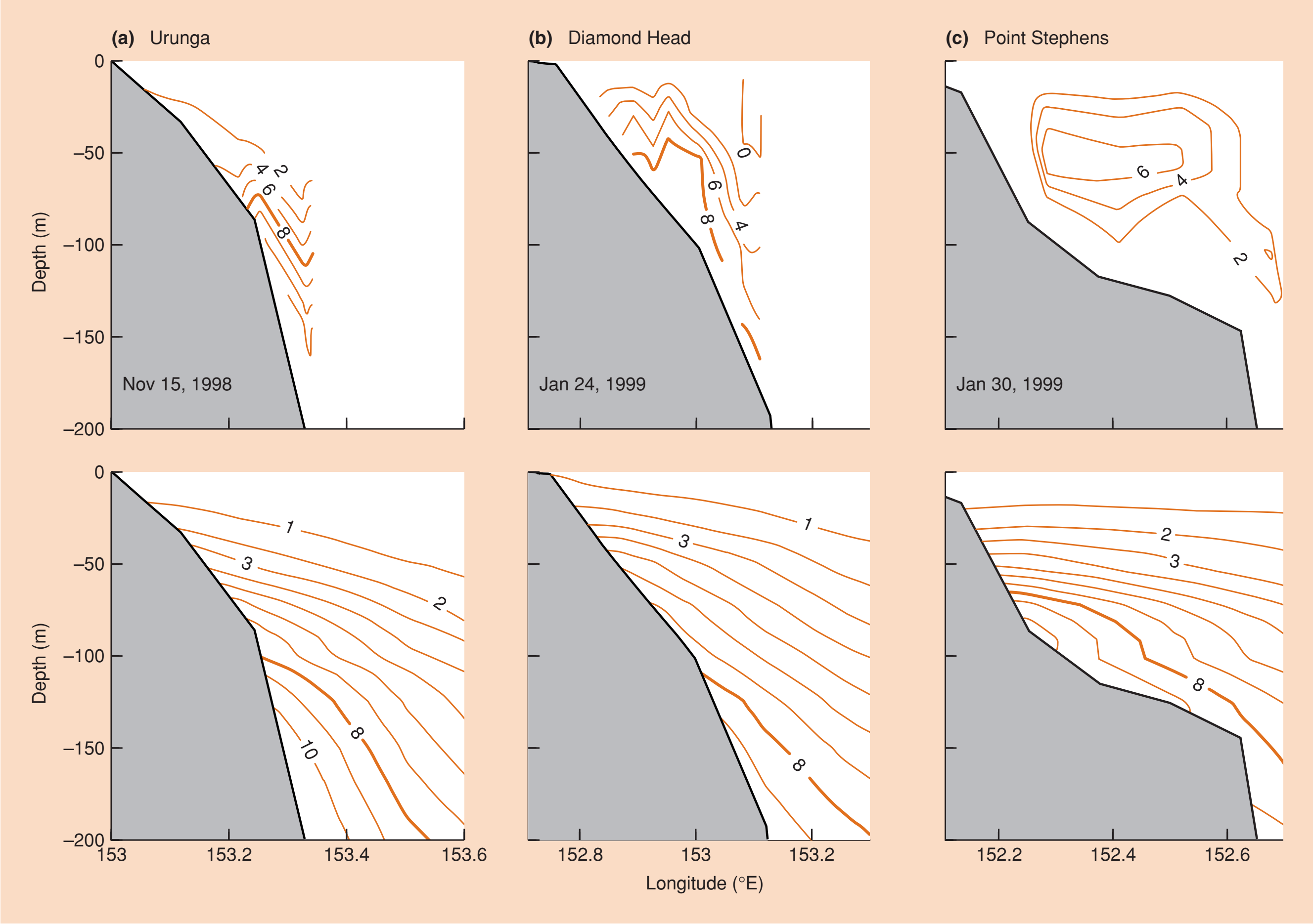


Figure 18.14 Contours of nitrate concentration during upwelling events along the New South Wales coast at: (a) Urunga (wind-driven), (b) Diamond Head (encroachment-driven), and (c) Point Stephens (separation-driven). The bottom graph in each case shows the mean nitrate concentrations that can be taken as characteristic of these sites in the absence of an upwelling event. Maximum concentration is 10 μmol l^{-1}. The contour interval is 1 or 2 μmol l^{-1} and the thick orange line represents 8 μmol l^{-1}. (After Roughan & Middleton, 2002.)

surface finds its way to the ocean bed. What reaches the ocean floor is consumed by the deep-sea biota, some is remineralized into dissolved organic form by decomposers, and a small proportion becomes buried in the sediment.

. . . which may follow a seasonal pattern

Just as we saw in terrestrial ecosystems, marked seasonal and interannual differences in nutrient flux and availability can be detected in the deep ocean. Thus, Figure 18.17a shows how chlorophyll *a* concentrations varied during the spring bloom at a site in the North Atlantic, reflecting a succession of dominant phytoplankton species. Large diatoms bloomed first, consuming almost all the available silicate (Figure 18.17b). Subsequently, a bloom of small flagellates used up the remaining nitrate. Over a longer timescale, a remarkable shift in the relative abundance of organic nitrogen and phosporus has been witnessed in the North Pacific. The ocean has traditionally been viewed as nitrogen-limited, but, when nitrogen limitation is extreme, nitrogen-fixing taxa such as *Trichodesmium* spp. grow over large areas and bring into play the inexhaustible pool of dissolved N_2 in the ocean. This has led to a decade-long shift in the N : P ratio in suspended particulate organic matter (Figure 18.17c). Under these circumstances, phosphorus, iron or some other nutrient will eventually limit productivity.

iron as a factor limiting ocean primary productivity?

About 30% of the world's oceans have long been known to have low productivity despite high concentrations of nitrate. The hypothesis that this paradox was due to the iron limitation of phytoplankton productivity has been tested in locations as different as the eastern equatorial Pacific and the open polar Southern Ocean (Boyd, 2002). Large infusions of dissolved iron

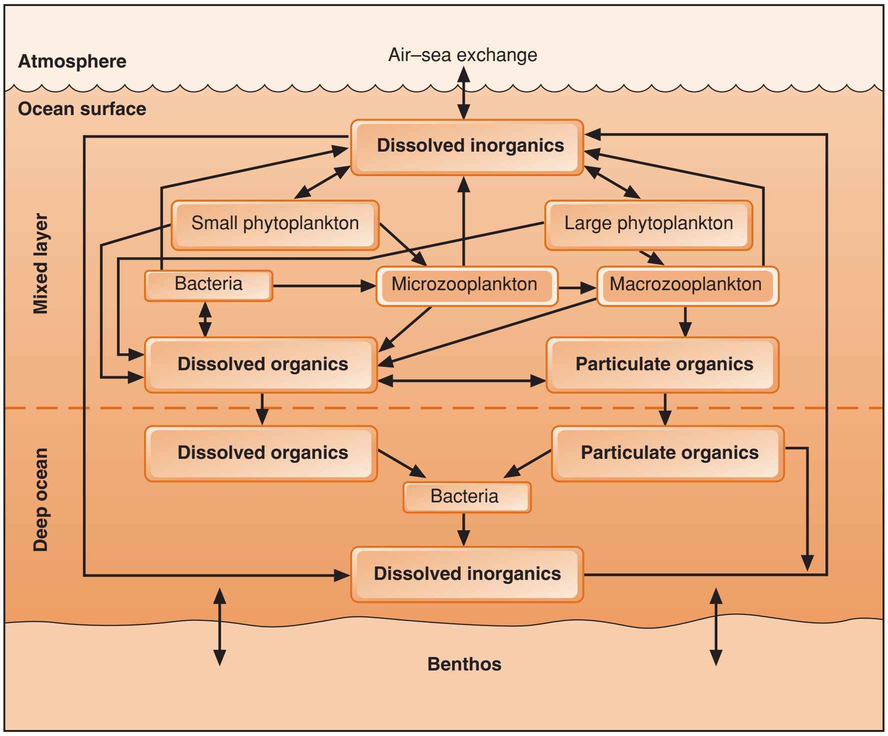


Figure 18.15 Biologically mediated transformations of carbon in the open ocean. (After Fasham *et al.*, 2001.)

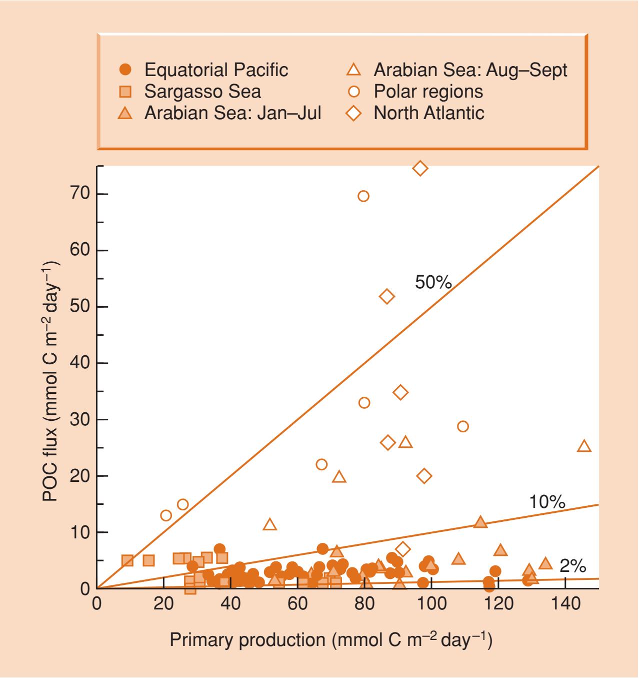


Figure 18.16 Relationship between the export of particulate organic carbon (POC) to the ocean depths, recorded at 100 m, and ocean primary productivity in the world's oceans. (After Buesseler, 1998.)

at sites in each ocean led in both cases to dramatic increases in primary productivity and decreases in nitrate and silicate, as these were taken up during algal production (the results are expressed as nitrate removal in Figure 18.18). Bacterial productivity tripled within a few days in both cases, and rates of herbivory by micrograzers (flagellates and ciliates) also increased, but less so in the polar situation (where dominance by a grazer-resistant, highly silicified diatom probably suppressed grazing). The metazoan community, dominated by copepods, showed relatively little change in either situation.

It is an intriguing thought that in places such as the eastern equatorial Pacific or polar Southern Ocean, blooms in productivity might sometimes be caused by long-distance wind transport of land-derived, iron-rich particles. This would mirror, but on a very different scale, the high productivity associated with inputs of land-derived, nutrient-rich water from rivers.

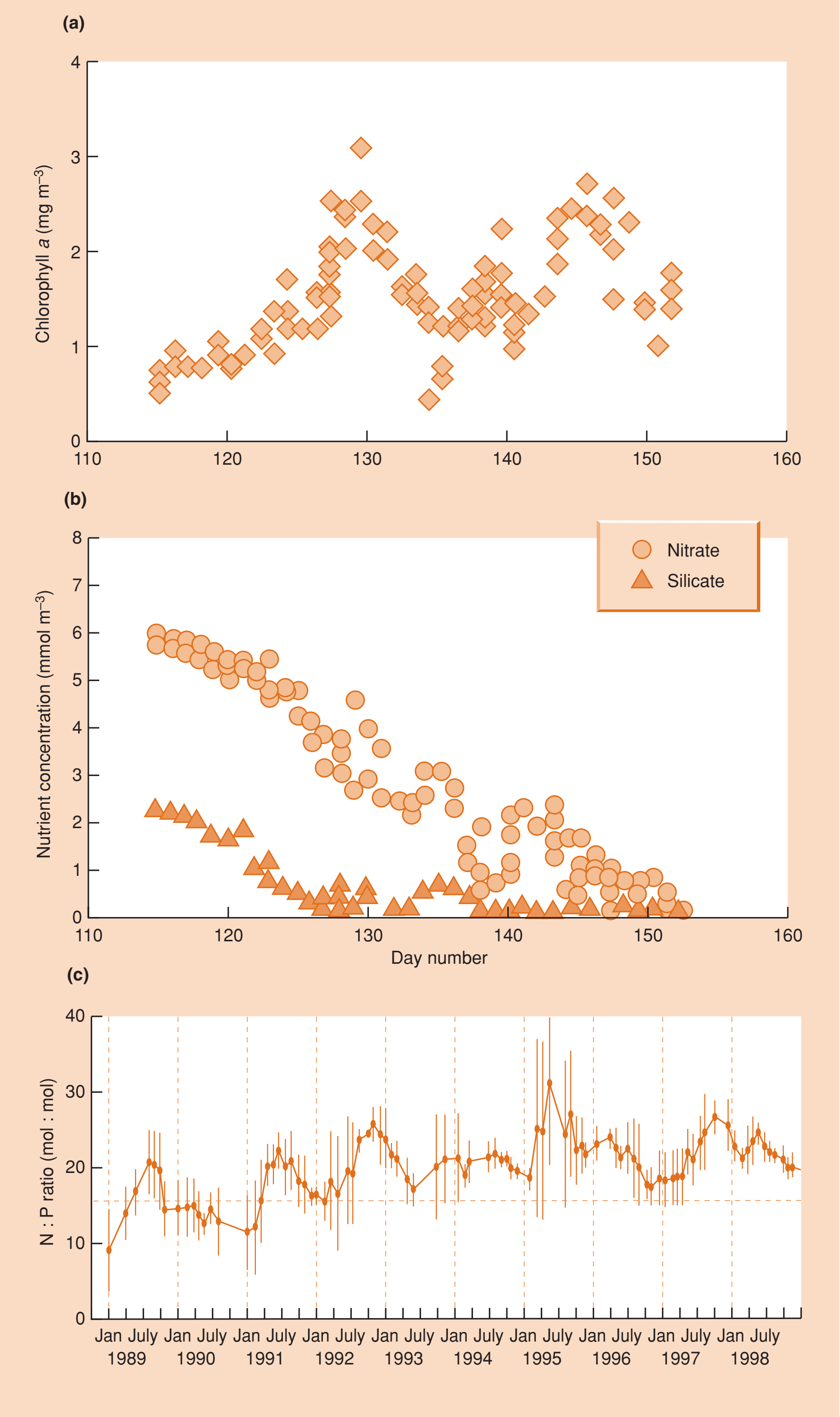


Figure 18.17 Patterns in (a) chlorophyll *a* and (b) silicate and nitrate concentrations during a spring bloom in the North Atlantic. Day number is days since January 1. (After Fasham *et al.*, 2001.) (c) Shift in the ratio of N : P in suspended particulate matter measured in the North Pacific Gyre. (After Karl, 1999.)

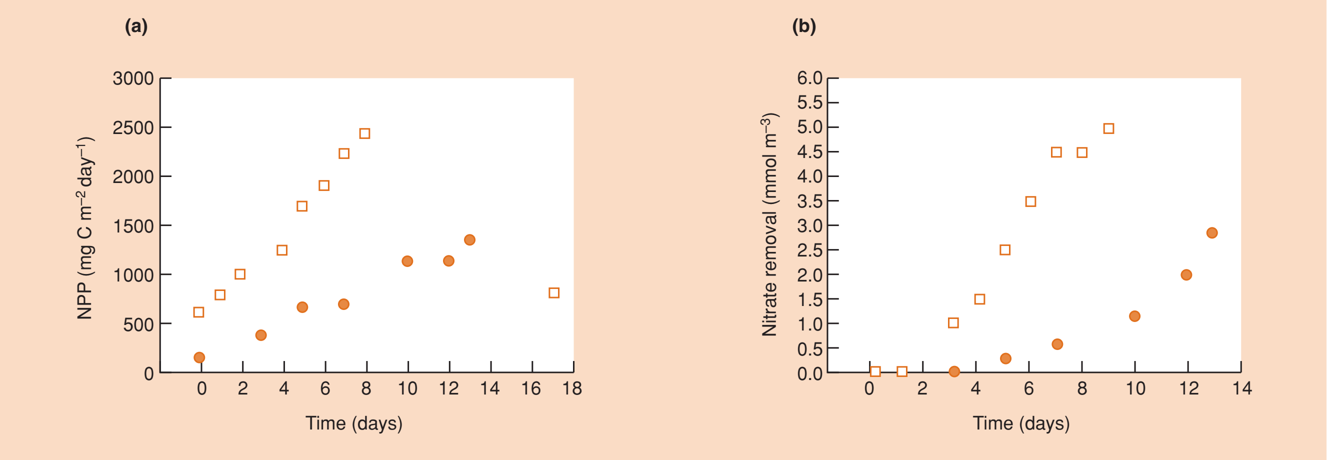


Figure 18.18 (a) Rates of depth-integrated net primary production (NPP) after iron addition at sites in the eastern equatorial Pacific Ocean (□) and polar Southern Ocean (●). (b) Nitrate removal during the time course of the two experiments. Note that silicate followed similar patterns. (After Boyd, 2002.)

18.4 Global biogeochemical cycles

Nutrients are moved over vast distances by winds in the atmosphere and by the moving waters of streams and ocean currents. There are no boundaries, either natural or political. It is appropriate, therefore, to conclude this chapter by moving to an even larger spatial scale to examine global biogeochemical cycles.

18.4.1 Hydrological cycle

The hydrological cycle is simple to conceive (although its elements are by no means always easy to measure) (Figure 18.19). The principal source of water is the oceans; radiant energy makes water evaporate into the atmosphere, winds distribute it over the surface of the globe, and precipitation brings it down to earth (with a net movement of atmospheric water from oceans to continents), where it may be stored temporarily in soils, lakes and icefields. Loss occurs from the land through evaporation and transpiration or as liquid flow through stream channels and groundwater aquifers, eventually to return to the sea. The major pools of water occur in the oceans (97.3% of the total for the biosphere; Berner & Berner, 1987), the ice of polar ice caps and glaciers (2.06%), deep in the groundwater (0.67%) and in rivers and lakes (0.01%). The proportion that is in transit at any time is very small – water draining through the soil, flowing along rivers and present as clouds and vapor in the atmosphere constitutes only about 0.08% of the total. However, this small percentage plays a crucial role, both by supplying the requirements for survival of living organisms and for community productivity, and because so many chemical nutrients are transported with the water as it moves.

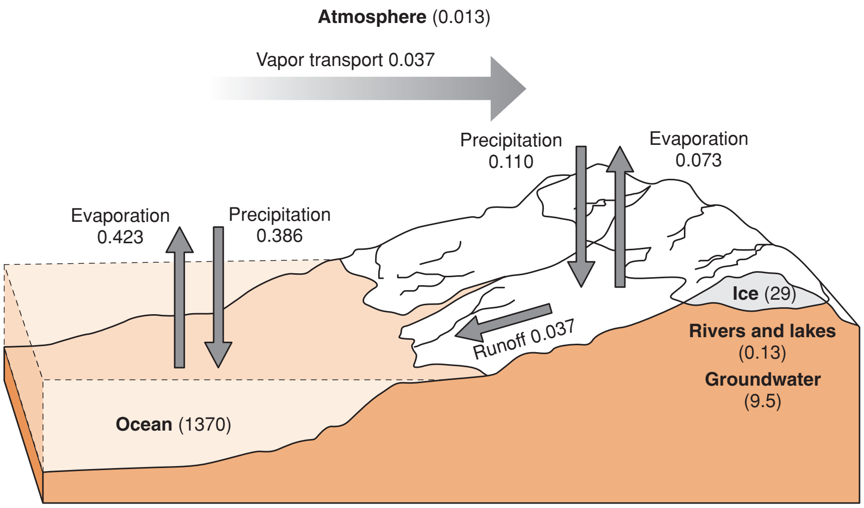


Figure 18.19 The hydrological cycle showing fluxes and sizes of reservoirs ($\times 10^6$ km^3). Values in parentheses represent the size of the various reservoirs. (After Berner & Berner, 1987.)

plants live between two counterflowing movements of water

The hydrological cycle would proceed whether or not a biota was present. However, terrestrial vegetation can modify to a significant extent the fluxes that occur. Plants live between two counterflowing movements of water (McCune & Boyce, 1992). One moves within the plant, proceeding from the soil into the roots, up through the stem and out from the leaves as transpiration. The other is deposited on the canopy as precipitation from where it may evaporate or drip from the leaves or flow down the stem to the soil. In the absence of vegetation, some of the incoming water would evaporate from the ground surface but the rest would enter the stream flow (via surface runoff and groundwater discharge). Vegetation can intercept water at two points on this journey, preventing some from reaching the stream and causing it to move back into the atmosphere by: (i) catching some in foliage from where it may evaporate; and (ii) preventing some from draining from the soil water by taking it up in the transpiration stream.

We have seen on a small scale how cutting down the forest in a catchment in Hubbard Brook can increase the throughput to streams of water together with its load of dissolved and particulate matter. It is small wonder that large-scale deforestation around the globe, usually to create new agricultural land, can lead to the loss of topsoil, nutrient impoverishment and increased severity of flooding.

Another major perturbation to the hydrological cycle will be global climate change resulting from human activities (see Section 18.4.6). The predicted temperature increase, with its concomitant changes to wind and weather patterns, can be expected to affect the hydrological cycle by causing some melting of polar caps and glaciers, by changing patterns of precipitation and by influencing the details of evaporation, transpiration and stream flow.

18.4.2 A general model of global nutrient flux

major nutrient compartments and fluxes in global biogeochemical cycles

The world's major abiotic reservoirs for nutrients are illustrated in Figure 18.20. The biotas of both terrestrial and aquatic habitats obtain some of their nutrient elements predominantly via the weathering of rock. This is the case, for example, for phosphorus. Carbon and nitrogen, on the other hand, derive mainly from the atmosphere – the first from CO_2 and the second from gaseous nitrogen, fixed by microorganisms in the soil and water. Sulfur derives from both atmospheric and lithospheric sources. In the following sections we consider phosphorus, nitrogen, sulfur and carbon in turn, and ask how human activities upset the global biogeochemical cycles of these biologically important elements.

18.4.3 Phosphorus cycle

phosphorus derives mainly from the weathering of rocks

The principal stocks of phosphorus occur in the water of the soil, rivers, lakes and oceans and in rocks and ocean sediments. The phosphorus

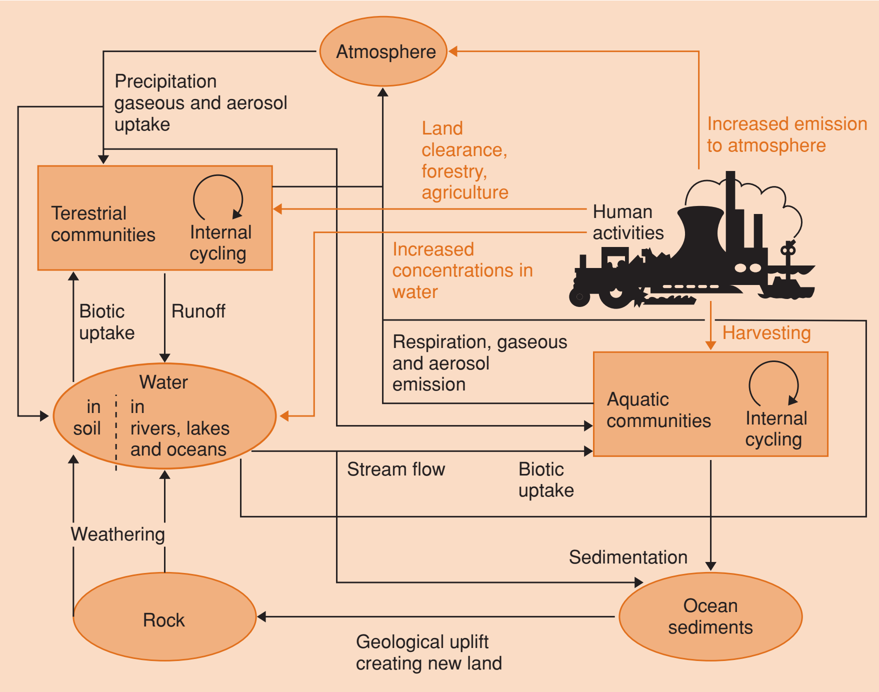


Figure 18.20 The major global pathways of nutrients between the abiotic 'reservoirs' of atmosphere, water (hydrosphere) and rock and sediments (lithosphere), and the biotic 'reservoirs' constituted by terrestrial and aquatic communities. Human activities (in color) affect nutrient fluxes through the terrestrial and aquatic communities both directly and indirectly, via their effects on global biogeochemical cycling through the release of extra nutrients into the atmosphere and water.

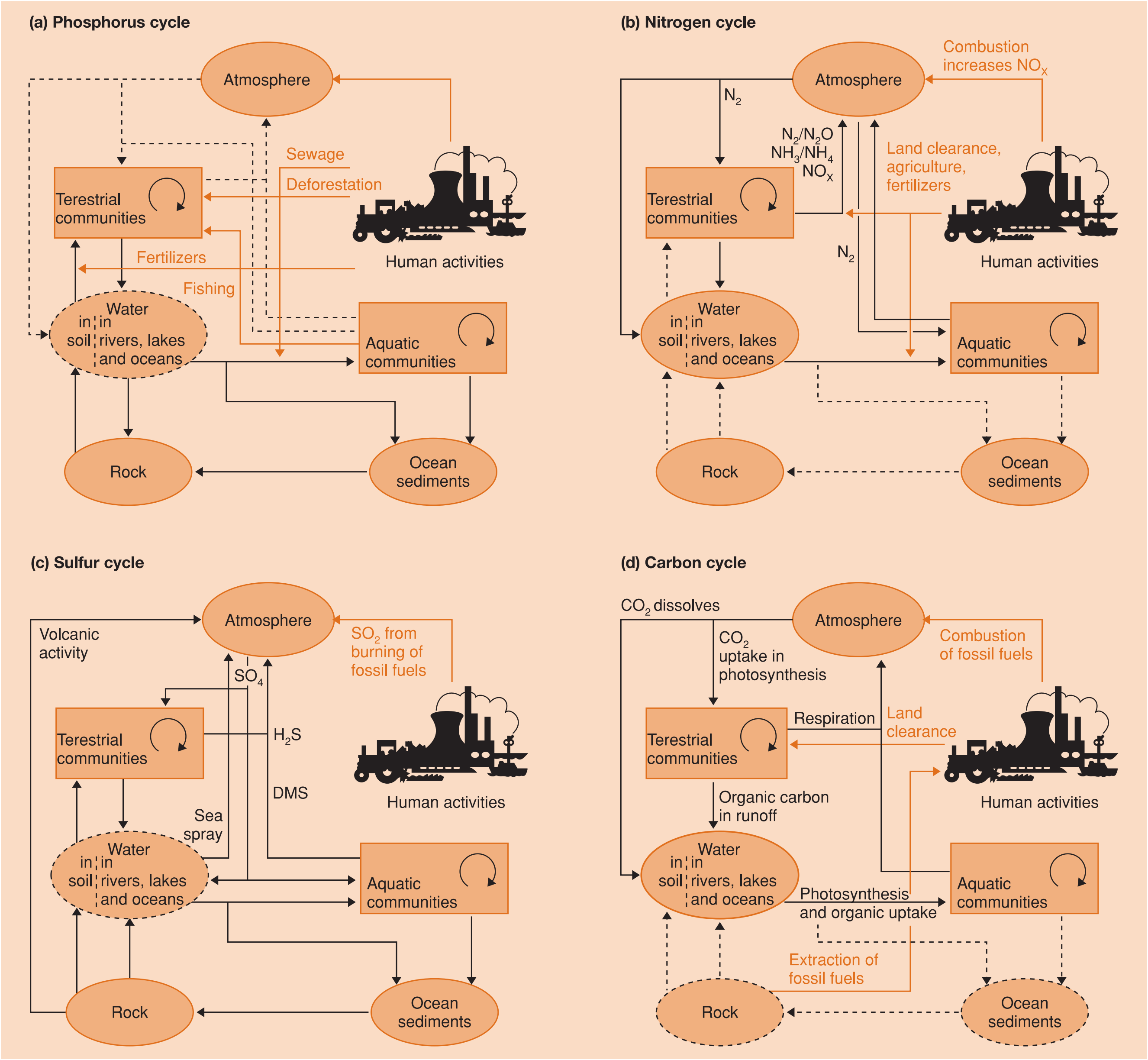


Figure 18.21 The main pathways of nutrient flux (black) and the perturbations caused by human activities (color) for four important nutrient elements: (a) phosphorus, (b) nitrogen, (c) sulfur (DMS, dimethylsufide), and (d) carbon. Insignificant compartments and fluxes are represented by dashed lines. (Based on the model illustrated in Figure 18.10, where further details can be found.)

cycle may be described as an 'open' cycle because of the general tendency for mineral phosphorus to be carried from the land inexorably to the oceans, mainly in rivers, but also to smaller extents in groundwater, or via volcanic activity and atmospheric fallout, or through abrasion of coastal land. The cycle may alternatively be termed a 'sedimentary cycle' because ultimately phosphorus becomes incorporated in ocean sediments (Figure 18.21a). We can unravel an intriguing story that starts in a terrestrial catchment area. A typical phosphorus atom, released from the rock by chemical weathering, may enter and cycle within the terrestrial community for years, decades or centuries before it is carried via groundwater into a stream, where it takes part in the nutrient spiraling described in Section 18.3.1. Within a short time of entering the stream (weeks, months or years), the atom is carried to the ocean. It then makes, on average, about 100 round trips between the surface and deep waters, each lasting perhaps 1000 years. During each trip, it is taken up by organisms that live at the ocean surface, before eventually settling into the deep again.

On average, on its 100th descent (after 10 million years in the ocean) it fails to be released as soluble phosphorus, but instead enters the bottom sediment in particulate form. Perhaps 100 million years later, the ocean floor is lifted up by geological activity to become dry land. Thus, our phosphorus atom will eventually find its way back via a river to the sea, and to its existence of cycle (biotic uptake and decomposition) within cycle (ocean mixing) within cycle (continental uplift and erosion).

human activities contribute the majority of phosphorus in inland waters . . .

Human activities affect the phosphorus cycle in a number of ways. Marine fishing transfers about 50 Tg (1 teragram = 10^{12} g) of phosphorus from the ocean to the land each year. Since the total oceanic pool of phosphorus is around 120 Pg (1 petagram = 10^{15} g), this reverse flow has negligible consequences for the ocean compartment. However, phosphorus from the fish catch will eventually move back through the rivers to the sea and, thus, fishing contributes indirectly to increased concentrations in inland waters. More than 13 Tg of phosphorus are dispersed annually over agricultural land as fertilizer (some derived from the marine fish catch) and a further 2 or 3 Tg as an additive to domestic detergents. Much of the former reaches the aquatic system as agricultural runoff, whereas the latter arrives in domestic sewage. In addition, deforestation and many forms of land cultivation increase erosion in catchment areas and contribute to artificially high amounts of phosphorus in runoff water. All told, human activities have almost doubled the inflow of phosphorus to the oceans above that which occurs naturally (Savenko, 2001).

. . . and cause eutrophication

An increase to phosphorus input to the oceans on this scale is likely to have increased productivity to some extent, but as the more concentrated water passes through rivers, estuaries, coastal waters and particularly lakes, its influence can be particularly profound. This is because phosphorus is often the nutrient whose supply limits aquatic plant growth. In many lakes worldwide, the input of large quantities of phosphorus from agricultural runoff and sewage and also of nitrogen (mainly as runoff from agricultural land) produces ideal conditions for high phytoplankton productivity. In such cases of cultural eutrophication (enrichment), the lake water becomes turbid because of dense populations of phytoplankton (often the blue-green species), and large aquatic plants are outcompeted and disappear along with their associated invertebrate populations. Moreover, decomposition of the large biomass of phytoplankton cells may lead to low oxygen concentrations, which kill fish and invertebrates. The outcome is a productive community, but one with low biodiversity and low esthetic appeal. The remedy is to reduce nutrient input; for example, by altering agricultural practices and by diverting sewage, or by chemically 'stripping' phosphorus from treated sewage before it is discharged. Where phosphate loading has been reduced in deep lakes, such as Lake Washington in North America, a reversal of the trends described above may occur within a few years (Edmonson, 1970). In shallow lakes, however, phosphorus stored in the sediment may continue to be released and the physical removal of some of the sediment may be called for (Moss *et al.*, 1988).

The effects of agricultural runoff and sewage discharge are localized, in the sense that only those waters that drain the catchment area concerned are affected. But the problem is pervasive and worldwide.

18.4.4 Nitrogen cycle

the nitrogen cycle has an atmospheric phase of overwhelming importance

The atmospheric phase is predominant in the global nitrogen cycle, in which nitrogen fixation and denitrification by microbial organisms are by far the most important (Figure 18.21b). Atmospheric nitrogen is also fixed by lightning discharges during storms and reaches the ground as nitric acid dissolved in rainwater, but only about 3–4% of fixed nitrogen derives from this pathway. Organic forms of nitrogen are also widespread in the atmosphere, some of which results from the reaction of hydrocarbons and oxides of nitrogen in polluted air masses. In addition, amines and urea are naturally injected as aerosols or gases from terrestrial and aquatic ecosystems; and a third source consists of bacteria and pollen (Neff *et al.*, 2002). While the atmospheric phase produces by far the most important input of nitrogen, there is also evidence that nitrogen from certain geological sources may fuel local productivity in terrestrial and freshwater communities (Holloway *et al.*, 1998; Thompson *et al.*, 2001). The magnitude of the nitrogen flux in stream flow from terrestrial to aquatic communities may be relatively small, but it is by no means insignificant for the aquatic systems involved. This is because nitrogen is one of the two elements (along with phosphorus) that most often limits plant growth. Finally, there is a small annual loss of nitrogen to ocean sediments.

In a model for the terrestrial part of the biosphere, nitrogen fixation accounts for the input of 211 Tg N year^{-1}. This is the predominant annual source of nitrogen and can be compared with the total amount stored in terrestrial vegetation and soil of 296 Pg year^{-1} (280 Pg year^{-1} of which is in the soil, and 90% of this in organic form) (Lin *et al.*, 2000).

humans impact on the nitrogen cycle in diverse ways

Human activities have a variety of far-reaching effects on the nitrogen cycle. Deforestation, and land clearance in general, leads to substantial increases in nitrate flux in the stream flow and N_2O losses to the atmosphere (see Section 18.2.2). In addition, technological processes yield fixed nitrogen as a by-product of internal combustion and in the production of fertilizers. The agricultural practice of planting legume crops, with their root nodules containing nitrogen-fixing bacteria, contributes further to nitrogen fixation. In fact, the amount of fixed nitrogen produced by these human activities is of the same order of magnitude as that produced by natural nitrogen fixation. The production of nitrogenous fertilizers (more than 50 Tg year^{-1}) is of particular significance because an appreciable proportion of fertilizer added to land finds its way into streams and lakes. The artificially raised concentrations of nitrogen contribute to the process of cultural eutrophication of lakes.

Human activities impinge on the atmospheric phase of the nitrogen cycle too. For example, fertilization of agricultural soils leads to increased runoff as well as an increase in denitrification, and the handling and spreading of manure in areas of intensive animal husbandry releases substantial amounts of ammonia to the atmosphere. Atmospheric ammonia (NH_3) is increasingly recognized as a major pollutant when it is deposited downwind of livestock farming areas (Sutton *et al.*, 1993). Since many plant communities are adapted to low nutrient conditions, an increased input of nitrogen can be expected to cause changes to community composition. Lowland heathland is particularly sensitive to nitrogen enrichment (this is a terrestrial counterpart to lake eutrophication) and, for example, more than 35% of former Dutch heathland has now been replaced by grassland (Bobbink *et al.*, 1992). Further sensitive communities include calcareous grasslands and upland herb and bryophyte floras, where declines in species richness have been recorded (Sutton *et al.*, 1993). The vegetation of some other terrestrial communities may be less sensitive, because it may reach a stage where nitrogen is not limited. Increased nitrogen deposition to forests, for example, can be expected to result initially in increased forest growth, but at some point the system becomes 'nitrogen-saturated' (Aber, 1992). Further increases in nitrogen deposition can be expected to 'break through' into drainage, with raised concentrations of nitrogen in stream runoff contributing to eutrophication of downstream lakes.

nitrogen and acid rain

There is clear evidence of increased NH_3 emissions during the past few decades and current estimates indicate that these account for 60–80% of anthropogenic nitrogen input to European ecosystems, at least in localized areas around livestock operations (Sutton *et al.*, 1993). The other 20–40% derives from oxides of nitrogen (NO_x), resulting from combustion of oil and coal in power stations, and from industrial processes and traffic emissions. Atmospheric NO_x is converted, within days, to nitric acid, which contributes, together with NH_3, to the acidity of precipitation within and downwind of industrial regions. Sulfuric acid is the other culprit, and we outline the consequences of acid rain in the next section, after dealing with the global sulfur cycle.

18.4.5 Sulfur cycle

In the global phosphorus cycle we have seen that the lithospheric phase is predominant (Figure 18.21a), whereas the nitrogen cycle has an atmospheric phase of overwhelming importance (Figure 18.21b). Sulfur, by contrast, has atmospheric and lithospheric phases of similar magnitude (Figure 18.21c).

the sulfur cycle has atmospheric and lithospheric phases of similar magnitude

Three natural biogeochemical processes release sulfur to the atmosphere: (i) the formation of the volatile compound dimethylsulfide (DMS) (by enzymatic breakdown of an abundant compound in phytoplankton – dimethylsulfonioproprionate); (ii) anaerobic respiration by sulfate-reducing bacteria; and (iii) volcanic activity. Total biological release of sulfur to the atmosphere is estimated to be 22 Tg S year^{-1}, and of this more than 90% is in the form of DMS. Most of the remainder is produced by sulfur bacteria that release reduced sulfur compounds, particularly H_2S, from waterlogged bog and marsh communities and from marine communities associated with tidal flats. Volcanic production provides a further 7 Tg S year^{-1} to the atmosphere (Simo, 2001). A reverse flow from the atmosphere involves oxidation of sulfur compounds to sulfate, which returns to earth as both wetfall and dryfall.

The weathering of rocks provides about half the sulfur draining off the land into rivers and lakes, the remainder deriving from atmospheric sources. On its way to the ocean, a proportion of the available sulfur (mainly dissolved sulfate) is taken up by plants, passed along food chains and, via decomposition processes, becomes available again to plants. However, in comparison to phosphorus and nitrogen, a much smaller fraction of the flux of sulfur is involved in internal recycling in terrestrial and aquatic communities. Finally, there is a continuous loss of sulfur to ocean sediments, mainly through abiotic processes such as the conversion of H_2S, by reaction with iron, to ferrous sulfide (which gives marine sediments their black color).

sulfur and acid rain

The combustion of fossil fuels is the major human perturbation to the global sulfur cycle (coal contains 1–5% sulfur and oil contains 2–3%). The SO_2 released to the atmosphere is oxidized and converted to sulfuric acid in aerosol droplets, mostly less than 1 μm in size. Natural and human releases of sulfur to the atmosphere are of similar magnitude and together account for 70 Tg S year^{-1} (Simo, 2001). Whereas natural inputs are spread fairly evenly over the globe, most human inputs are concentrated in and around industrial zones in northern Europe and eastern North America, where they can contribute up to 90% of the total (Fry & Cooke, 1984). Concentrations decline progressively downwind from sites of production, but they can still be high at distances of several hundred kilometers. Thus, one nation can export its SO_2 to other countries; concerted international political action is required to alleviate the problems that arise.

Water in equilibrium with CO_2 in the atmosphere forms dilute carbonic acid with a pH of about 5.6. However, the pH of acid precipitation (rain or snow) can average well below 5.0, and values as low as 2.4 have been recorded in Britain, 2.8 in

Scandinavia and 2.1 in the USA. The emission of SO_2 often contributes most to the acid rain problem, though together NO_x and NH_3 account for 30–50% of the problem (Mooney *et al.*, 1987; Sutton *et al.*, 1993).

We saw earlier how a low pH can drastically affect the biotas of streams and lakes (see Chapter 2). Acid rain (see Section 2.8) has been responsible for the extinction of fish in thousands of lakes, particularly in Scandinavia. In addition, a low pH can have far-reaching consequences for forests and other terrestrial communities. It can affect plants directly, by breaking down lipids in foliage and damaging membranes, or indirectly, by increasing leaching of some nutrients from the soil and by rendering other nutrients unavailable for uptake by plants. It is important to note that some perturbations to biogeochemical cycles arise through indirect, 'knock-on' effects on other biogeochemical components. For example, alterations in the sulfur flux in themselves are not always damaging to terrestrial and aquatic communities, but the effect of sulfate's ability to mobilize metals such as aluminum, to which many organisms are sensitive, may indirectly lead to changes in community composition. (In another context, sulfate in lakes can reduce the ability of iron to bind phosphorus, releasing the phosphorus and increasing phytoplankton productivity (Caraco, 1993).)

Provided that governments show the political will to reduce emissions of SO_2 and NO_x (for example, by making use of techniques already available to remove sulfur from coal and oil), the acid rain problem should be controllable. Indeed reductions in sulfur emissions have occurred in various parts of the world.

18.4.6 Carbon cycle

opposing forces of photosynthesis and respiration drive the global carbon cycle

Photosynthesis and respiration are the two opposing processes that drive the global carbon cycle. It is predominantly a gaseous cycle, with CO_2 as the main vehicle of flux between the atmosphere, hydrosphere and biota. Historically, the lithosphere played only a minor role; fossil fuels lay as dormant reservoirs of carbon until human intervention in recent centuries (Figure 18.21d).

Terrestrial plants use atmospheric CO_2 as their carbon source for photosynthesis, whereas aquatic plants use dissolved carbonates (i.e. carbon from the hydrosphere). The two subcycles are linked by exchanges of CO_2 between the atmosphere and oceans as follows:

$$\text{atmospheric } CO_2 \rightleftharpoons \text{dissolved } CO_2$$
$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \text{ (carbonic acid).}$$

In addition, carbon finds its way into inland waters and oceans as bicarbonate resulting from weathering (carbonation) of calcium-rich rocks such as limestone and chalk:

$$CO_2 + H_2O + CaCO_3 \rightleftharpoons CaH_2(CO_3)_2.$$

Respiration by plants, animals and microorganisms releases the carbon locked in photosynthetic products back to the atmospheric and hydrospheric carbon compartments.

CO_2 in the atmosphere has increased significantly because of . . .

The concentration of CO_2 in the atmosphere has increased from about 280 parts per million (ppm) in 1750 to more than 370 ppm today and it is still rising. The pattern of increase recorded at the Mauna Loa Observatory in Hawaii since 1958 is shown in Figure 18.22. (Note the cyclical decreases in CO_2 associated with higher rates of photosynthesis during summer in the northern hemisphere – reflecting the fact that most of the world's landmass is north of the equator.)

. . . the combustion of fossil fuels . . .

We discussed this increase in atmospheric CO_2, and the associated exaggeration in the greenhouse effect, in Sections 2.9.1 and 2.9.2, but armed with a more comprehensive appreciation of carbon budgets, we can now revisit this subject. The principal causes of the increase has been the combustion of fossil fuels and, to a much smaller extent, the kilning of limestone to produce cement (the latter produces less than 2% of that produced by fossil fuel burning). Together, during the period 1980–95, these accounted for a net increase in the atmosphere averaging 5.7 (± 0.5) Pg C $year^{-1}$ (Houghton, 2000).

. . . and exploitation of tropical forest

Land-use change has caused a further 1.9 (± 0.2) Pg of carbon to enter the atmosphere each year. The exploitation of tropical forest causes a significant release of CO_2, but the precise effect depends on whether forest is cleared for permanent agriculture, shifting agriculture or timber production. The burning that follows most forest clearance quickly converts some of the vegetation to CO_2, while decay of the remaining vegetation releases CO_2 over a more extended period. If forests have been cleared to provide for permanent agriculture, the carbon content of the soil is reduced by decomposition of the organic matter, by erosion and sometimes by mechanical removal of the topsoil. Clearance for shifting agriculture has similar effects, but the regeneration of ground flora and secondary forest during the fallow period sequesters a proportion of the carbon originally lost. Shifting agriculture and timber extraction involve 'temporary' clearance in which the net release of CO_2 per unit area is significantly less than is the case for 'permanent' clearance for agriculture or pasture. Changes to land use in nontropical terrestrial communities seem to have had a negligible effect on the net release of CO_2 to the atmosphere.

some of the extra CO_2 dissolves in the oceans . . . or is taken up by terrestrial plants

The total amount of carbon released each year to the atmosphere

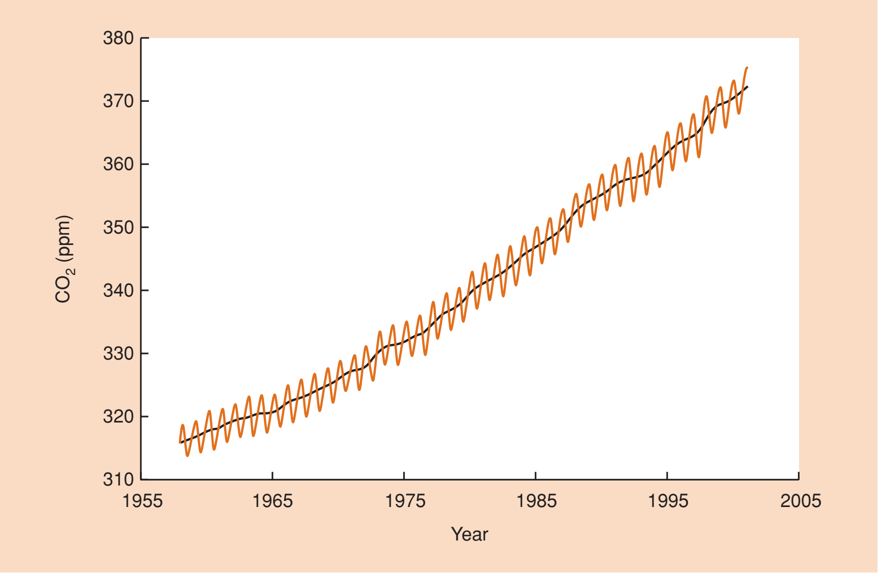


Figure 18.22 Concentration of atmospheric carbon dioxide (CO_2) at the Mauna Loa Observatory, Hawaii, showing the seasonal cycle (resulting from changes in photosynthetic rate) and the long-term increase that is due largely to the burning of fossil fuels. (Courtesy of the Climate Monitoring and Diagnostics Laboratory of the National Oceanic and Atmospheric Administration.)

by human activities (7.6 Pg C year^{-1}; see Section 2.9.1) can be compared with the 100–120 Pg C year^{-1} released naturally by respiration of the world's biota (Houghton, 2000). Where does the extra CO_2 go? The observed increase in atmospheric CO_2 accounts for 3.2 (± 1.0) Pg C year^{-1} (i.e. 42% of the human inputs). Much of the rest, 2.1 (± 0.6) Pg C year^{-1}, dissolves in the oceans. This leaves 2.3 Pg C year^{-1}, which is generally put down to a residual terrestrial sink, the magnitude, location and causes of which are uncertain, but are believed to involve increased terrestrial productivity in northern mid-latitude regions (i.e. part of the increase in CO_2 may serve to 'fertilize' terrestrial communities and be assimilated into extra biomass) and the recovery of forests from earlier disturbances (Houghton, 2000).

accurate prediction of future changes in carbon emissions is a pressing matter

There is considerable year-to-year variation in the estimates of CO_2 sources and sinks, and of the increase in the atmosphere (Figure 18.23). Indeed, this variation is what allowed standard errors to be placed on average values in the previous paragraphs. The declines in atmospheric increase in CO_2 between 1981 and 1982 followed dramatic rises in oil prices, while the declines in 1992 and 1993 followed the economic collapse of the Soviet Union. In 1997–98 (not shown in Figure 18.23), a remarkable wildfire in a small part of the globe doubled the growth rate of CO_2 in the atmosphere. Massive forest fires in Indonesia produced a carbon emission of about 1 Pg in just a few weeks. The burned areas included vast deposits of peat, which lost 25–85 cm of their depth during the fire, and most of the released carbon came from this source rather than the burning of wood. The fires in Indonesia were particularly serious due to a combination of circumstances – drought caused by the 1997–98 El Niño event, the thickness of peat present, and particular logging practices that allowed the vegetation and soil to dry out (Schimel & Baker, 2002). The accurate prediction of future changes in carbon emissions is a pressing matter, but it will be a difficult task because so many variables – climatic, political and sociological – impinge on the carbon balance. We return to the many dimensions of the ecological challenges facing mankind at the very end of the book (see Section 22.5.3).

Summary

Living organisms expend energy to extract chemicals from their environment, hold on to them and use them for a period, and then lose them again. In this chapter, we consider the ways in which the biota on an area of land, or within a volume of water, accumulates, transforms and moves matter between the various living and abiotic components of the ecosystem. Some abiotic compartments occur in the *atmosphere* (carbon in carbon dioxide, nitrogen as gaseous nitrogen), some in the rocks of the *lithosphere* (calcium, potassium) and others in the *hydrosphere* – the water of soils, streams, lakes or oceans (nitrogen in dissolved nitrate, phosphorus in phosphate).

Nutrient elements are available to plants as simple inorganic molecules or ions and can be incorporated into complex organic carbon compounds in biomass. Ultimately, however, when the carbon compounds are metabolized to carbon dioxide, the mineral nutrients are released again in simple inorganic form. Another plant may then absorb them, and so an individual atom of a nutrient element may pass repeatedly through one food chain after another. By its very nature, each joule of energy in a high-energy

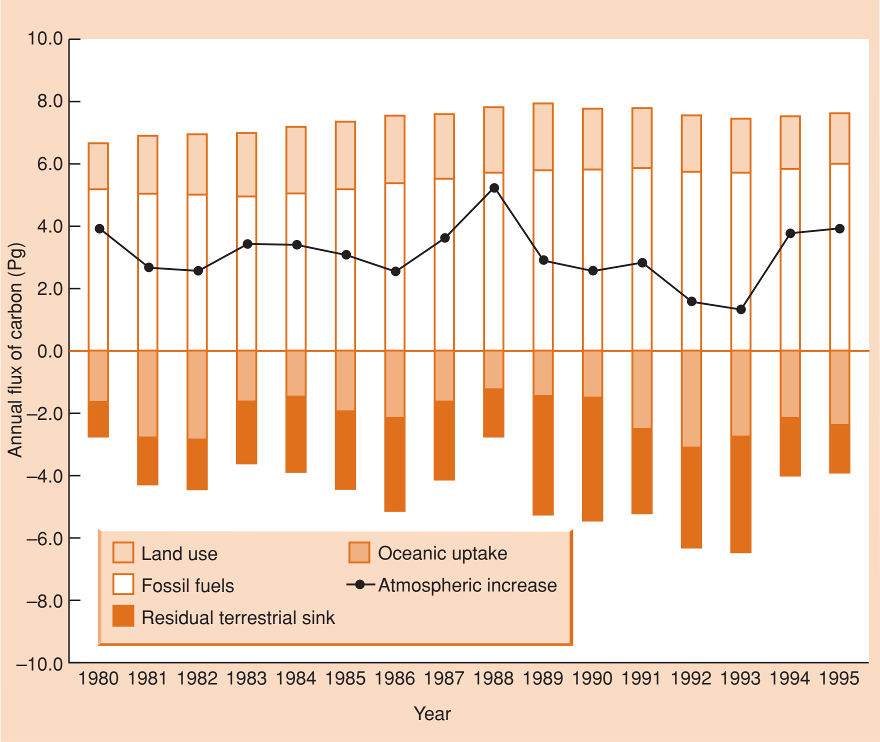


Figure 18.23 Annual variations in the atmospheric increase in carbon dioxide (circles and black line) and in carbon released (histograms above the midline) or accumulated (histograms below the midline) in the global carbon cycle from 1980 to 1995. (After Houghton, 2000.)

compound can be used only once, whereas chemical nutrients can be used again, and repeatedly recycled (although nutrient cycling is never perfect).

We discuss the ways that nutrients are gained and lost in ecosystems and note that inputs and outputs of a given nutrient may be in balance. However, this is by no means always so, in which case the ecosystem is a net source or sink for the nutrient in question. We discuss the components of nutrient budgets, and the factors affecting inputs and outputs, in forests, streams, lakes, estuaries and oceans.

Because nutrients are moved over vast distances by winds in the atmosphere and by the moving waters of streams and ocean currents, we conclude the chapter by examining global biogeochemical cycles. The principal source of water in the hydrological cycle is the oceans; radiant energy makes water evaporate into the atmosphere, winds distribute it over the surface of the globe, and precipitation brings it down to earth. Phosphorus derives mainly from the weathering of rocks (lithosphere); its cycle may be described as sedimentary because of the general tendency for mineral phosphorus to be carried from the land inexorably to the oceans where ultimately it becomes incorporated in sediments. The sulfur cycle has an atmospheric phase and a lithospheric phase of similar magnitude. In contrast, the atmospheric phase is predominant in both the carbon and nitrogen cycles. Photosynthesis and respiration are the two opposing processes that drive the global carbon cycle while nitrogen fixation and denitrification by microbial organisms are of particular importance in the nitrogen cycle. Human activities contribute significant inputs of nutrients to ecosystems and disrupt local and global biogeochemical cycles.

Chapter 19

The Influence of Population Interactions on Community Structure

19.1 Introduction

interspecific competition may determine which, and how many, species can coexist

Individual species can influence the composition of whole communities in a variety of ways. Every species provides resources for others that prey upon or parasitize them, but some species (trees, for example) provide a wide range of resources that are used by a large number of consumer species (discussed in Chapter 3). Thus, oak trees can be very influential in determining the composition and diversity of the communities of which they are part by providing acorns, leaves, stemwood and roots for their specialist herbivores as well as a similar range of dead organic materials that are exploited by detritivores and decomposers (see Chapter 11). Species may also help determine community composition and diversity by influencing conditions (see Chapter 2). Thus, large plants create microhabitats that encompass the niche requirements of many smaller plants and animals, whilst large animals provide a range of conditions on and in their bodies that are exploited by a variety of parasites (see Chapter 12). During succession we have also seen that some early colonizers facilitate the entry of later species by changing conditions in a way that favors the latter (see Chapter 16). We will not dwell further on these processes.

The current chapter pays particular attention to the way that competition, predation and parasitism can shape communities. The ideas we present reflect a debate that has been central to ecology for the last four decades. As we explain below, there are sound theoretical reasons for expecting interspecific competition to be important in shaping communities by determining which, and how many, species can coexist. Indeed, the prevalent view amongst ecologists in the 1970s was that competition was of overriding importance (MacArthur, 1972; Cody, 1975). Subsequently, the conventional wisdom has moved away from this monolithic view to one giving more prominence to nonequilibrial and stochastic factors, such as physical disturbance and inconstancy in conditions (see Chapter 16), and to an important role for predation and parasitism (e.g. Diamond & Case, 1986; Gee & Giller, 1987; Hudson & Greenman, 1998). We first consider the role of interspecific competition in theory and practice before proceeding to the other population interactions that in some communities and for some organisms make competition much less influential.

19.2 Influence of competition on community structure

The view that interspecific competition plays a central and powerful role in the shaping of communities was first fostered by the competitive exclusion principle (see Chapter 8) which says that if two or more species compete for the same limiting resource, then all but one of them will be driven to extinction. More sophisticated variants of the principle, namely the concepts of limiting similarity, optimum similarity and niche packing (see Chapter 8), have suggested a limit to the similarity of competing species, and thus, a limit to the number of species that can be fitted into a particular community before niche space is fully saturated. Within this theoretical framework, interspecific competition is obviously important, because it excludes particular species from some communities, and determines precisely which species coexist in others. The crucial question, however, is: ‘how important are such theoretical effects in the real world?’

19.2.1 Prevalence of current competition in communities

competition is not always of overriding importance

There is no argument about whether competition *sometimes* affects community structure; nobody doubts that it does. Equally, nobody claims that competition is of overriding importance in each and every case. In a community where the species are competing with one another on a day-to-day or minute-by-minute basis, and where the environment is homogeneous, it is indisputable that competition will have a powerful effect on community structure. Suppose instead, though, that other factors prevent competition from progressing to competitive exclusion, by depressing densities or periodically reversing competitive superiority. In this context, Hutchinson (1961) noted how phytoplankton communities generally exhibit high diversity despite limited opportunities for resource partitioning (his 'paradox of the plankton') and suggested that short-term fluctuations in conditions (e.g. temperature) or resources (light or nutrients) might prevent competitive exclusion and permit high diversity. Floder *et al.* (2002) tested this hypothesis by comparing species diversity of inocula of natural phytoplankton communities in microcosms maintained at high (100 μmol photons m^{-2} s^{-1}) or low (20 μmol photons m^{-2} s^{-1}) light levels with diversities achieved when light levels were periodically switched from high to low and back again every 1, 3, 6 or 12 days in a 49-day experiment. As predicted by Hutchinson, diversities were higher under fluctuating conditions, where interspecific competition was less likely to proceed to competitive exclusion (Figure 19.1).

literature reviews suggest competition is widespread . . .

Perhaps the most direct way of determining the importance of competition in practice is from the results of experimental field manipulations, in which one species is removed from or added to the community, and the responses of the other species are monitored. Two important surveys of field experiments on interspecific competition were published in 1983. Schoener (1983) examined the results of all the experiments he could find – 164 studies in all – and noted that approximately equal numbers of studies had dealt with terrestrial plants, terrestrial animals and marine organisms, but that studies of freshwater organisms amounted to only about half the number in the other groups. Amongst the terrestrial studies, however, most were concerned with temperate regions and mainland populations and relatively few dealt with phytophagous (plant-eating) insects. Any conclusions were therefore bound to be subject to the limitations imposed by what ecologists had chosen to look at. Nevertheless, Schoener found that approximately 90% of the studies had demonstrated the existence of interspecific competition, and that the figures were 89, 91 and 94% for terrestrial, freshwater and marine organisms, respectively. Moreover, if he looked at single species or small groups of species (of which there were 390) rather than at whole studies which may have dealt with several groups of species, 76% showed effects of competition at least sometimes, and 57% showed effects in all the conditions under which they were examined. Once again, terrestrial, freshwater and marine organisms gave very similar figures. Connell's (1983) review was less extensive than Schoener's: 72 studies in six major journals, dealing with a total of 215 species and 527 different experiments. Interspecific competition was demonstrated in most of the studies, in more than half of the species, and in approximately 40% of the experiments. In contrast to Schoener, Connell found that interspecific competition was more prevalent in marine than in terrestrial organisms, and also that it was more prevalent in large than in small organisms.

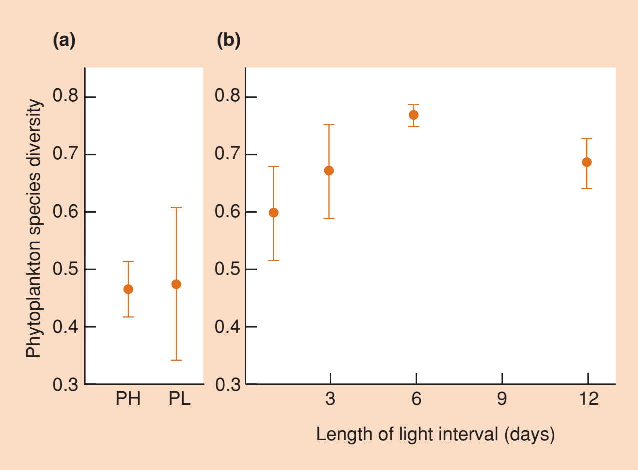


Figure 19.1 Average phytoplankton species diversity (Shannon diversity index, ± SE) at the end of 49-day experiments (a) under constant light conditions and (b) under fluctuating light intensity. PH, permanent high light intensity; PL, permanent low light intensity. (After Floder *et al.*, 2002.)

Taken together, Schoener's and Connell's reviews certainly seem to indicate that active, current interspecific competition is widespread. Its percentage occurrence amongst species is admittedly lower than its percentage occurrence amongst whole studies. However, this is to be expected, since, for example, if four species are arranged along a single niche dimension and all adjacent species competed with each other, this would still be only three out of six (or 50%) of all possible pairwise interactions.

. . . but are the data biased?

Connell also found, however, that in studies of just one pair of species, interspecific competition was almost always apparent, whereas with more species the prevalence dropped markedly (from more than 90% to less than 50%). This can be explained to some extent by the argument outlined above, but it may also indicate biases in the particular pairs of species studied, and in the studies that are actually reported (or accepted by journal editors). It is highly likely that many pairs of species are chosen for study because they are 'interesting' (because competition between them is suspected) and if none is found this is simply not reported. Judging the prevalence of competition from such studies is rather like judging the prevalence of debauched clergymen from the 'gutter press'. Bias in the choice of studies is a real problem, only partially alleviated in investigations of larger groups of species when a number of 'negatives' can be conscientiously reported alongside one or a few 'positives'. Thus the results of surveys, such as those by Schoener and Connell, exaggerate, to an unknown extent, the frequency of competition.

the strength of competition is likely to vary from community to community

As previously noted, phytophagous insects were poorly represented in Schoener's data, but reviews of phytophagous insects have tended to suggest either that competition is relatively rare in the group overall (Strong *et al.*, 1984) or at least in certain types of phytophagous insects, for example 'leaf-biters' (Denno *et al.*, 1995). There are also examples of 'vacant niches' for phytophagous insects: feeding sites or feeding modes on a widespread plant that are utilized by insects in one part of the world, but not in another part of the world where the native insect fauna is different (Figure 19.2). This failure to saturate the niche space also argues against a powerful role for interspecific competition. On a more general level, it has been suggested that herbivores *as a whole* are seldom food-limited, and are therefore not likely to compete for common resources (Hairston *et al.*, 1960; Slobodkin *et al.*, 1967; see Section 20.2.5). The bases for this suggestion are the observations that green plants are normally abundant and largely intact, they are rarely devastated, and most herbivores are scarce most of the time. Schoener found the proportion of herbivores exhibiting interspecific competition to be significantly lower than the proportions of plants, carnivores or detritivores.

Taken overall, therefore, current interspecific competition has been reported in studies on a wide range of organisms and in some groups its incidence may be particularly obvious, for example amongst sessile organisms in crowded situations. However, in other groups of organisms, interspecific competition may have little or no influence. It appears to be relatively rare among herbivores generally, and particularly rare amongst some types of phytophagous insect.

19.2.2 Structuring power of competition

Atkinson and Shorrock's simulations

Even when competition is potentially intense, the species concerned may nevertheless coexist. This has been highlighted in theoretical studies of model communities in which species compete for patchy and ephemeral resources, and in which species themselves have aggregated distributions, with each species distributed independently of the others (e.g. Atkinson & Shorrocks, 1981; Shorrocks & Rosewell, 1987; see Chapter 8). The species exhibited 'current competition' (like that in Schoener's and Connell's surveys), in

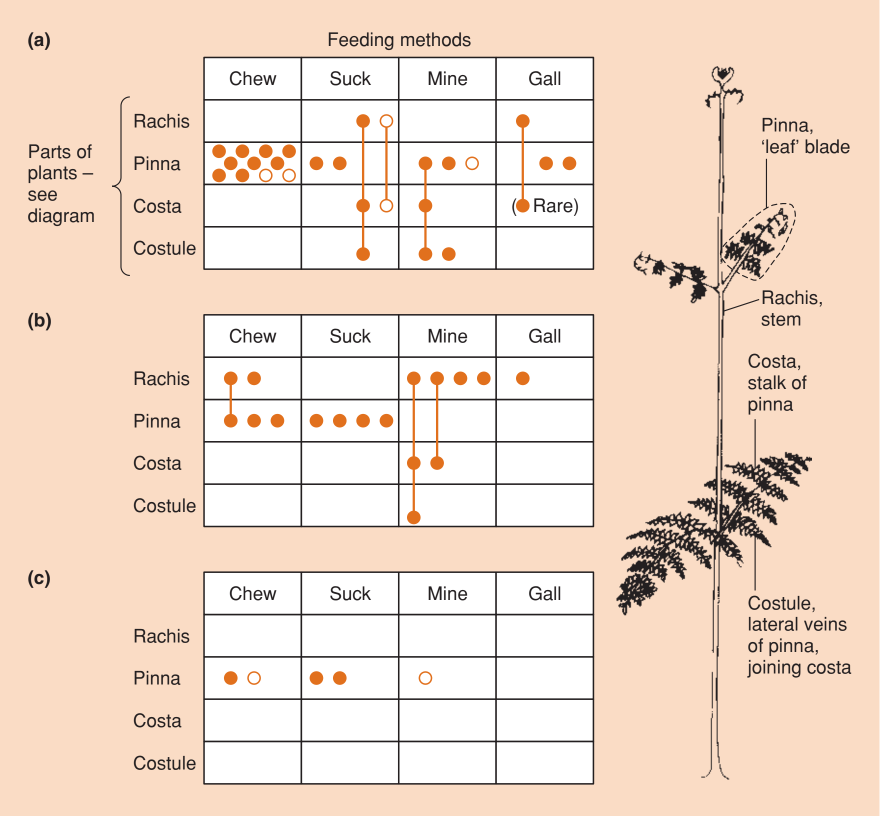


Figure 19.2 Feeding sites and feeding methods of herbivorous insects attacking bracken (*Pteridium aquilinum*) on three continents. (a) Skipwith Common in northern England; the data are derived from both a woodland and a more open site. (b) Hombrom Bluff, a savanna woodland in Papua New Guinea. (c) Sierra Blanca in the Sacramento Mountains of New Mexico and Arizona, USA; as at Skipwith, the data here are derived from both an open and a wooded site. Each bracken insect exploits the frond in a characteristic way. Chewers live externally and bite large pieces out of the plant; suckers puncture individual cells or the vascular system; miners live inside tissues; and gall-formers do likewise but induce galls. Feeding sites are indicated on the diagram of the bracken frond. Feeding sites of species exploiting more than one part of the frond are joined by lines. ●, open and woodland sites; ○, open sites only. (After Lawton, 1984.)

that the removal of one species led to an increase in the abundance of others. But, despite the fact that competition coefficients were high enough to lead to competitive exclusion in a uniform environment, the patchy nature of the environment and the aggregative behaviors of individuals of the species made coexistence possible without any niche differentiation. Thus, even if interspecific competition is actually affecting the abundance of populations, it need not determine the species composition of the community. In a field study of 60 insect taxa (Diptera and Hymenoptera) that exploit the patchy resources provided by 66 mushroom taxa, Wertheim *et al.* (2000) found insect coexistence could be explained by intraspecific aggregation in the manner described above, while resource partitioning was judged not to contribute detectably to biodiversity.

the ghost of competition past

On the other hand, even when interspecific competition is absent or difficult to detect, this does not necessarily mean that it is unimportant as a structuring force. Species may not compete at present because selection in the past favored an avoidance of competition, and thus a differentiation of niches (Connell's 'ghost of competition past' – see Chapter 8). Alternatively, unsuccessful competitors may already have been driven to extinction; the present, observed species may then simply be those that are able to exist because they compete very little or not at all with other species. Furthermore, species may compete only rarely (perhaps during population outbreaks), or only in localized patches of especially high density, but the results of such competition may be crucial to their continued existence at a particular location. In all of these cases, interspecific competition must be seen as a powerful influence on community structure, affecting which species coexist and the precise nature of those species. Yet, this influence will not be reflected in the level of current competition. It is clear that the intensity of current competition may sometimes be linked only weakly to the structuring power of competition within the community.

expectations from competition theory

This weak link has led a number of community ecologists to carry out studies on competition that do not rely on the existence of current competition. The approach has been first to predict what a community *should* look like if interspecific competition was shaping it or had shaped it in the past, and then to examine real communities to see whether they conform to these predictions.

The predictions themselves emerge readily from conventional competition theory (see Chapter 8).

1. Potential competitors that coexist in a community should, at the very least, exhibit niche differentiation (see Section 19.2.3).
2. This niche differentiation will often manifest itself as morphological differentiation (see Section 19.2.4).
3. Within any one community, potential competitors with little or no niche differentiation would be unlikely to coexist. Their distributions in space should therefore be negatively associated: each should tend to occur only where the other is absent (see Section 19.2.5).

In the following sections, we will discuss studies that deal with the documentation of patterns consistent with a role for competition in structuring communities.

19.2.3 Evidence from community patterns: niche differentiation

The various types of niche differentiation in animals and plants were outlined in Chapter 8. On the one hand, resources may be utilized differentially. This may express itself directly within a single habitat, or as a difference in microhabitat, geographic distribution or temporal appearance if the resources are themselves separated spatially or temporally. Alternatively, species and their competitive abilities may differ in their responses to environmental conditions. This too can express itself as either microhabitat, geographic or temporal differentiation, depending on the manner in which the conditions themselves vary.

19.2.3.1 Niche complementarity

evidence from community patterns . . .

. . . in anemone fishes in Papua New Guinea, . . .

In one study of niche differentiation and coexistence, a number of species of anemone fish were examined near Madang in Papua New Guinea (Elliott & Mariscal, 2001). This region has the highest reported species richness of both anemone fishes (nine) and their host anemones (10). Each individual anemone is typically occupied by individuals of just one species of anemone fish because the residents aggressively exclude intruders (although aggressive interactions are less frequently observed between anemone fish of very different sizes). Anemones seem to be a limiting resource for the fishes because almost all the anemones were occupied, and when some were transplanted to new sites they were quickly colonized and the abundance of adult fish increased. Surveys at three replicate reef sites in four zones (nearshore, mid-lagoon, outer barrier reef and offshore: Figure 19.3a) showed that each anemone fish was primarily associated with a particular species of anemone and each showed a characteristic preference for a particular zone (Figure 19.3b). Different anemone fish that lived with the same anemone were typically associated with different zones. Thus, *Amphiprion percula* occupied the anemone *Heteractis magnifica* in nearshore zones, while *A. perideraion* occupied *H. magnifica* in offshore zones. Elliott and Mariscal concluded that coexistence of the nine anemone fishes on the limited anemone resource was possible because of the differentiation of their niches, together with the ability of small anemone fish species (*A. sandaracinos* and *A.*

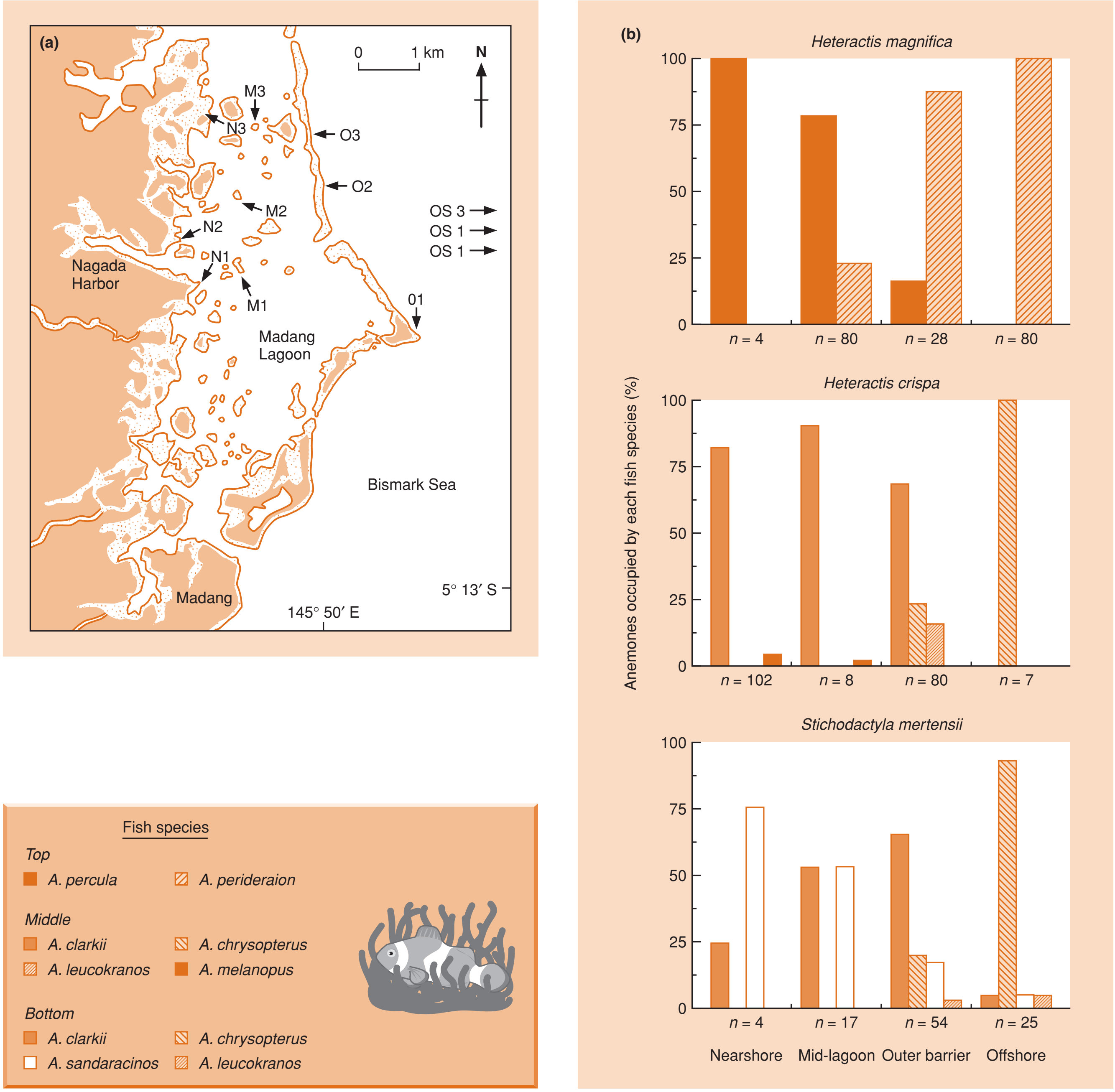


Figure 19.3 (a) Map showing the location of three replicate study sites in each of four zones within and outside Madang Lagoon (N, nearshore; M, mid-lagoon; O, outer barrier reef; OS, offshore reef). The white areas indicate water, heavy stippling represents coral reef and light stippling represents land. (b) The percentage of three common species of anenome (*Heteractis magnifica*, *H. crispa* and *Stichodactyla mertensii*) occupied by different anemone fish species (*Amphiprion* spp., in key on left) in each of four zones. The number of anenomes censused in each zone is shown by *n*. (After Elliott & Mariscal, 2001.)

leucokranos) to cohabit the same anemone with larger species. The pattern is consistent with what would be expected of communities molded by competition (specifically predictions 1 and 3 above).

Two further points, illustrated by the anemone fish, are worth highlighting. First, they can be considered to be a guild, in that they are a group of species that exploit the same class of environmental resources in a similar way (Root, 1967). If interspecific competition is to occur at all, or if it has occurred in the past, then it will be most likely to occur, or to have occurred, within guilds. But this does *not* mean that guild members necessarily compete or have necessarily competed: the onus is on ecologists to demonstrate that this is the case.

The second point about the anemone fish is that they demonstrate *niche complementarity*. That is, within the guild as a whole, niche differentiation involves several niche dimensions, and species that occupy a similar position along one dimension (anemone species used) tend to differ along another dimension (zone occupied). Complementary differentiation along several dimensions has also been reported for guilds as diverse as lizards (Schoener, 1974), bumblebees (Pyke, 1982), bats (McKenzie & Rolfe, 1986), rainforest carnivores (Ray & Sunquist, 2001) and tropical trees (Davies *et al.*, 1998), as described next.

19.2.3.2 Niche differentiation in space

. . . in trees in Borneo, . . .

Trees vary in their capacity to use resources such as light, water and nutrients. A study in Borneo of 11 tree species in the genus *Macaranga* showed marked differentiation in light requirements, from extremely high light-demanding species such as *M. gigantea* to shade-tolerant species such as *M. kingii* (Figure 19.4a). The average light levels intercepted by the crowns of these trees tended to increase as they grew larger, but the ranking of the species did not change. The shade-tolerant species were smaller (Figure 19.4b) and persisted in the understory, rarely establishing in disturbed microsites (e.g. *M. kingii*), in contrast to some of the larger, high-light species that are pioneers of large forest gaps (e.g. *M. gigantea*). Others were associated with intermediate light levels and can be considered small gap specialists (e.g. *M. trachyphylla*). The *Macaranga* species were also differentiated along a second niche gradient, with some species being more common on clay-rich soils and others on sand-rich soils (Figure 19.4b). This differentiation may be based on nutrient availability (generally higher in clay soils) and/or soil moisture availability (possibly lower in the clay soils because of thinner root mats and humus layers). As with the anemone fish, there is evidence of niche complementarity among the *Macaranga* species. Thus, species with similar light requirements differed in terms of preferred soil textures, especially in the case of the shade-tolerant species.

The apparent niche partitioning by *Macaranga* species was partly related to horizontal heterogeneity in resources (light levels in relation to gap size, distribution of soil types) and partly to vertical heterogeneity (height achieved, depth of root mat).

Ectomycorrhizal fungi have also been shown to exploit resources differentially in the vertical plane in the floor of a pine (*Pinus resinosa*) forest. Until recently, it was not possible to study the *in situ* distribution of ectomycorrhizal hyphae, but now DNA analyses allow the identification of putative species (even in the absence of species names) and permit their distributions to be compared. The forest soil had a well-developed litter layer above a fermentation layer (the F layer) and a thin humified layer (the H layer), with mineral soil beneath (the B horizon). Of the 26 species separated by the DNA analysis, some were very largely restricted to the litter layer (group A in Figure 19.5), others to the F layer (group D), the H layer (group E) or the B horizon (group F). The remaining species were more general in their distributions (groups B and C).

19.2.3.3 Niche differentiation in time

. . . in preying mantids in North America . . .

Intense competition may, in theory, be avoided by partitioning resources in horizontal or vertical space, as in the examples above, *or* in time (Kronfeld-Schor & Dayan, 2003), for example, by a staggering of life cycles through the year. It is notable that two species of mantids, which feature as predators in many parts of the world, commonly coexist both in Asia and North America. *Tenodera sinensis* and *Mantis religiosa* have life cycles that are 2–3 weeks out of phase. To test the hypothesis that this asynchrony serves to reduce interspecific competition, the timing of their egg hatch was experimentally synchronized in replicated field enclosures (Hurd & Eisenberg, 1990). *T. sinensis*, which normally hatches earlier, was unaffected by *M. religiosa*. In contrast, the survival and body size of *M. religiosa* declined in the presence of *T. sinensis*. Because these mantids are both competitors for shared resources and predators of each other, the outcome of this experiment probably reflects a complex interaction between the two processes.

. . . and in tundra plants in Alaska

In plants too, resources may be partitioned in time. Thus, tundra plants growing in nitrogen-limited conditions in Alaska were differentiated in their timing of nitrogen uptake, as well as the soil depth from which it was extracted and the chemical form of nitrogen used. To trace how tundra species differed in their uptake of different nitrogen sources, McKane *et al.* (2002) injected three chemical forms labeled with the rare isotope ^{15}N (inorganic ammonium, nitrate and organic glycine) at two soil depths (3 and 8 cm) on two occasions (June 24 and August 7) in a $3 \times 2 \times 2$ factorial design. Concentration of the ^{15}N tracer was measured in each of five common tundra plants in 3–6 replicates of each treatment 7 days after application. The five plants proved to be well differentiated in their use of nitrogen sources (Figure 19.6). Cottongrass (*Eriophorum vaginatum*) and the cranberry bush (*Vaccinium vitis-idaea*) both relied on a combination of glycine and ammonium, but cranberry obtained more of these forms early in the growing season and at a shallower depth than cottongrass. The evergreen shrub *Ledum palustre* and the dwarf birch (*Betula nana*) used mainly ammonium but *L. palustre* obtained more of this form early in the season while the birch exploited it later. Finally, the grass *Carex bigelowii* was the only species to use mainly nitrate. Here, niche complementarity can be seen along three niche dimensions and differences in timing of use may help explain the coexistence of these species on a limited resource.

19.2.3.4 Niche differentiation – apparent or real? Null models

the aim of demonstrating that patterns are not generated merely by chance

Many cases of apparent resource partitioning have been reported. It is likely, however, that studies failing to detect such differentiation have tended to go unpublished. It is always possible, of course, that these 'unsuccessful' studies are flawed and incomplete, and that they have failed to deal with the relevant niche dimensions; but a number have been sufficiently beyond reproach to raise the possibility that in certain groups resource partitioning is not an important feature. Strong (1982) studied a group of hispine beetles (Chrysomelidae) that commonly coexist as adults in the rolled leaves of *Heliconia* plants. These long-lived tropical beetles are closely related, eat the same food and occupy the same habitat. They would appear to be good candidates for demonstrating resource partitioning. Yet, Strong could find no evidence of segregation, except in the case of just one of the 13 species studied, which was segregated weakly from a number of others. The beetles lack any aggressive behavior, either within or between species; their host specificity does not change as a function of co-occupancy of leaves with other species that might be competitors; and the levels of food and habitat are commonly not limiting for these beetles, which suffer heavily from parasitism and predation. In these species, resource partitioning associated with interspecific competition does not appear to structure the community. As we have seen, this may well be true of many phytophagous insect communities. Plant

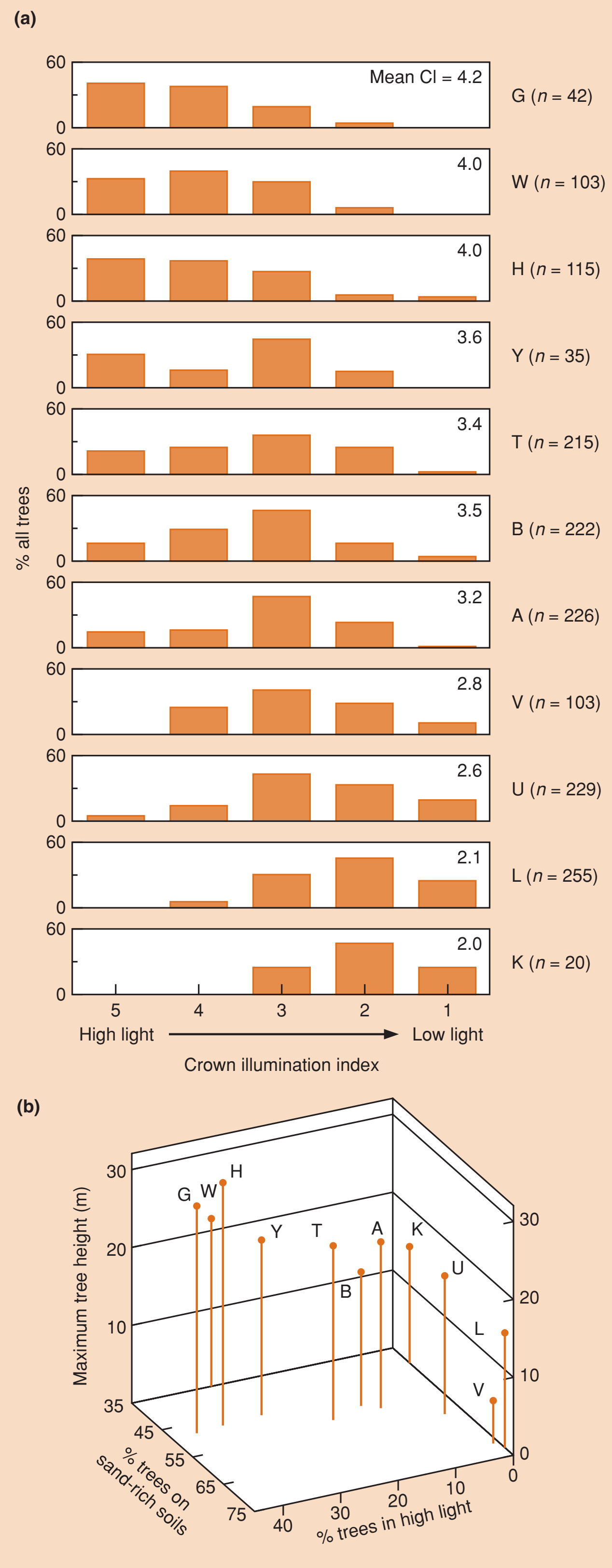


Figure 19.4 (*right*) (a) Percentage of individuals in each of five crown illumination classes for 11 *Macaranga* species (sample sizes in parentheses). (b) Three-dimensional distribution of the 11 species with respect to maximum height, the proportion of stems in high light levels (class 5 in (a)) and proportion of stems in sand-rich soils. Each species of *Macaranga* is denoted by a single letter: G, *gigantean*; W, *winkleri*; H, *hosei*; Y, *hypoleuca*; T, *triloba*; B, *beccariana*; A, *trachyphylla*; K, *kingii*; U, *hullettii*; V, *havilandii*; L, *lamellata*. (After Davies *et al.*, 1998.)

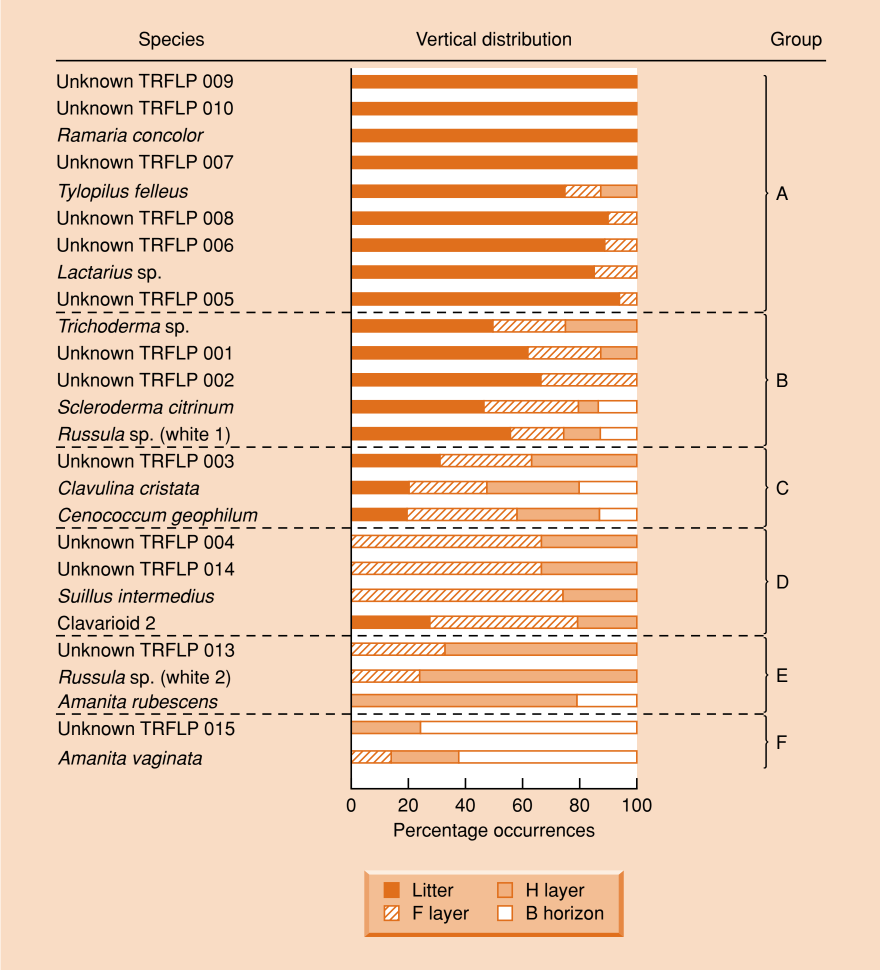


Figure 19.5 The vertical distribution of 26 ectomycorrhizal fungal species in the floor of a pine forest determined by DNA analysis. Most have not been named formally but are shown as a code (TRFLP, terminal restriction fragment length polymorphism). The vertical distribution histograms show the percentage of occurrences of each species in litter, the F layer, the H layer and the B horizon. (After Dickie *et al.*, 2002.)

studies involving taxa as diverse as phytoplankton (see Figure 19.1) and trees (Brokaw & Busing, 2000) have similarly failed to provide evidence consistent with a strong role for niche partitioning in promoting coexistence and species diversity. Whilst patterns consistent with a niche differentiation hypothesis are reasonably widespread, they are by no means universal.

null hypotheses are intended to ensure statistical rigor

Moreover, a number of workers, notably Simberloff and Strong, have criticized what they see as a tendency to interpret 'mere differences' as confirming the importance of interspecific competition. Such reports beg the question of whether the differences are large enough or regular enough to be different from what might be found at random among a set of species. This problem led to an approach known as *null model analysis* (Gotelli, 2001). Null models are models of actual communities that retain certain of the characteristics of their real counterparts, but reassemble the components at random, specifically excluding the consequences of biological interactions. In fact, such analyses are attempts to follow a much more general approach to scientific investigation, namely the construction and testing of *null hypotheses*. The idea (familiar to most readers in a statistical context) is that the data are rearranged into a form (the null model) representing what the data would look like in the absence of the phenomenon under investigation (in this case species interactions, particularly interspecific competition). Then, if the actual data show a significant statistical difference from the null hypothesis, the null hypothesis is rejected and the action of the phenomenon under investigation is strongly inferred. Rejecting (or falsifying) the absence of an effect is reckoned to be better than confirming its presence, because there are well-established statistical methods for testing whether things are significantly different (allowing falsification) but none for testing whether things are 'significantly similar'.

a null model of food resource use in lizard communities . . .

Lawlor (1980) looked at 10 North American lizard communities, consisting of 4–9 species, for which he had estimates of the amounts of each of

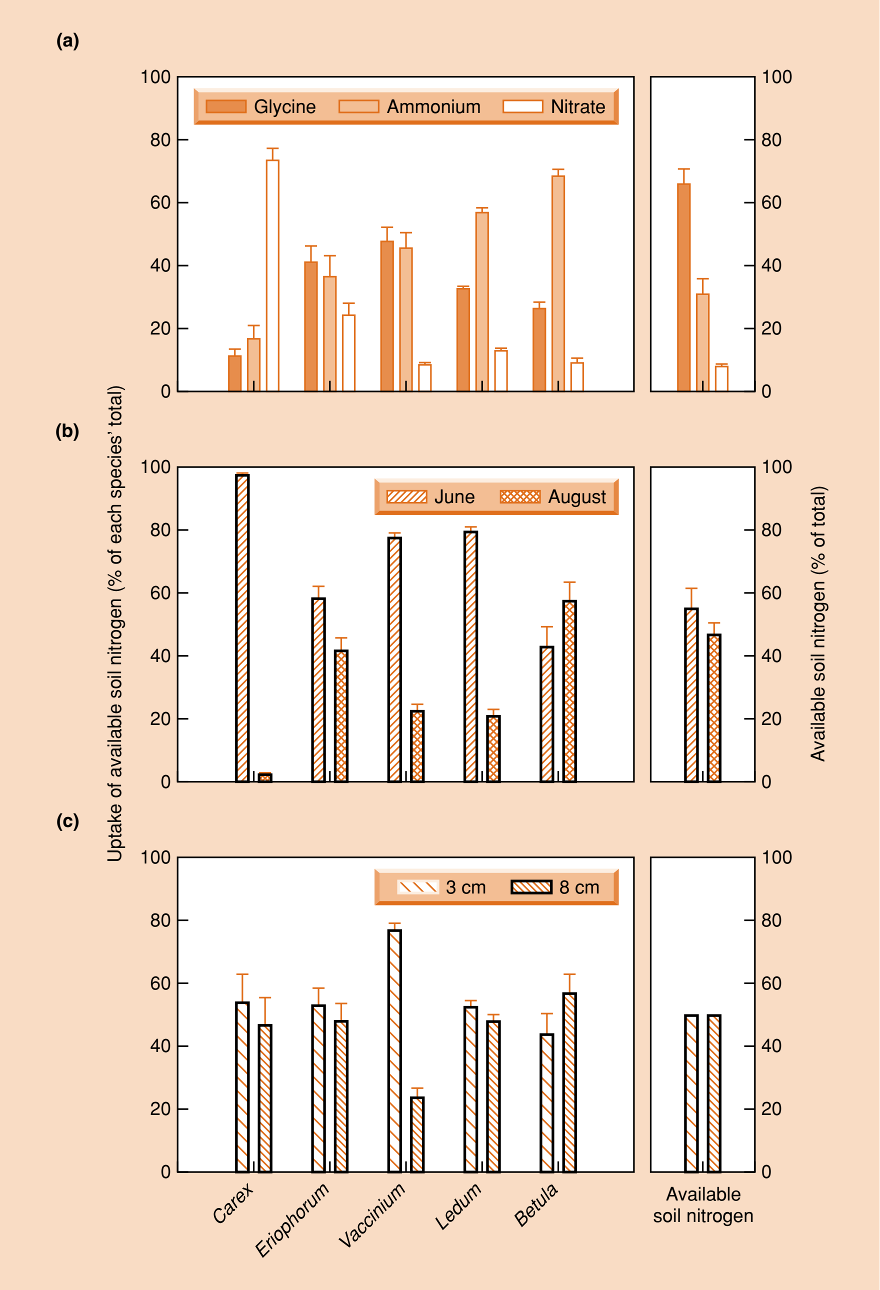


Figure 19.6 Mean uptake of available soil nitrogen (± SE) in terms of (a) chemical form, (b) timing of uptake and (c) depth of uptake by the five most common species in tussock tundra in Alaska. Data are expressed as the percentage of each species' total uptake (left panels) or as the percentage of the total pool of nitrogen available in the soil (right panels). (After McKane *et al.*, 2002.)

20 food categories consumed by each species in each community (data from Pianka, 1973). A number of null models of these communities were created (see below), which were then compared with their real counterparts in terms of their patterns of overlap in resource use. If competition is or has been a significant force in determining community structure, the niches should be spaced out, and overlap in resource use in the real communities should be less than predicted by the null models.

Lawlor's analysis was based on the 'electivities' of the consumer species, where the electivity of species *i* for resource *k* was the proportion of the diet of species *i* which consisted of resource *k*. Electivities therefore ranged from 0 to 1. These electivities were in turn used to calculate, for each pair of species in a community, an index of resource-use overlap, which itself varied between 0 (no overlap) and 1 (complete overlap). Finally, each community was characterized by a single value: the mean resource overlap for all pairs of species present.

. . . based on four 'reorganization algorithms'

The null models were of four types, generated by four 'reorganization algorithms' (RA1–RA4, Figure 19.7). Each retained a different aspect of the structure of the original community whilst randomizing the remaining aspects of resource use.

RA1 retained the minimum amount of original community structure. Only the original number of species and the original number of resource categories were retained. Observed electivities (including zeros) were replaced in every case by random values between 0 and 1. This meant that there were far fewer zeros than in the original community. The niche breadth of each species was therefore increased.

RA2 replaced all electivities, *except zeros*, with random values. Thus, the qualitative degree of specialization of each consumer was retained (i.e. the number of resources consumed to any extent by each species was correct).

RA3 retained not only the original qualitative degree of specialization but also the original consumer niche breadths. No randomly generated electivities were used. Instead, the original sets of values were rearranged. In other words, for each consumer, all electivities, both zeros and non-zeros, were randomly reassigned to the different resource types.

RA4 reassigned only the non-zero electivities. Of all the algorithms, this one retained most of the original community structure.

Each of the four algorithms was applied to each of the 10 communities. In every one of these 40 cases, 100 'null model' communities were generated and the corresponding 100 mean values of resource overlap were calculated. If competition were important in the real community, these mean overlaps should exceed the real community value. The real community was therefore considered to have a *significantly* lower mean overlap than the null model ($P < 0.05$) if five or fewer of the 100 simulations gave mean overlaps less than the real value.

the lizards appear to pass the test . . .

The results are shown in Figure 19.7. Increasing the niche breadths of all consumers (RA1) resulted in the highest mean overlaps (significantly higher than the real communities). Rearranging the observed non-zero electivities (RA2 and RA4) also always resulted in mean overlaps

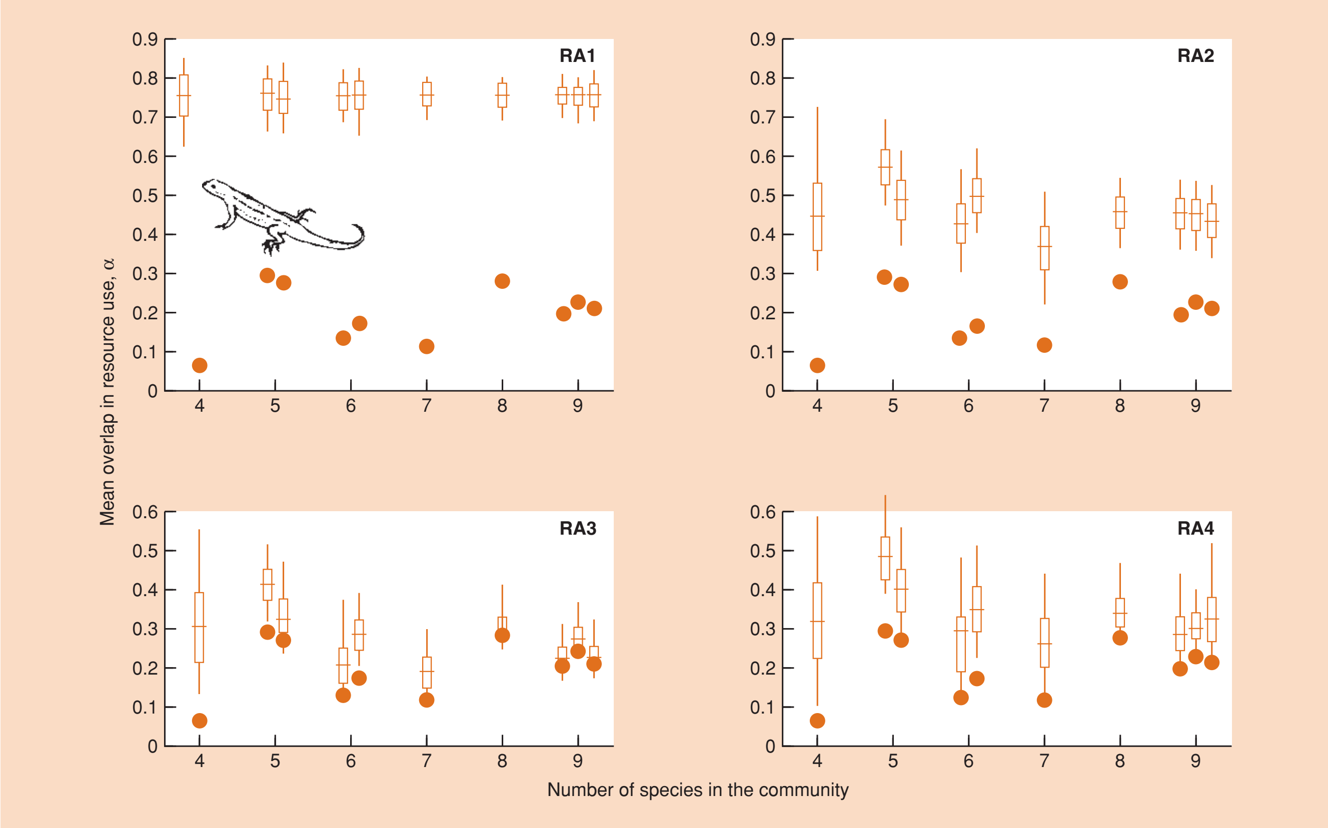


Figure 19.7 The mean indices of resource-use overlap for each of Pianka's (1973) 10 North American lizard communities are shown as solid circles. These can be compared, in each case, with the mean (horizontal line), standard deviation (vertical rectangle) and range (vertical line) of mean overlap values for the corresponding set of 100 randomly constructed communities. The analysis was performed using four different reorganization algorithms (RAs), as described in the text. (After Lawlor, 1980.)

that were significantly higher than those actually observed. With RA3, on the other hand, where all electivities were reassigned, the differences were not always significant. But in all communities, the algorithm mean was higher than the observed mean. In the case of these lizard communities, therefore, the observed low overlaps in resource use suggest that the niches are segregated, and that interspecific competition plays an important role in community structure.

. . . whereas grassland ants do not

A study similar to that in Figure 19.7 concerned spatial and temporal niche partitioning in grassland ant communities in Oklahoma (Albrecht & Gotelli, 2001). In this case, there was little evidence of niche partitioning on a seasonal basis. However, on a smaller spatial scale, at individual bating stations there was significantly less spatial niche overlap than expected by chance. This pattern of results – sometimes a role for competition is confirmed, sometimes not – has been the general conclusion from the null model approach.

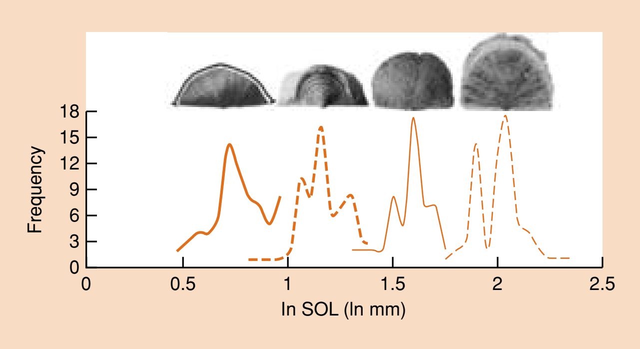


Figure 19.8 Distributions of strophomenide body outline length (SOL) of samples of four coexisting species of strophomenide brachiopods collected from a late Ordovician (*c.* 448–438 million years before present) marine sediment in Indiana, USA. The species shown, from left to right, are *Eochonetes clarksvillensis*, *Leptaena richmondensis*, *Strophomena planumbona* and *Rafinesquina alternata*. (After Hermoyian *et al.*, 2002.)

19.2.4 Evidence from morphological patterns

Hutchinson's 'rule' about size ratios of coexisting species applied to brachiopods

Where niche differentiation is manifested as morphological differentiation, the spacing out of niches can be expected to have its counterpart in regularity in the degree of morphological difference between species belonging to a guild. Specifically, a common feature claimed for animal guilds that appear to segregate strongly along a single-resource dimension is that adjacent species tend to exhibit regular differences in body size or in the size of feeding structures. Hutchinson (1959) was the first to catalog many examples, drawn from vertebrates and invertebrates, of sequences of potential competitors in which average individuals from adjacent species had weight ratios of approximately 2.0 or length ratios of approximately 1.3 (the cube root of 2.0). This 'rule' also seems to hold approximately for guilds as different as coexisting cuckoo-doves (mean body weight ratio of 1.9; Diamond, 1975), bumblebees (mean proboscis length ratio for worker bees of 1.32; Pyke, 1982), weasels (mean canine diameter ratio of between 1.23 and 1.50; Dayan *et al.*, 1989) and even fossil brachiopods (between 1.48 and 1.57 for body outline length, an index of the size of the brachiopod's feeding organ; Hermoyian *et al.*, 2002). Models of competition do not predict specific values for size ratios that might apply across a range of organisms and environments, and whether the apparent regularity is an empirical quirk usually remains to be determined. In the case of the brachiopod community (Figure 19.8), however, Hermoyian *et al.* (2002) built 100,000 null models that each drew four species at random from the complete strophomenide brachiopod fossil fauna (74 taxa) and calculated size ratios between adjacent species. On the basis of their results, they rejected the null hypothesis ($P < 0.03$) that the observed ratios could have arisen from randomly selected taxa, supporting the hypothesis of limiting similarity.

are extinctions more likely for very similar competitors?

If interspecific competition does in fact shape a community, it will often do so through a process of selective extinction. Species that are too similar will simply fail to persist together. The detailed records of ornithologists from the six main Hawaiian islands during the period 1860–1980 allowed Moulton and Pimm (1986) to estimate, at least to the nearest decade, when each species of passerine bird was introduced and if and when it became extinct. In the records, overall, there were 18 pairs of congeneric species present at the same time on the same island. Of these, six pairs persisted together; in nine cases one species became extinct; and in three cases both species died out (the last category was ignored in the analysis because the outcome is not compatible with pairwise competitive exclusion). In cases where one species became extinct the species pair was morphologically more similar than in cases where both species persisted: the average percentage difference in bill length was 9 and 22%, respectively. This statistically significant result is consistent with the competition hypothesis.

Moulton and Pimm's approach was informative because it invoked historical data, providing a glimpse of the elusive workings of the 'ghost of competition past'. An evolutionary perspective has been even more explicitly incorporated by the use of 'cladistic analysis', which allows us to reconstruct phylogenies (evolutionary trees) based on similarities and differences between species in their DNA molecules and/or in morphological (or other biologically meaningful) characteristics.

Figure 19.9 Phylogenies of lizards in the genus *Anolis* (a) on Puerto Rico and (b) on Jamaica. For each species, size (snout–vent length, mm) and ecomorph are shown: cg, crown-giant; gb, grass–bush; tc, trunk–crown; tg, trunk–ground; tw, twig. (After Losos, 1992.)

evidence from the divergent evolution of lizards on islands

The results of such an analysis of the *Anolis* lizards of Puerto Rico (Figure 19.9a) are consistent with the hypothesis of divergent evolution in body size (Losos, 1992). The two-species stage in evolution (the first, lowermost node in Figure 19.9a) was composed of species with markedly different snout–vent lengths (SVL – a standard index of size for lizards) of approximately 38 and 64 mm (*A. occultus* and the ancestor of all the remaining types, respectively) whilst sizes at the three-species stage (the next node) were 38, 64 and 127 mm. In Jamaica, on the other hand (Figure 19.9b), no such pattern is observed; the two- and three-species stages were composed of species of similar size (61 and 73 mm, then 57, 61 and 73 mm SVL). However, the phylogenies of the two islands show remarkable consistency when viewed from the point of view of patterns in 'ecomorphs' – each distinct in morphology, ecology and behavior. On both islands, the two-morph stage was composed of a short-legged twig ecomorph, which crawls slowly on narrow supports on the periphery of trees, and a generalist ancestral species. At the three-morph stage, too, both islands possessed the same assembly – a twig ecomorph, one specialized at foraging in the tree crown and a trunk–ground type, the latter being robust and long-legged and using its jumping and running abilities to forage on the ground. At the four-morph stage the patterns were again identical, each having added a trunk–crown type. Only at the five-morph stage was there a difference – the grass–bush morph was the last to evolve on Puerto Rico, but its counterpart has never appeared on Jamaica (Figure 19.10). Note that on each island a morph usually consists of a single species of *Anolis*, but Puerto Rico has several trunk–ground and grass–bush species. This phylogenetic analysis is consistent with the hypothesis that the faunal assembly on both Puerto Rico and Jamaica has occurred via sequential microhabitat partitioning, with morphological differences perhaps being related to differences in microhabitat utilization. Extending this work to further islands, Losos *et al.* (1998) confirmed that adaptive radiation in similar environments can produce strikingly similar evolutionary outcomes.

19.2.5 Evidence from negatively associated distributions

evidence from 'checkerboard' distributions in . . . . . . island birds . . .

A number of studies have used patterns in distribution as evidence for the importance of interspecific competition. Foremost amongst these is Diamond's (1975) survey of the land birds living on the islands of the Bismarck Archipelago off the coast of New Guinea. The most striking evidence comes from distributions that Diamond refers to as 'checkerboard'. In these, two or more ecologically similar species (i.e. members of the same guild) have mutually exclusive but interdigitating distributions such that any one island supports only one of the species (or none at all). Figure 19.11 shows this for two small, ecologically similar cuckoo-dove species: *Macropygia mackinlayi* and *M. nigrirostris*.

A null model approach to the analysis of distributional differences involves comparing the pattern of species co-occurrences at a suite of locations with that which would be expected by chance. An excess of negative associations would then be consistent with a role for competition in determining community structure.

. . . and native and exotic plants on islands in a lake

Thorough censuses of both native and exotic (introduced) plants occurring on 23 small islands in Lake Manapouri in the South Island of New Zealand (Wilson, 1988b), were the basis for computing a standard index of association for every pair of species:

$$d_{ik} = (O_{ik} - E_{ik})/\mathrm{SD}_{ik} \tag{19.1}$$

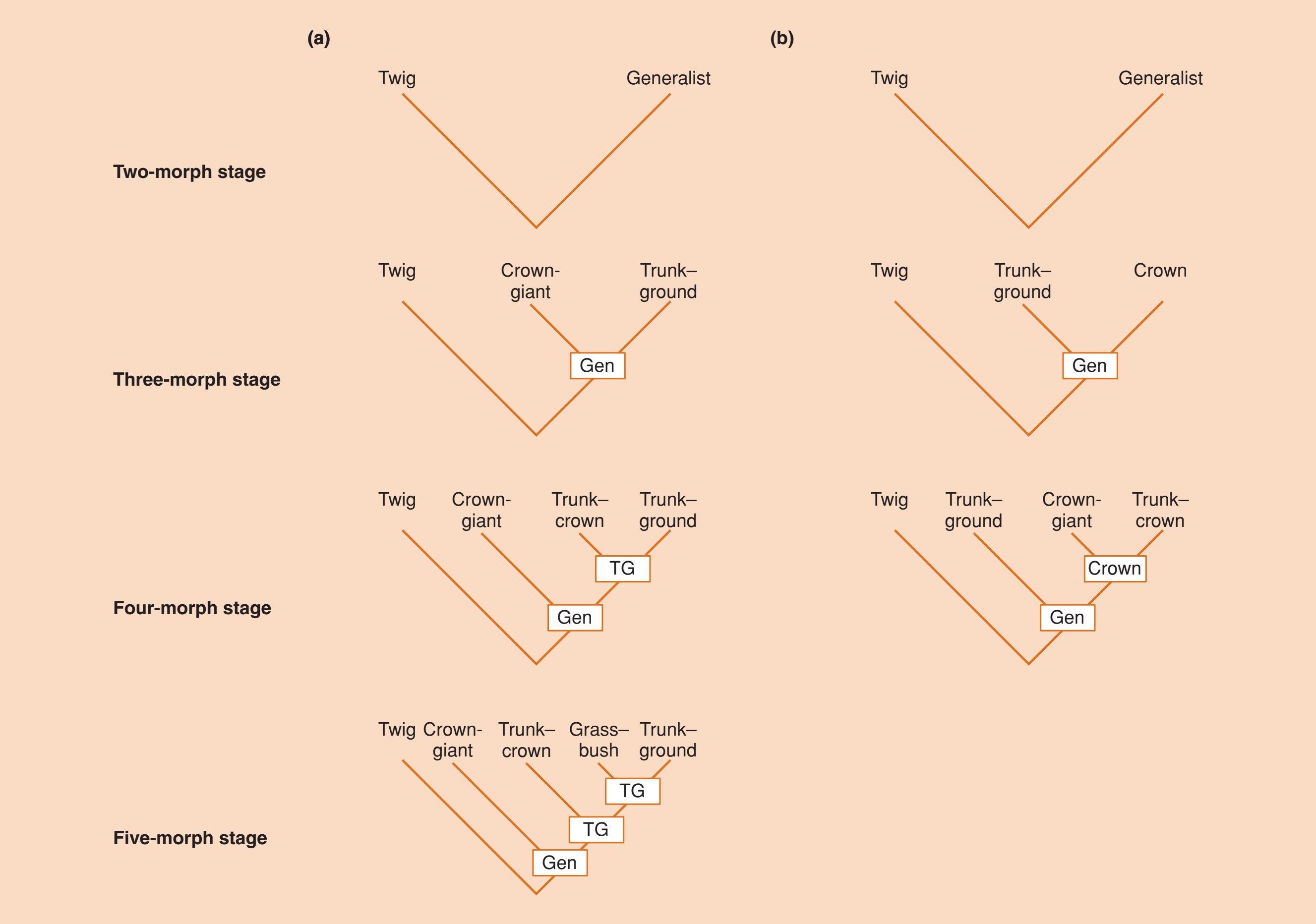


Figure 19.10 The evolution of *Anolis* communities (a) on Puerto Rico and (b) on Jamaica for two-, three-, four- and, in the case of Puerto Rico, five-ecomorph communities. Labels at nodes in the trees are the estimated ecological characteristics of the ancestors. (After Losos, 1992.)

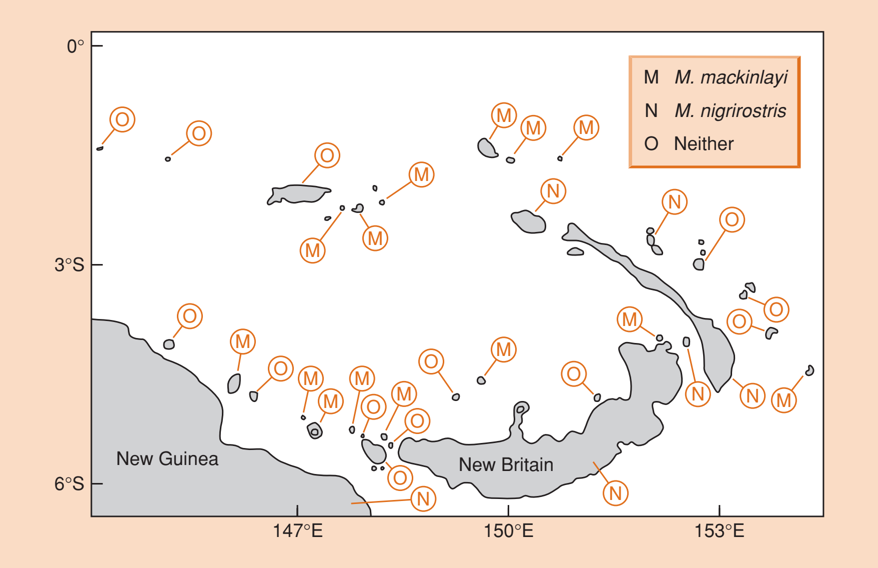


Figure 19.11 Checkerboard distribution of two small *Macropygia* cuckoo-dove species in the Bismarck region. Islands whose pigeon faunas are known are designated as M (*M. mackinlayi* resident), N (*M. nigrirostris* resident) or O (neither species resident). Note that most islands have one of these species, no island has both and some islands have neither. (After Diamond, 1975.)

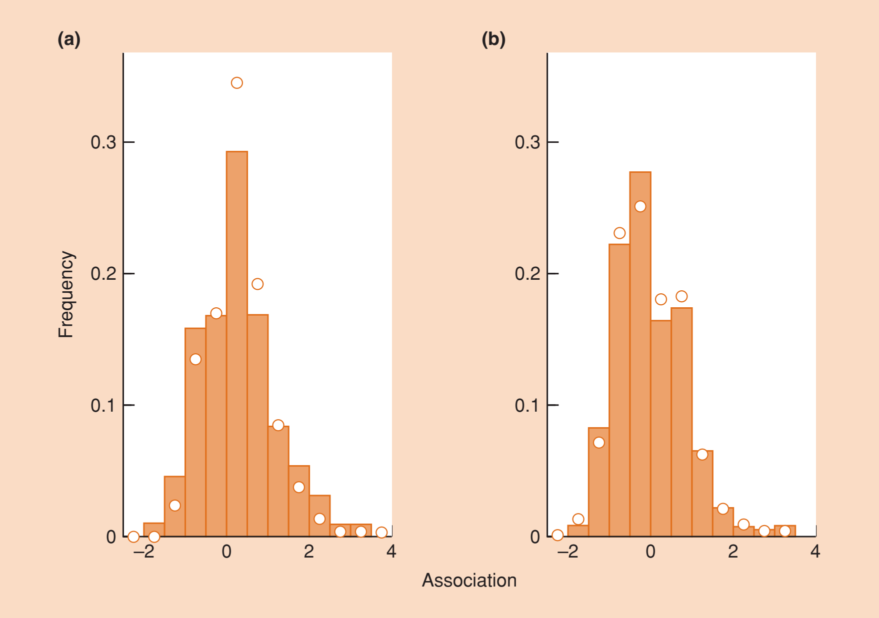


Figure 19.12 A comparison between the observed values of association between pairs of (a) native plant species and (b) exotic plant species on islands in Lake Manapouri (histograms), and the distributions expected on the basis of a neutral model (○). (After Wilson, 1988b.)

where d_{ik} is the difference between the observed (O_{ik}) and the expected (E_{ik}) number of islands shared by species i and k, expressed in terms of the standard deviation of the expected number (SD_{ik}).

The resulting sets of association values for the real communities of native and exotic species are presented as histograms in Figure 19.12. These can be compared with null model communities in which island species richnesses and species frequencies of occurrence were fixed at those observed, but species occurrences on islands were randomized (Wilson, 1987). One thousand randomizations were performed, yielding a mean frequency in each d_{ik} category (the circles in Figure 19.12). The analysis of native plants showed an excess of negative associations (highly statistically significant for the bottom four categories) and of positive associations (highly significant for the top five categories), with a corresponding deficit of associations near zero. In contrast, the analysis of exotic plants showed no significant departure from the null model.

In the case of native species, the excess of negative associations is consistent with the action of competitive exclusion, and this is particularly likely for the woody species. However, we cannot rule out an explanation based on a tendency of particular pairs of species to occur in different habitats, which themselves are not represented on every island (Wilson, 1988b). The most likely explanation for the excess of positive associations amongst native plants is a tendency for certain species to occur in the same habitats. The agreement of exotic species with the null model may reflect their generally weedy status and effective colonization abilities, or it may indicate that the exotics have not yet reached an equilibrium distribution (Wilson, 1988b).

The number of checkerboard pairs in a community can be readily calculated by counting the number of unique pairs of species that never co-occur. A less strict version of Diamond's assembly rule that 'some pairs of species never coexist' can be assessed using the C score of Stone and Roberts (1990). This index also measures the degree to which species co-occur but does not require perfect segregation between species. The C score is calculated for each pair of species as $(R_i - S)(R_j - S)$ where R_i and R_j are the number of sites where species i and j occur, and S is the number of sites in which both species co-occur. This score is then averaged over all possible pairs of species in the matrix. For a community structured by competitive interactions, the number of checkerboard pairs should be greater and the C score should be larger than expected by chance.

comparison of taxonomic groups

Gotelli and McCabe (2002) checked the generality of negatively associated distributions (in support of a structuring role for competition) in a meta-analysis of various taxonomic groups in 96 data sets that reported the distribution of species assemblages across sets of replicated sites. For every real data set, 1000 randomized versions were prepared and an index of association d_{ik} was computed (as in Wilson, 1988b) but Gotelli and McCabe called this index the standardized effect size (SES). The results of this analysis for all 96 data sets together support the predictions that the C score and the number of checkerboard pairs should be larger than expected by chance (Figure 19.13a, b). The null hypothesis in each case is that the mean SES should be zero (real communities not different from simulated communities) and that 95% of the values should lie between −2.0 and +2.0. The null hypothesis can be rejected in both cases. Figure 19.13c shows that

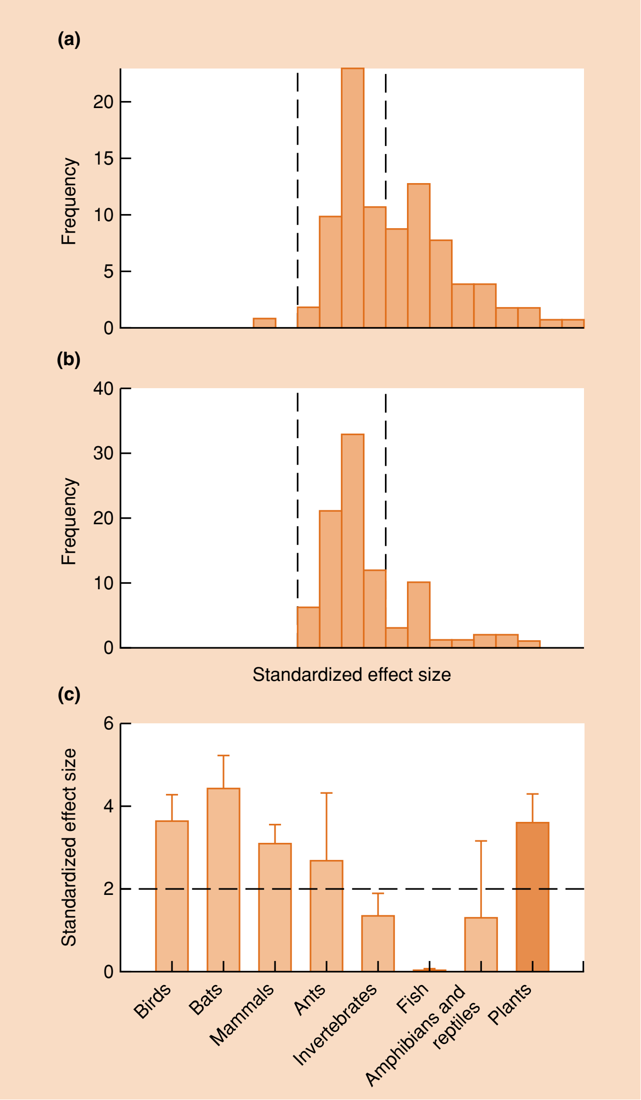


Figure 19.13 Frequency histograms for standardized effect sizes measured for 96 presence–absence matrices taken from the literature in the case of (a) the C score and (b) the number of species pairs forming perfect checkerboard distributions. (c) Standardized effect sizes for the C score for different taxonomic groups. The dashed line indicates an effects size of 2.0, which is the approximate 5% significance level. (After Gotelli & McCabe, 2002.)

plants and homeothermic vertebrates tend to have higher SESs for the C score, indicating stronger tendencies towards negative species associations than the poikilotherms have (invertebrates, fish and reptiles), with the exception of ants.

Gotelli and McCabe (2002) do not go so far as to claim they have performed a definitive test of the role of competition. They note that some species may exhibit 'habitat checkerboards' because they have affinities to nonoverlapping habitats. Others may reveal 'historical checkerboards', co-occurring infrequently because of restricted dispersal since allopatric speciation (i.e. having speciated in different places). However, these results add further weight to a widespread role for competition in structuring communities.

19.2.6 Appraisal of the role of competition

We can now draw a number of conclusions about the evidence for competition discussed in this section.

1. Interspecific competition is a possible and indeed a plausible explanation for many aspects of the organization of many communities – but it is not often a proven explanation.
2. One of the main reasons for this is that active, current competition has been studied and demonstrated in only a small number of communities. Its actual prevalence overall can be judged only imperfectly from the results and considerations discussed above.
3. As an alternative to current competition, the ghost of competition past can always be invoked to account for present-day patterns. But it can be invoked so easily because it is impossible to observe directly and therefore is difficult to disprove.
4. The communities chosen for study may not be typical. The ecologists observing them have usually been specifically interested in competition, and they may have selected appropriate, 'interesting' systems. Studies that fail to show niche differentiation may often have been considered 'unsuccessful' and are likely to have gone largely unreported.
5. The community patterns uncovered, even where they appear to support the competition hypothesis, often have alternative explanations. For example, species that have negatively associated distributions may have recently speciated allopatrically, and their distributions may still be expanding into one another's ranges.
6. The recurring alternative explanation to competition as the cause of community patterns is that these have arisen simply by chance. Niche differentiation may occur because the various species have evolved independently into specialists, and their specialized niches happen to be different. Even niches arranged along a resource dimension at random are bound to differ to some extent. Similarly, species may differ in their distribution because each has been able, independently, to colonize and establish itself in only a small proportion of the habitats that are suitable for it. Ten blue and 10 red balls thrown at random into 100 boxes are almost certain to end up with different distributions. Hence, competition cannot be inferred from mere 'differences' alone. But, what sorts of differences *do* allow the action of competition to be inferred? This is the domain of the null model approach.

7 The aim of the null model approach, whether applied to niche differentiation, morphological patterns or negatively associated distribution patterns, is undoubtedly worthy. We need to guard against the temptation to see competition in a community simply because we are looking for it. On the other hand, the approach is bound to be of limited use unless it is applied to groups (usually guilds) within which competition may be expected. In its favor, the null model approach concentrates the minds of investigators, and it can stop them from jumping to conclusions too readily. Ultimately, though, it can never take the place of a detailed understanding of the field ecology of the species in question, or of manipulative experiments designed to reveal competition by increasing or reducing species abundances (Law & Watkinson, 1989). It can only be part of the community ecologist's armory.

8 Interspecific competition is certain to vary in importance from community to community: it has no single, general role. For example, it appears frequently to be important in vertebrate communities, particularly those of stable, species-rich environments, and in communities dominated by sessile organisms such as plants and corals; whilst, for example, in some phytophagous insect communities it is less often important. A challenge for the future is to understand why some guilds show evidence for a role for competition, such as regularity in size ratios, whilst others do not (Hopf *et al.*, 1993).

9 Finally, we should not lose sight of the fact that community organization in field studies is almost certain to be influenced by more than one kind of population interaction; for example the anenome fish (see Section 19.2.3.1) and ectomycorrhizal fungal cases (see Section 19.2.3.2) both involved mutualism as well as competition, and the mantids in Section 19.2.3.3 were intraguild predators as well as competitors. The interaction between predation and competition can be particularly influential, as we shall see in Section 19.4.

19.3 Equilibrium and nonequilibrium views of community organization

It is possible to conceive of a world with just one species of plant (or herbivore) with supreme performance over an enormous range of tolerance. In this scenario the most competitive species (the one that is most efficient at converting limited resources into descendants) would be expected to drive all less competitive species to extinction. The species richness we witness in real communities is a clear demonstration of the failure of evolution to produce such supreme species. An extension of this competitive argument holds that diversity can be explained through a partitioning of resources amongst competing species whose requirements do not overlap completely, as discussed in detail in Section 19.2. However, this argument rests on two assumptions that are not necessarily always valid.

The first assumption is that the organisms are actually competing, which in turn implies that resources are limiting. But there are many situations where physical disturbances, such as storms on a rocky shore or frequent fires, may hold down the densities of populations so that resources are not limiting and individuals do not compete for them. The role of physical disturbances, and the associated patch dynamics view of communities, were discussed in Chapter 16. In an exactly analogous manner, the action of predators or parasites is often a disturbance in the 'normal' course of a competitive interaction; the resulting mortality may open up a gap for colonization in a way that is sometimes indistinguishable from that of battering by waves on a rocky shore or a hurricane in a forest.

The second assumption is that when competition is operating and resources are in limited supply, one species will inevitably exclude another. But in the real world, when no year is exactly like another, and no square centimeter of ground exactly the same as the next, the process of competitive exclusion may not proceed to its monotonous end. Any force that continually changes direction at least delays, and may prevent, an equilibrium or a stable conclusion being reached. Any force that simply interrupts the process of competitive exclusion may prevent extinction and enhance species richness.

equilibrium and nonequilibrium theories

A basic distinction can thus be made between *equilibrium* and *nonequilibrium* theories. An equilibrium theory, like the one concerned with niche differentiation, helps us to focus attention on the properties of a system at an equilibrium point – time and variation are not the central concern. A nonequilibrium theory, on the other hand, is concerned with the transient behavior of a system away from an equilibrium point, and specifically focuses our attention on time and variation. Of course, it would be naive to think that any real community has a precisely definable equilibrium point, and it is wrong to ascribe this view to researchers who are associated with equilibrium theories. The truth is that investigators who focus attention on equilibrium points have in mind that these are merely states towards which systems tend to be attracted, but about which there may be greater or lesser fluctuation. In one sense, therefore, the contrast between equilibrium and nonequilibrium theories is a matter of degree. However, this difference of focus is instructive in unraveling the important role of temporal heterogeneity in communities.

Thus, predators and parasites, like physical disturbances, can interrupt the process of competitive exclusion, influence profoundly the outcome of competitive processes, and impose their own order on community organization. Predation and parasitism can also affect community structure through the process of 'apparent competition' (see Section 8.6), where one or more prey or host species suffers from the actions of predators or parasites that are sustained by the presence of other species of prey or hosts. We turn to predation and parasitism in the next two sections.

19.4 The influence of predation on community structure

19.4.1 Effects of grazers

Lawn-mowers are relatively unselective predators capable of maintaining a close-cropped sward of vegetation. Darwin (1859) was the first to notice that the mowing of a lawn could maintain a higher richness of species than occurred in its absence. He wrote that:

> If turf which has long been mown, and the case would be the same with turf closely browsed by quadrupeds, be let to grow, the most vigorous plants gradually kill the less vigorous, though fully grown plants; thus out of 20 species growing on a little plot of mown turf (3 feet by 4 feet) nine species perished from the other species being allowed to grow up freely.

grazing can increase plant species richness (exploiter-mediated coexistence) . . .

Grazing animals are usually more choosy than lawn-mowers, and this is clearly demonstrated by the occurrence in the neighborhood of rabbit (*Oryctolagus cuniculus*) burrows of plants which for chemical or physical reasons are unacceptable as food to the rabbits (including the poisonous deadly nightshade *Atropa belladonna* and the stinging nettle *Urtica dioica*). Nevertheless, many grazers seem to have a similar general effect to lawn-mowers. Thus, in one experiment, grazing by oxen (*Bos taurus*) and zebu cows (*Bos taurus indicus*) in natural pasture in the Ethiopian highlands was manipulated to provide a no-grazing control and four grazing intensity treatments (several replicates of each) in two sites. Figure 19.14 shows how the mean number of plant species varied in the sites in October, the period when plant productivity was at its highest (Mwendera *et al.*, 1997). Significantly more species occurred at intermediate levels of grazing than where there was no grazing or heavier grazing ($P < 0.05$). In the ungrazed plots, several highly competitive plant species, including the grass *Bothriochloa insculpta*, accounted for 75–90% of ground cover. At intermediate levels of grazing, however, the cattle apparently kept the aggressive, competitively dominant grasses in check and allowed a greater number of plant species to persist. But at very high intensities of grazing, species numbers were reduced as the cattle were forced to turn from heavily grazed, preferred plant species to less preferred species, driving some to extinction. Where grazing pressure was particularly intense, grazing-tolerant species such as *Cynodon dactylon* became dominant.

. . . but not always

The composition of plant communities in different grazing regimes clearly depends on a variety of species traits. First, competitively superior species can be expected to dominate in the absence of grazing. A particularly striking example has been provided by Paine (2002), who reported that the exclusion of macroherbivores (urchins, chitons and limpets) from a North American rocky intertidal zone caused the multispecies kelp community to collapse to a virtual monoculture of *Alaria marginata*; this was 10 times more productive than its grazed counterpart (86.0 versus 8.6 kg wet mass m^{-2} $year^{-1}$). Second, we have seen that plant species with physical or chemical characteristics that deter grazers are likely to be more strongly represented in grazed locations. Bullock *et al.* (2001) have also noted that while certain dominant grasses decreased in importance in response to sheep grazing, most dicotyledonous species increased in abundance, at least at certain times of year. Moreover, summer grazing produced an increased representation of plant species best able to colonize gaps.

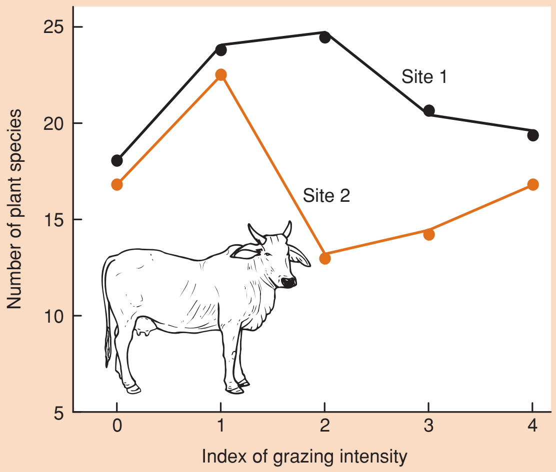


Figure 19.14 Mean species richness of pasture vegetation in plots subjected to different levels of cattle grazing in two sites in the Ethiopian highlands in October. 0, no grazing; 1, light grazing; 2, moderate grazing; 3, heavy grazing; 4, very heavy grazing (estimated according to cattle stocking rates). (After Mwendera *et al.*, 1997.)

exploiter-mediated coexistence is more likely in nutrient-rich situations

When predation promotes the coexistence of species amongst which there would otherwise be competitive exclusion (because the densities of some or all of the species are reduced to levels at which competition is relatively unimportant), this is known generally as '*exploiter-mediated coexistence*'. Many examples of this phenomenon have been reported, such as that in Figure 19.14, but grazer-mediated coexistence is far from universal. Proulx and Mazumder (1998) performed a meta-analysis of 44 reports of the effects of grazing on plant species richness from lake, stream, marine, grassland and forest ecosystems. Their conclusion was that the outcome was strongly related to whether the studies had been performed in nutrient-rich or nutrient-poor situations. All

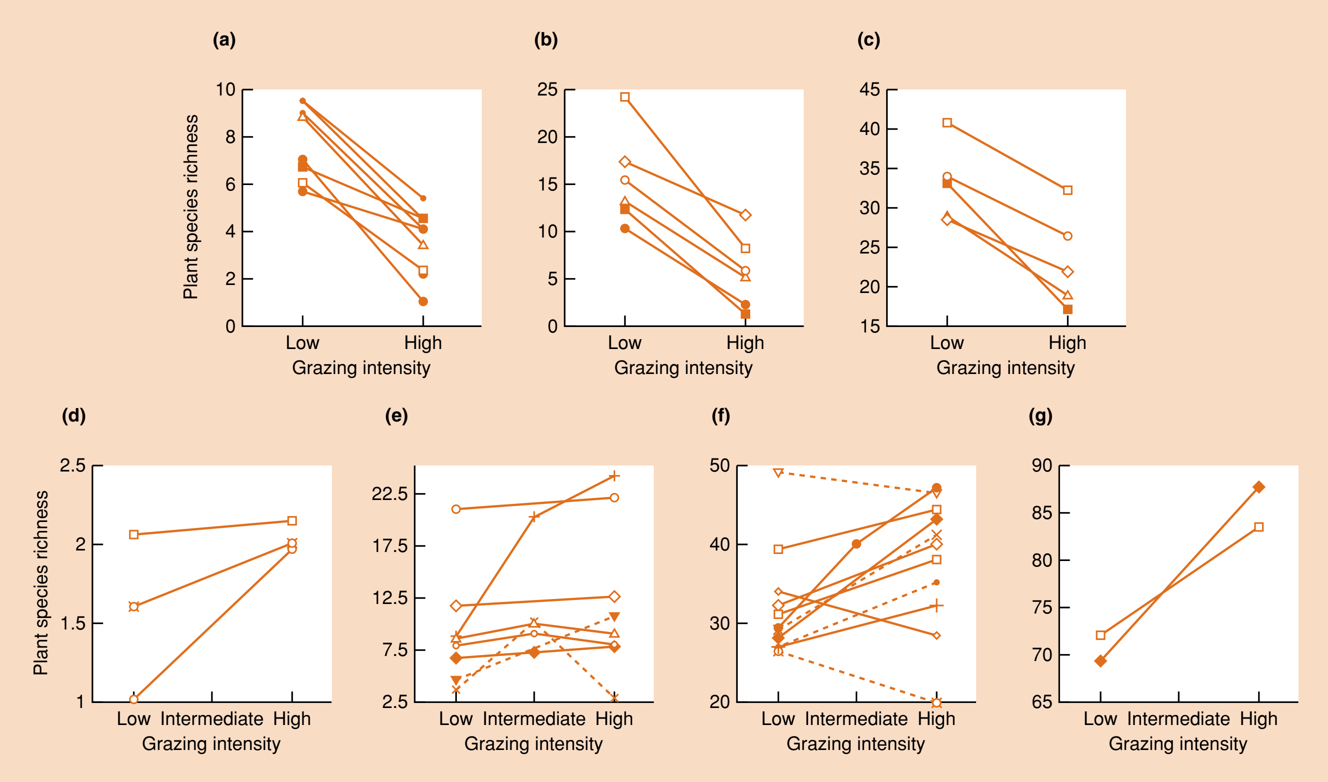


Figure 19.15 (a–c) Species richness under contrasting grazing pressure (low or high) in nonenriched or nutrient-poor ecosystems. The different lines show the results of different aquatic or terrestrial studies and are presented in three panels simply for clarity. (d–g) Species richness under contrasting grazing pressure (low, intermediate or high) in various enriched or nutrient-rich ecosystems. (After Proulx & Mazumder, 1998.)

19 studies from nonenriched or nutrient-poor ecosystems exhibited significantly lower species richness under high grazing than under low grazing (Figure 19.15a–c). In contrast, 14 of 25 comparisons from enriched or nutrient-rich ecosystems showed significantly higher species richness under high grazing (indicating grazer-mediated coexistence) (Figure 19.15d–g). Nine of the remaining 11 nutrient-rich studies showed no difference with grazing regime whilst two showed a decline in species richness. The lack of grazer-mediated coexistence in unproductive situations may reflect the poor growth potential of the less competitive species that, in nutrient-rich circumstances, would be released from competitive domination as a result of grazing.

community responses to grazing depend on productivity . . .

Osem *et al.* (2002) focused on the interactive effects of grazing and productivity in a study of annual herbaceous plant communities in Mediterranean semiarid rangeland in Israel. They recorded the response of the community to protection from sheep grazing in four neighboring topographic situations – south-facing slopes, north-facing slopes, hilltops and wadi (dry stream) shoulders (Figure 19.16). Annual above-ground primary productivity was measured each year for 4 years at the peak season in the four fenced subplots per site and was found to be typical of semiarid ecosystems (10–200 g dry matter m^{-2}) except on wadi shoulders (up to 700 g dry matter m^{-2}). The measured values were taken to represent 'potential' productivity in the adjacent grazed subplots. Grazing only increased plant species richness in the most productive site (wadi) (Figure 19.16d). In the other, less productive sites, species richness was unaffected or declined with grazing. These results are consistent with those reported by Proulx and Mazumder (1998) and support the long-standing proposal of Huston (1979) that grazing should change diversity in opposite ways in resource-poor and resource-rich ecosystems.

Figure 19.17a and b plots species richness in relation to potential productivity individually for all subplots and all years (because precipitation and productivity varied both spatially and temporally) for both grazed and ungrazed locations. Under grazing, species richness was positively related to productivity over the whole range measured. In the absence of grazers, however, a positive relationship only occurred in low-productivity sites. Osem *et al.* (2002) hypothesize (Figure 19.17c) that at low productivity, plant growth and diversity are limited by the soil resources of water and nutrients, while at higher productivity (with its associated larger

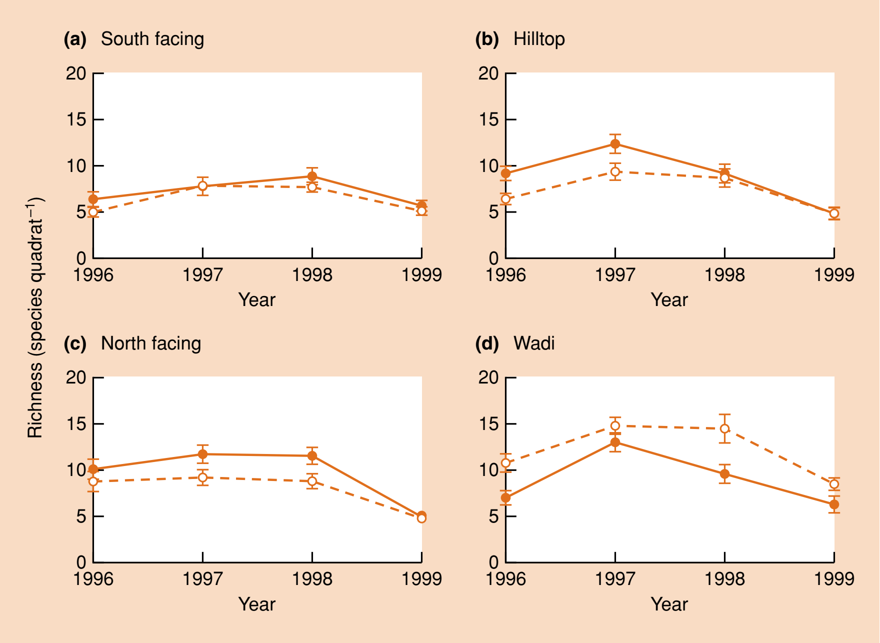


Figure 19.16 Species richness (per 20 × 20 cm quadrats) in four topographic sites in Israel in April: (a) south-facing slopes, (b) hilltops, (c) north-facing slopes, and (d) wadis. ●, ungrazed subplots; ○, grazed subplots. (After Osem *et al*., 2002.)

biomass) competition is predominantly for the canopy resource of light. Thus, in the low productivity range, richness was either unaffected or reduced by grazing, probably because of plant removal and trampling. In the high productivity wadi sites, however, species richness continued to increase with grazing, most likely because of a reduction in light competition through removal of the palatable larger species.

. . . and plant species traits

Taken overall, then, the way that plant species richness responds to grazing depends partly on grazing intensity, but also on the evolutionary history of the plant community and thus the particular plant species traits that are represented, as well as the primary productivity of the ecosystem in question. An increase in species richness in response to grazing can be expected if grazers feed preferentially on competitively dominant species, a prediction that has received support in situations as diverse as cattle grazing in Ethiopia (see above) and periwinkles (*Littorina littorea*) feeding on algae in rocky tide pools (Lubchenco, 1978). Conversely, a reduction in species richness can be expected if the preferred food plants are competitively inferior, as was the case for periwinkles feeding on algae on emergent substrata in Lubchenco's study.

19.4.2 The effect of carnivores

predator-mediated coexistence on a rocky shore . . .

The rocky intertidal zone also provided the location for pioneering work by Paine (1966) on the influence of a top carnivore on community structure. The starfish *Pisaster ochraceus* preys on sessile filter-feeding barnacles and mussels, and also on browsing limpets and chitons and a small carnivorous whelk. These species, together with a sponge and four macroscopic algae, form predictable associations on rocky shores of the Pacific coast of North America. Paine removed all the starfish from a typical piece of shoreline about 8 m long and 2 m deep, and continued to exclude them for several years. At irregular intervals, the density of invertebrates and the cover of benthic algae were assessed in the experimental area and in an adjacent control site. The latter remained unchanged during the study. Removal of *P. ochraceus*, however, had dramatic consequences. Within a few months, the barnacle *Balanus glandula* settled successfully. Later, barnacles were crowded out by mussels (*Mytilus californianus*), and eventually the site became dominated by the latter. All but one of the species of algae disappeared, apparently through lack of space, and the browsers tended to move away, partly because space was limited and partly due to lack of suitable food. Overall, the removal of starfish led to a reduction in the number of species from 15 to eight. The main influence of the starfish *Pisaster* appears to be to make space available for competitively subordinate species. It cuts a swathe free of barnacles and, most importantly, free of the dominant mussels that would otherwise outcompete other invertebrates and algae for space. Once again, there is exploiter-mediated coexistence. Note that this argument applies specifically to the primary space occupiers, such as mussels, barnacles and macroalgae. In contrast, the number of less conspicuous species associated with living and dead mussel shells would be expected to increase in the bed that develops after *Pisaster* removal (more than 300 species of animals and plants occur in mussel beds; Suchanek, 1992).

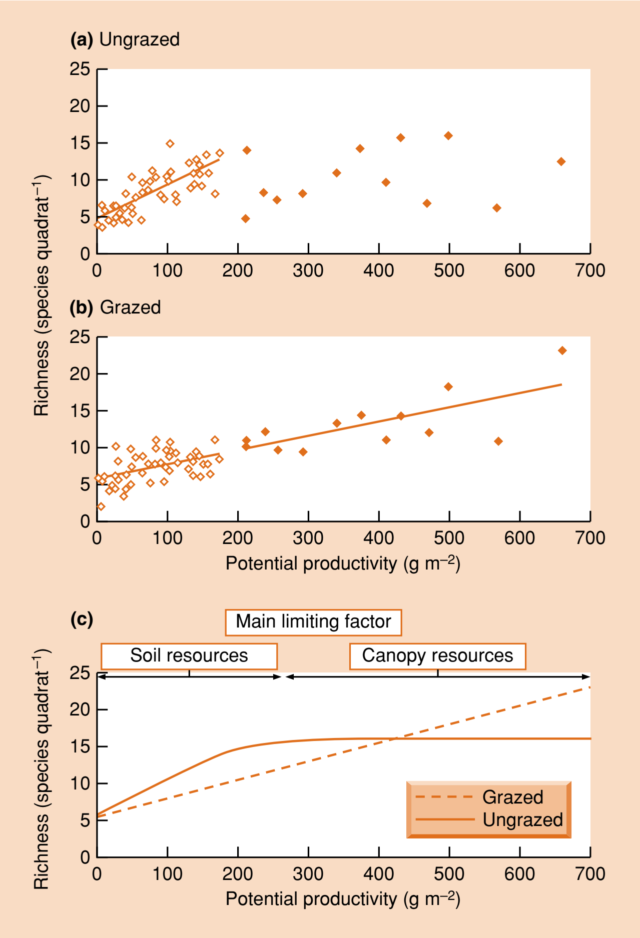


Figure 19.17 Relationship between annual above-ground productivity (measured in ungrazed subplots) and species richness in (a) ungrazed and (b) grazed subplots. Open symbols represent low productivity subplots (< 200 g dry matter m^{-2}; hilltop, south- and north-facing slopes in all years plus wadi in the dry 1999 season). Closed symbols represent high productivity subplots (> 200 g dry matter m^{-2}; wadi sites in years other than 1999). (c) Conceptual model of the relationship between productivity and species richness in grazed and ungrazed semiarid Mediterranean rangeland. (After Osem *et al.*, 2002.)

. . . but not in hydrothermal vent communities

Experiments similar to those of Paine have been performed in the more challenging environment of hydrothermal vents at a depth of 2500 m in the eastern tropical Pacific Ocean (Micheli *et al.*, 2002). Colonization of replicate recruitment substrates (10 cm basalt cubes) was monitored for 5 months at increasing distances from the vent in three sites in the presence and absence (exclusion cages) of predators (fish and crabs). In terms of reduced prey abundance (particularly two gastropods endemic to vents – the limpet *Lepetodrilus elevatus* and the snail *Cyathermia naticoides*), the effects of predation were strongest near the vent where productivity and the overall abundance of invertebrates were greatest. Species richness, which generally declined with distance from the vent, was usually lower in the presence of predators (but only statistically significantly so at the Worm Hole site – Figure 19.18). The reason for a lack of predator-mediated coexistence is unknown.

predator-mediated coexistence among passerine birds . . .

Turning now to terrestrial ecosystems, in a study of nine Scandinavian islands, pigmy owls (*Glaucidium passerinum*) occurred on only four of the islands, and the pattern of occurrence of three species of passerine birds in the genus *Parus* showed a striking relationship with this distribution (Table 19.1). The five islands without the predatory owl were home to only one species, the coal tit (*Parus ater*). However, in the presence of the owl, the coal tit was always joined by two larger tit species, the willow tit (*P. montanus*) and the crested tit (*P. cristatus*). Kullberg and Ekman (2000) argue that the smaller coal tit is superior in exploitation competition for food. The two larger species, however, have an advantage via interference competition for foraging sites close to the trunk of trees where they are safer from predators; in other words the larger species are less affected than the coal tit by predation from the owl. It seems that the owl may be responsible for predator-mediated coexistence, by reducing the competitive dominance enjoyed by coal tits in its absence.

. . . but not among communities of insects or spiders

However, an increase in species richness with predation is by no means universal in terrestrial ecosystems. Spiller and Schoener (1998) reviewed a

Table 19.1 Area, distance to mainland and occurrence of breeding pairs of pygmy owls and three species of tit. (After Kullberg & Ekman, 2000.)

Island	*Area (km^2)*	*Distance to mainland (km)*	*Pygmy owl*	*Coal tit*	*Willow tit*	*Crested tit*
Åland	970	50	+	+	+	+
Ösel	3000	15	+	+	+	+
Dagö	989	10	+	+	+	+
Karlö	200	7	+	+	+	+
Gotland	3140	85		+		
Öland	1345	4		+		
Bornholm	587	35		+		
Hanö	2.2	4		+		
Visingsö	30	6		+		

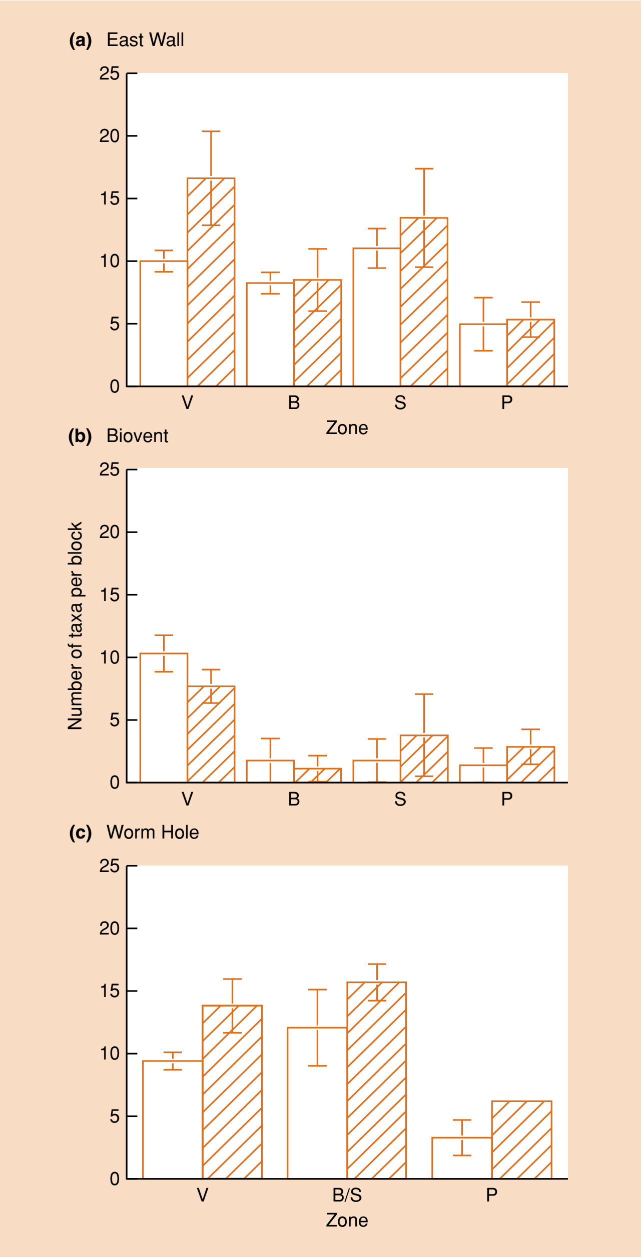


Figure 19.18 Patterns of invertebrate species richness (worms in the order Vestimentifera (class Pogonophora), worms in the class Polychaeta, gastropods, bivalves and crustaceans) per implanted recruitment substrate after 5 months at three sites with two experimental treatments: (a) East Wall, (b) Biovent, and (c) Worm Hole. The results are presented for four zones whose boundaries are based on water temperature and dominant benthic invertebrates (at increasing distances from the hydrothermal vent: Vestimentiferan (V), bivalve (B), suspension-feeder (S) and periphery (P)). The two middle zones were combined at the Worm Hole site. Experimental treatments: □, uncaged; ▨, caged to exclude mobile predators – fish and crabs. (After Micheli *et al*., 2002.)

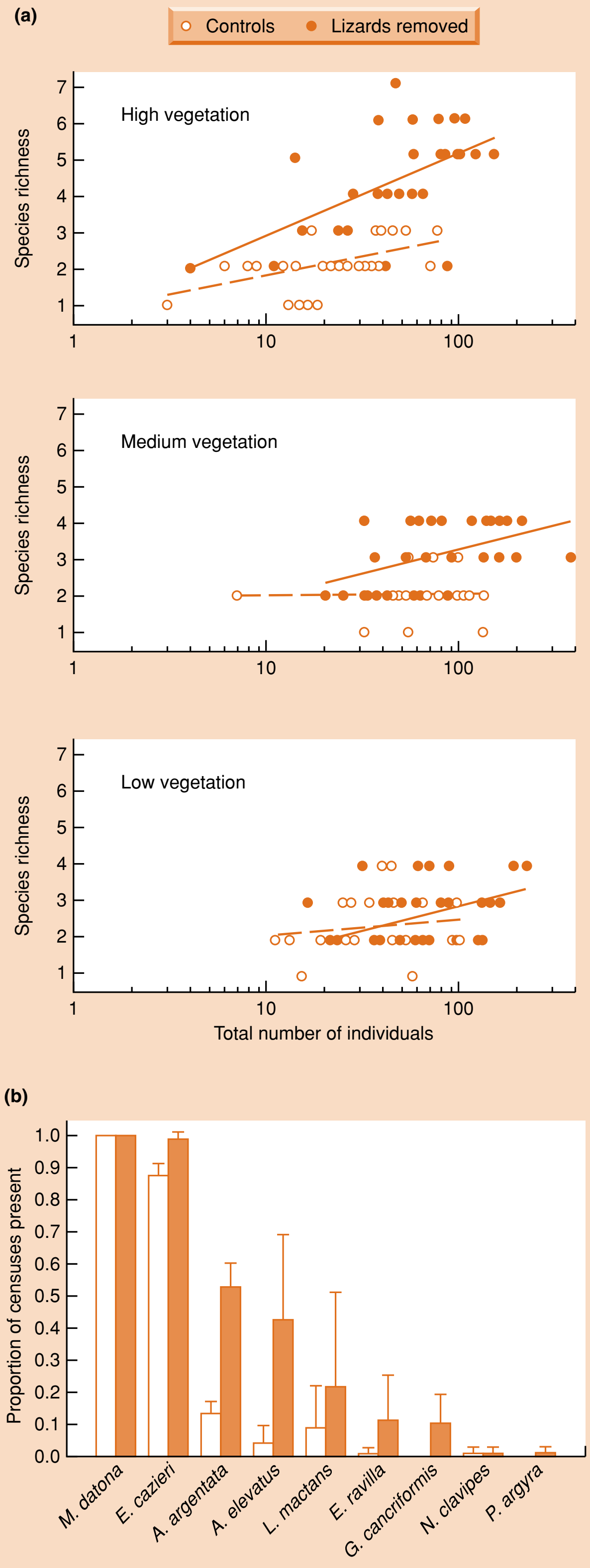
number of studies involving birds preying upon grasshoppers, rodents upon carabid beetles and lizards upon web spiders and concluded that these predators usually reduced prey richness or had no effect. In their own study in the Bahamas, they censused spider populations at 2-month intervals for 4.5 years in enclosures (three replicates) containing or lacking lizards. Species richness was dramatically increased by the exclusion of lizards (mainly *Anolis sagrei*) at high and medium levels in the vegetation (Figure 19.19a). The lizards preyed preferentially upon rare species of spiders (Figure 19.19b), resulting in increased dominance of the already abundant *Metapeira datona*, a species whose relative invulnerability to predation is probably due to its small size and habit of living in a suspended retreat rather than in the middle of the web.

predator dietary preferences may modify the outcome

As was the case with grazers, the manner in which prey species richness responds to predation no doubt depends partly on predation intensity, partly on ecosystem productivity, and partly on the particular characteristics of the prey species. Once again we have seen increases in prey species richness where carnivores feed preferentially on competitively dominant prey (starfish feeding on mussels, pygmy owls feeding on coal tits) and a decrease where the preferred prey are competitively inferior (lizards feeding on spiders).

frequency-dependent selection may sometimes enhance diversity

Another reason for contrasting effects of consumers on lower trophic levels relates to their prey-selection behavior. They seldom simply take potential prey species from a community in turn, bringing each to extinction before turning to the next. Selection is moderated by the time or energy spent in search for the preferred prey (see Chapter 9), and many species take a mixed diet. However, others switch sharply from one type of prey to another, taking disproportionately more of the most common acceptable types of prey. In theory, such behavior could lead to the coexistence of a large number of relatively rare species (a frequency-dependent form of exploiter-mediated coexistence). In this context, there is evidence that predation on the seeds of tropical trees is often more intense where the seeds are more dense (beneath and near the adult that produced them) (Connell, 1979); the herbivorous butterfly *Battus philenor* forms search images for leaf shape when foraging for its two larval host plants, and concentrates on whichever happens to be the more common (Rausher, 1978); the freshwater zooplanktivorous fish *Rutilus rutilus* switches from large planktonic waterfleas, its preferred prey, to small sediment-dwelling waterfleas when the density of the former falls below about 40 per liter (Townsend *et al*., 1986); and piscivorous coral reef fish (*Cephalopholis boenak* and *Pseudochromis fuscus*) concentrate on highly abundant cardinal fish (mainly *Apogon fragilis*) when these are present, leaving recruits of many other fish species relatively unmolested (Webster & Almany, 2002). However, such frequency-



dependent selection is not a general rule and may not be common. For one thing, some species are so highly specialized that switching is not an option – giant pandas are specialists on bamboo shoots and specialization in diet is equally extreme amongst many phytophagous insects. Moreover, in other cases a predator may be sustained by one prey type whilst exterminating others. This has been claimed for the introduced snake *Boiga irregularis*, on the small island of Guam, midway between Japan and New Guinea. Coincident with its arrival in the early 1950s, and its subsequent spread through Guam, most of the 18 native bird species have declined dramatically and seven are now extinct. Savidge (1987) argues that by including abundant small lizards in its diet, *B. irregularis* has maintained high densities whilst exterminating the more vulnerable bird species.

19.5 Influence of parasitism on community structure

parasites may drive vulnerable host species extinct

The incidence of a parasite, like that of other types of exploiter, may determine whether or not a host species occurs in an area. Thus, the extinction of nearly 50% of the endemic bird fauna of the Hawaiian Islands has been attributed in part to the introduction of bird pathogens such as malaria and bird pox (van Riper *et al*., 1986); and changes in the distribution of the North American moose (*Alces alces*) have been associated with the parasitic nematode *Pneumostrongylus tenuis* (Anderson, 1981). Probably the largest single change wrought in the structure of communities by a parasite has been the destruction of the chestnut (*Castanea dentata*) in North American forests, where it had been a dominant tree over large areas until the introduction of the fungal pathogen *Endothia parasitica*, probably from China.

a microparasite with subtle direct and indirect effects in a stream community

Like grazers and carnivores, parasites can cause more subtle effects too. In many streams in Michigan, USA, larvae of the herbivorous caddis-fly *Glossosoma nigrior* play a key role in the community because their foraging maintains attached algae at very low levels, with negative consequences for most other stream herbivores

Figure 19.19 (*left*) (a) Spider species richness plotted against total number of individuals (all censuses) in the presence and absence of lizards at three heights in the vegetation. For a given number of individuals, enclosures without lizards (●) contained a greater number of spider species than enclosures with lizards (○) except low in the vegetation. (b) Mean proportion of censuses in which each web spider was recorded per enclosure in the presence (□) and absence of lizards (■). Error bars ± SD. (After Spiller & Schoener, 1998.)

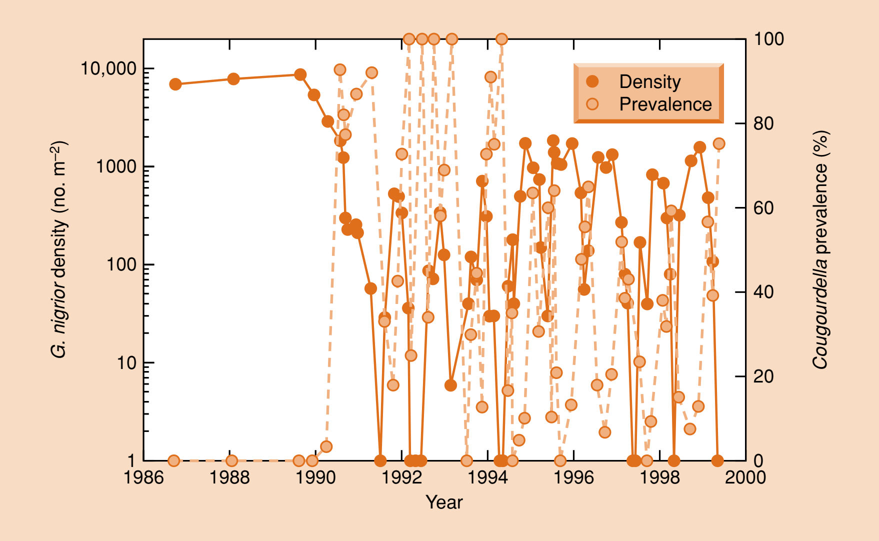


Figure 19.20 *Glossosoma nigrior* density in Seven Mile Creek, Michigan, and the percentage of the population infected (prevalence) by *Cougourdella*. (After Kohler, 1992.)

(Kohler, 1992). *G. nigrior* is subject to sporadic outbreaks of a highly specific microsporidian microparasite, *Cougourdella*, which result in dramatic whole stream reductions in *G. nigrior* density that may be maintained for years. In Seven Mile Creek, for example, the mean *G. nigrior* density was 6285 per m^2 in the 10 generations before a parasite outbreak in 1990 but it averaged 164 per m^2 for the next decade (Figure 19.20). The decline of *G. nigrior* leads to increased abundance of its food resource (Figure 19.21a). As a result, several herbivores (Figure 19.21b–d), including a species that was previously absent or extremely rare (Figure 19.21e), increased in abundance after the streams had experienced a parasite-caused decline in *G. nigrior*. Thus, by reducing the abundance of the competitively dominant herbivore, the parasite increased herbivore equitability (one aspect of species diversity) and may have been responsible for an increase in species richness. This example, therefore, has the hallmarks of parasite-mediated coexistence The parasite was also responsible for further effects – increased algal abundance seems to have resulted in more fine particulate dead organic matter (through sloughing off of algal cells) fueling an increase in the density of filter-feeders (Figure 19.21f), and the increase in abundance of vulnerable herbivore species (*G. nigrior* is relatively invulnerable to predators) led to increased densities of predaceous caddis-flies (*Rhyacophila manistee*) and stoneflies (*Paragnetina media*) (Figure 19.21g).

parasite-mediated coexistence in Caribbean lizards . . .

In terrestrial ecosystems, too, there are apparent examples of parasite-mediated coexistence. For example, the malarial parasite *Plasmodium azurophilum* infects two *Anolis* lizards on the Caribbean island of St Martin. One of the lizards, thought to be the competitive dominant, is widespread throughout the island while the other is only found in a limited area. Schall (1992) reported that the superior competitor was much more likely to be infected by the parasite and, intriguingly, the two species only coexisted where the parasite was present. Once again, though, this is far from a universal pattern. For example, the invading grey squirrel (*Sciurus carolensis*) is displacing the resident red squirrel (*S. vulgaris*) throughout much of its range in Britain. At least part of the reason seems to be that the invader has brought with it a parapox virus that has little discernible effect on the grey squirrel but a dramatic adverse effect on the health of the native red squirrel (Tompkins *et al*., 2003).

. . . but not in songbirds

Brood parasites (see Section 12.2.3), such as brown-headed cowbirds (*Molothrus ater*), might also be expected to affect the composition or richness of the communities in which they operate. De Groot and Smith (2001) made use of a cowbird reduction program in a pine (*Pinus banksiana*) forest in Michigan (designed to protect one of the cowbird's hosts, the endangered Kirtland's warbler *Dendroica kirtlandii*) to investigate whether the songbird community as a whole was affected by a reduction in the density of the brood parasite. Their results provided no support for parasite-mediated coexistence, nor was there a change in community composition or an increase in the representation of songbird species known to be unsuitable as hosts for cowbirds.

parasites that influence species that are themselves strong community interactors

Parasites may sometimes influence community composition not by altering the outcome of competitive interactions but through an impact on a key member of the community that acts as an ecosystem engineer (*sensu* Jones *et al.*, 1994, 1997). The juvenile stages of the trematode *Curtuteria australis* encyst in the foot of cockles, *Austrovenus stutchburyi*, and impair the burrowing ability of the cockles. This results in heavily infected cockles remaining stranded at the surface of the sediments, where they are easy prey

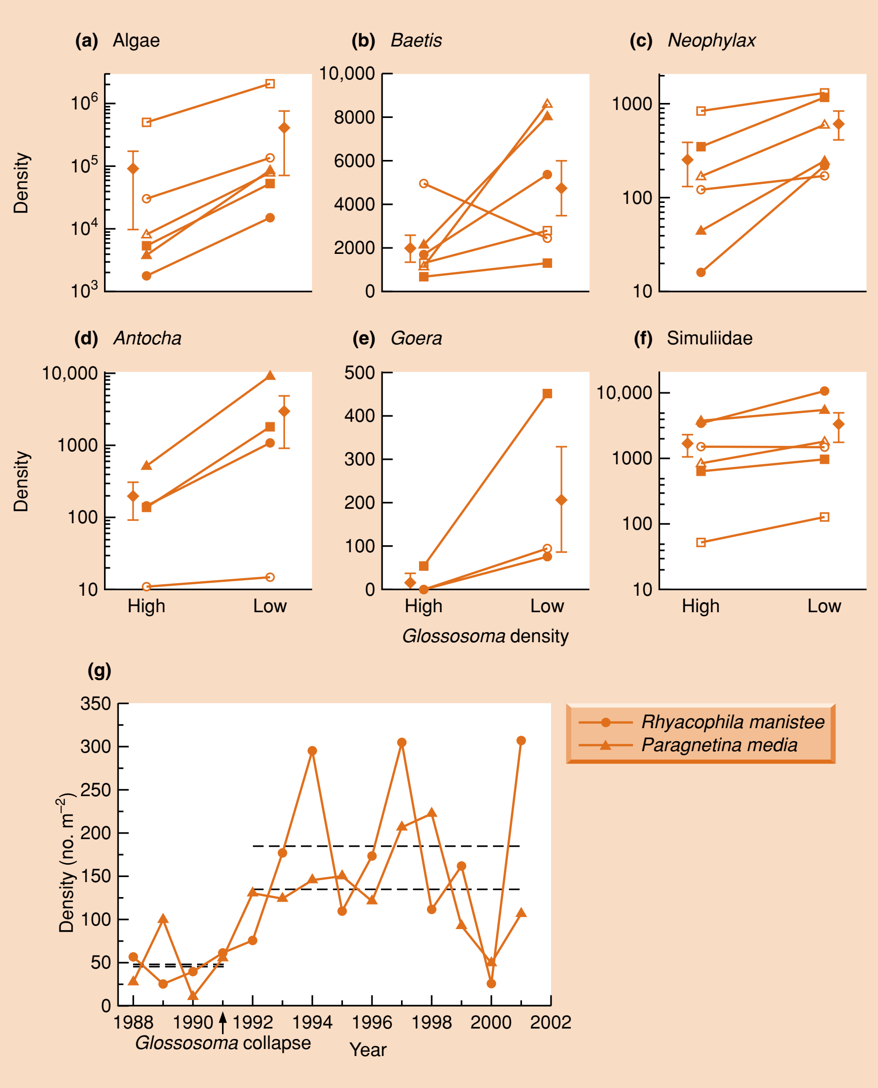


Figure 19.21 Mean densities of (a) attached algae (cells cm^{-2}), (b–e) herbivorous insects (number m^{-2}) and (f) filter-feeders (number m^{-2}), in relation to *Glossosoma nigrior* density (high, before a parasite outbreak; low, during a parasite outbreak) in six streams. Lines connect data points for each of the six streams; the points with error bars (± 1 SE) are the overall means. (g) Predator densities before and after a parasite-induced reduction of *G. nigrior* in Silver Creek (dashed lines show mean densities before and after the collapse). (After Kohler & Wiley, 1997.)

for oystercatchers, the trematode's definitive host (Thomas & Poulin, 1998; Mouritsen, 2002). Cockles, the dominant bivalves in New Zealand soft-sediment intertidal zones, are normally buried 2–3 cm under the sediment surface. But in areas of intense parasitism, large numbers protrude from the sediment or lie on its surface, increasing surface heterogeneity and changing patterns of water flow and sedimentation. Mouritsen and Poulin (2005) manipulated the density of surface cockles by creating plots with 30 or 100 surface cockles added to compare with control plots with naturally few cockles at the surface. After 6 months, there were significantly more species of macrofaunal invertebrates (polychaetes, molluscs, crustaceans, etc.) in the treatments with added surface cockles and the densities of a variety of taxa were greater in these experimental plots (Figure 19.22).

19.6 Appraisal of the effects of predators and parasites

1 Selective predators are likely to act to enhance species richness in a community if their preferred prey are competitively dominant and in situations where community productivity is high. It seems likely that there is some general correlation between palatability to predators and high growth rates. If the production of chemical and physical defenses by prey requires a sacrifice of resources used in growth and reproduction, we might expect species that are competitive dominants in the absence of predators (and hence, which devote resources to competition rather than defense) to suffer excessively from their presence. Thus, selective predators may often enhance

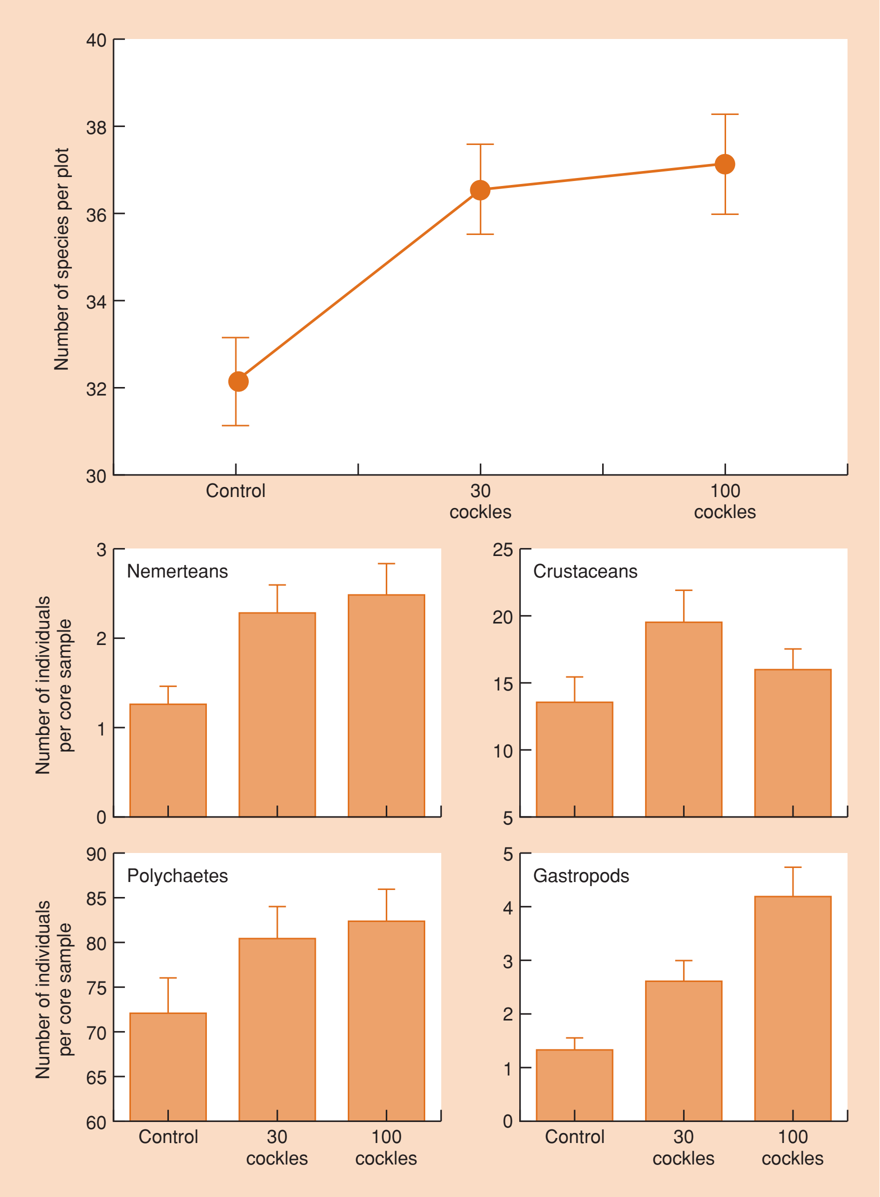


Figure 19.22 Manipulation of the density of cockles at the sediment surface, mimicking variation in infection levels by the trematode *Curtuteria australis*, and its effect on intertidal communities. Mean (± 1 SE) species richness of macrofaunal invertebrate species per plot and mean density of several invertebrate taxa in three experimental treatments (0, 30 and 100 cockles added to a 1 m^2 plot). All means are derived from five core samples taken per plot, with seven plots per treatment. (After Mouritsen & Poulin, 2005)

species richness. If the predators act in a frequency-dependent manner their action should be even stronger. Even very generalist predators may increase community diversity through exploiter-mediated coexistence, because if prey are attacked simply in proportion to their abundance, it will be those species that are assimilating resources and producing biomass and offspring most rapidly (the competitive dominants) that will be most abundant, and will therefore be most severely set back by predation. Note, however, that predators seem just as frequently to cause a reduction in species richness, or to have no effect.

2 An intermediate intensity of predation is most likely to be associated with high prey species richness, since too low an intensity may not prevent competitive exclusion of inferior prey species, whilst too high an intensity may itself drive preferred prey to extinction. (Note, however, that 'intermediate' is difficult to define *a priori*.)

3 The role of predators and parasites in shaping community structure may often be least significant in communities where physical conditions are more severe, variable or unpredictable (Connell, 1975). In sheltered coastal sites, predation appears to be a dominant force shaping community structure

(Paine, 1966), but in exposed rocky tidal communities where there is direct wave action, predators seem to be scarce and to have a negligible influence on community structure (Menge & Sutherland, 1976; Menge *et al*., 1986). Deep-sea hydrothermal vents provide an exception to these generalizations, probably because the physically severe circumstances close to the vents also engender very high levels of productivity.

4 The effects of animals on a community often extend far beyond just those due to the cropping of their prey. Burrowing animals (such as earthworms, rabbits and porcupines) and mound-builders (ants and termites) – and parasitized cockles – all create disturbances and act as ecosystem engineers (by modifying the physical structure of the environment) (Wilby *et al*., 2001). Their activities provide local heterogeneities, including sites for new colonists to become established and for microsuccessions to take place. Larger grazing animals introduce a mosaic of nutrient-rich patches, as a result of dunging and urinating, in which the local balance of other species is profoundly changed. Even the footprint of a cow in a wet pasture may so change the microenvironment that it is now colonized by species that would not be present were it not for the disturbance (Harper, 1977). The predator is just one of the many agents disturbing community equilibrium.

5 Carnivores that also feed at other trophic levels (omnivores) may have particularly far-reaching consequences for the community. For example, omnivorous freshwater crayfish can influence the composition of plants (which they consume), herbivores and carnivores (which they consume or with which they compete), and even detritivores because their extreme omnivory includes feeding on dead plant and animal material (Usio & Townsend, 2002, 2004). Moreover, they can also act as ecosystem engineers by dislodging animals and detritus as they move or burrow through the substrate (Statzner *et al*., 2000).

19.7 Pluralism in community ecology

communities are not necessarily structured by a single biotic process

It would be wrong to replace one monolithic view of community organization (the overriding importance of competition and niche differentiation) with another (the overriding importance of forces such as predation and disturbance that make competition much less influential). Certainly, communities structured by competition are not a general rule, but neither necessarily are communities structured by any single agency. Most communities are probably organized by a mixture of forces – competition, predation, disturbance and recruitment – although their relative importance may vary systematically, with competition and predation figuring more prominently in communities where recruitment levels are high (Menge & Sutherland, 1987) and in less disturbed environments (Menge & Sutherland, 1976; Townsend, 1991).

physical conditions can moderate the effects of predators and parasites

In an elegant series of experiments, Wilbur (1987) investigated the interactions between competition, predation and disturbance as they influenced four species of frog and toad that occur in North American ponds. In the absence of predators, tadpoles of *Scaphiopus holbrooki* were competitively dominant whilst, at the opposite extreme, *Hyla chrysoscelis* had a very low competitive status (Figure 19.23a). The presence of predatory salamanders, *Notophthalmus viridescens*, did not alter the total number of tadpoles reaching metamorphosis, but relative abundances were shifted because *S. holbrooki*, the competitive dominant, was selectively eaten (Figure 19.23b). Finally, Wilbur subjected his tadpole communities, in the presence and absence of predators, to water loss, to simulate a natural drying regime (disturbance). The influence of competition was to slow growth and retard the

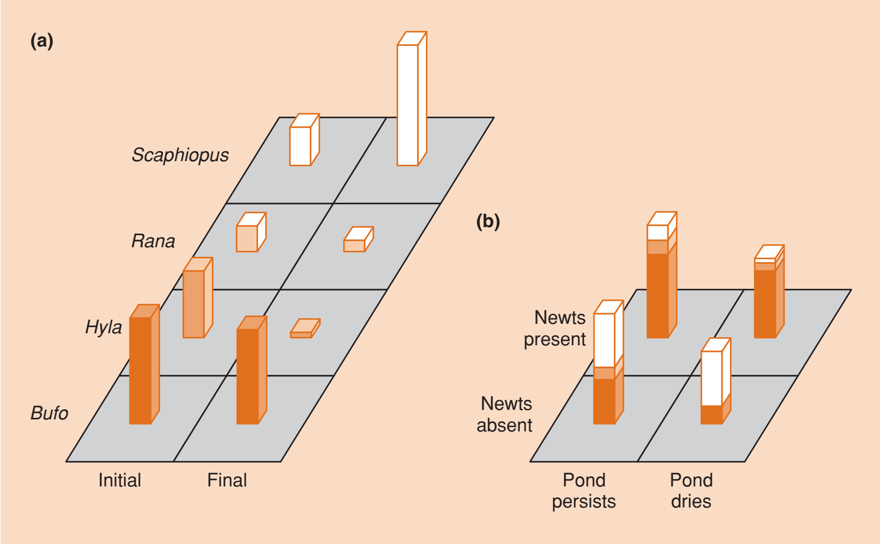
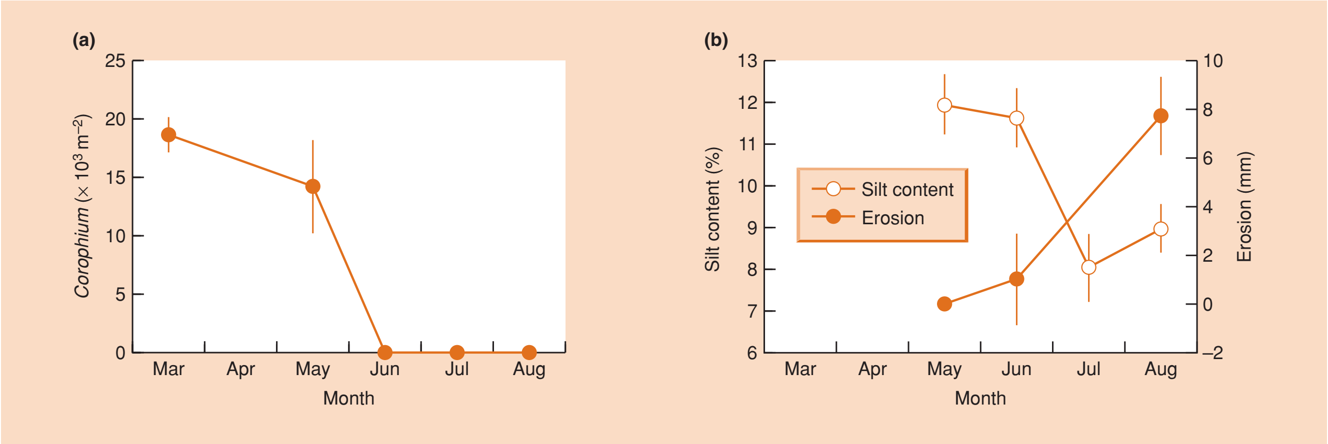


Figure 19.23 (a) Relative abundance of tadpoles of each of four species introduced at high density into ponds (initial), and the relative abundances of metamorphs at the end of the experiment (final). (b) Number of metamorphs of four species in the absence and presence of predatory salamanders, and in ponds which persist or which dry up 100 days into the experiment. (After Wilbur, 1987; Townsend, 1991a.)



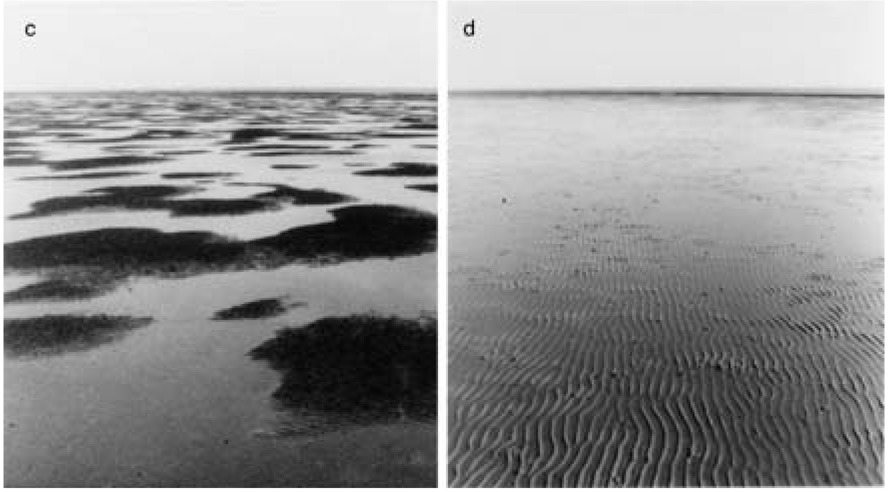


Figure 19.24 Extermination of a dense intertidal amphipod population by microphallid trematodes and the consequent changes in sediment characteristics and topography of the mudflat. (a) Mean density (± SE) of *Corophium volutator*. (b) Mean silt content (particles < 63 μm) and substrate erosion. (c) The topography of the *Corophium* bed before the parasite-induced *C. volutator* die-off. (d) The topography of the flat a few months after the disappearance of amphipods. (After Mouritsen & Poulin, 2002 and Mouritsen *et al.*, 1998. Reproduced by permission of K. Mouritsen)

timing of metamorphosis, thus increasing the risk of desiccation in drying ponds. *S. holbrooki* had the shortest larval period and made up a greater proportion of metamorphs in the drying experiment without predators. The presence of predators ameliorated the impact of competition, allowing surviving tadpoles of several species to grow rapidly enough to metamorphosize before the ponds dried up.

The consequences of parasitism may also be moderated by physical conditions. The mud snail *Hydrobia ulvae* and the amphipod *Corophium volutator* dominate the benthic macrofaunal community on intertidal mudflats in the Danish Wadden Sea. These two species serve as first and second intermediate hosts, respectively, to microphallid trematodes, with sandpipers (*Calidris* spp.) as definitive hosts. The trematode eggs are expelled in the bird's droppings and the detritus-feeding snails accidentally eat them. The parasite larvae hatch and reproduce inside the snail, releasing into the water on a daily basis vast numbers of swimming cercariae that seek out an amphipod. As a consequence of a temperature-dependent release of cercariae from the snails, the parasites cause intensity-dependent mortality in the amphipod hosts, which itself increases rapidly with increasing temperature (Mouritsen & Jensen, 1997). *C. volutator* normally increases rapidly during spring and summer, commonly achieving densities exceeding 80,000 individuals per m^2 in early fall (Mouritsen *et al.*, 1997). Because these amphipods make permanent U-shaped burrows that stabilize the substrate, and because of their patchy distribution, *Corophium*-dominated mudflats have a characteristic topography with a mosaic of elevated plateaux (high-density patches) and sediment depressions (low-density patches) (Mouritsen *et al.*, 1998). In this state, the *Corophium* bed is very stable even during strong onshore gales. But during the spring of 1990, ambient temperatures were unusually high and so was the prevalence of microphallid infections in the snail population, resulting in a massive release of cercariae from the snails and, within 5 weeks, the complete collapse of the amphipod population (Figure 19.24a) (Jensen & Mouritsen, 1992). As the sediment-stabilizing amphipods disappeared, the plateaux of the former *Corophium* bed (which covered about 80 ha) were subject to significant erosion (Figure 19.24b). The characteristic mudflat topography eventually vanished (Figure 19.26c, d) with dramatic consequences for many other mudflat macroinvertebrates, including species of nemertinea, polychaeta, gastropoda, bivalvia and crustacea.

remember that some biotic interactions are positive in their effects

We began this chapter by noting the diversity of ways in which a single species can affect communities and ecosystems. It would be wrong to finish it with the impression that competition, predation and parasitism are the principal population interactions that determine community organization. Facilitation is also of major significance, though once again its significance varies with physical conditions. Thus, the presence of a canopy of the seaweed *Ascophyllum nodosum* at its upper intertidal boundary in communities in the Gulf of Maine reduced maximum daily rock temperatures by 5–10°C and evaporative losses by an order of magnitude, with positive outcomes for recruitment, growth and survivorship of a range of benthic organisms (Bertness *et al.*, 1999). In fact, nearly half of the recorded population interactions in this zone were positive (facilitation) rather than negative (competitive or predatory). On the other hand, at *A. nodosum*'s lower boundary, rather than ameliorating physical conditions (these are not so severe deeper in the intertidal zone) the seaweed canopy provided excellent conditions for herbivores and carnivores and consumer pressure was severe.

Positive interactions among terrestrial plant species have also been demonstrated in many communities (Wilson & Agnew, 1992; Jones *et al.*, 1994). Plants sometimes benefit their neighbors by reducing the likelihood of consumption by herbivores. Thus, Callaway *et al.* (2000) examined the role played by two competitively dominant and highly unpalatable plants, the physically defended thistle *Cirsium obvalatum* and the chemically defended *Veratrum lobelianum*. Both have invaded grazed meadows in the central Caucasus in the Republic of Georgia. Forty four percent (15/34) of all species in the study were rare (< 1.0% cover) in open meadow, but occurred at significantly higher covers under *C. obvalatum* and *V. lobelianum* (i.e. within a 60 × 60 cm plot containing one of the unpalatable species). Eight species were only found under an unpalatable species, and the communities associated with them had 78–128% more species in flower or fruit than in the open meadow sites. It seems that tasty species may avoid being eaten, and grow and reproduce better, if they associate with an unpalatable neighbor.

Finally, we have seen how the effects of predators and parasites are not restricted to their prey/hosts or even just those species with which they or their prey compete. Sometimes the effects extend beyond a single, or adjacent, trophic level to spread throughout the food web. This was the case, for example, for starfish (see Section 19.4.2), parasitized caddis larvae (see Section 19.5) and omnivorous crayfish (see Section 19.6). We turn our attention to the complex workings of whole food webs in the next chapter.

Summary

Individual species can influence the composition of whole communities in a variety of ways. In this chapter we pay particular attention to the manner in which competition, predation and parasitism can shape communities.

The view that interspecific competition plays a central and powerful role in the shaping of communities was first fostered by the competitive exclusion principle, with its implication of a limit to the similarity of competing species, and thus a limit to the number of species that can be fitted into a particular community before niche space is fully saturated. There is no argument about whether competition sometimes affects community structure, nor does it play an overriding role in every case. Thus, other factors may prevent competition from progressing to competitive exclusion, by depressing densities or periodically reversing competitive superiority. Moreover, even when competition is intense, the species may coexist if they have aggregated distributions, with each species distributed independently of the others.

Evidence from community studies of niche differentiation for important resources in space and time is consistent with a role for competition in determining community composition. However, the documentation of mere differences among species is insufficient. The approach has been to build null models of actual communities that retain certain of the characteristics of their real counterparts (in terms of diets, feeding morphologies or distributions of coexisting species) but reassemble the components at random, excluding the consequences of competition. Comparisons of predicted and observed patterns have sometimes supported a role for competition, but by no means in all cases.

Grazing animals sometimes increase plant species richness (exploiter-mediated coexistence) by interrupting the process of competitive exclusion, thus imposing their own order on community composition. Plant coexistence is more likely to be fostered by grazers in nutrient-rich situations, and where the preferred food plants would otherwise be competitively superior to less preferred ones.

Carnivorous animals may, likewise, increase the species richness of prey. This has been recorded for rocky shore invertebrates and woodland bird communities, but not for deep-sea vent communities or in terrestrial insect and spider studies. The outcome for species richness in the face of predation again depends on a number of factors, including the pattern of dietary preference and the relative competitive status of the prey.

The incidence of a parasite, like that of other types of exploiter, may determine whether or not a host species occurs in an area; parasites can cause more subtle effects too, by influencing species that are themselves strong interactors or ecosystem engineers in terrestrial, freshwater and marine communities. Parasites are sometimes responsible for exploiter-mediated coexistence.

Communities are not necessarily structured by a single biotic process and the role of consumers in shaping community structure can be expected to be modified according to abiotic conditions. Biotic effects may often be least significant in communities where physical conditions are more severe, variable or unpredictable.

Chapter 20

Food Webs

20.1 Introduction

In the previous chapter we began to consider how population interactions can shape communities. Our focus was on interactions between species occupying the same trophic level (interspecific competition) or between members of adjacent trophic levels. It has already become clear, however, that the structure of communities cannot be understood solely in terms of direct interactions between species. When competitors exploit living resources, the interaction between them necessarily involves further species – those whose individuals are being consumed – while a recurrent effect of predation is to alter the competitive status of prey species, leading to the persistence of species that would otherwise be competitively excluded (consumer-mediated coexistence).

In fact, the influence of a species often ramifies even further than this. The effects of a carnivore on its herbivorous prey may also be felt by any plant population upon which the herbivore feeds, by other predators and parasites of the herbivore, by other consumers of the plant, by competitors of the herbivore and of the plant, and by the myriad of species linked even more remotely in the food web. This chapter is about food webs. In essence, we are shifting the focus to systems usually with at least three trophic levels and 'many' (at least more than two) species.

The study of food webs lies at the interface of community and ecosystem ecology. Thus, we will focus both on the population dynamics of interacting species in the community (species present, connections between them in the web, and interaction strengths) and on the consequences of these species interactions for ecosystem processes such as productivity and nutrient flux.

First, we consider the incidental effects – repercussions further away in the food web – when one species affects the abundance of another (Section 20.2). We examine indirect, 'unexpected' effects in general (Section 20.2.1) and then specifically the effects of 'trophic cascades' (Sections 20.2.3 and 20.2.4). This leads naturally to the question of when and where the control of food webs is 'top-down' (the abundance, biomass or diversity at lower trophic levels depends on the effects of consumers, as in a trophic cascade) or 'bottom-up' (a dependence of community structure on factors acting from lower trophic levels, such as nutrient concentration and prey availability) (Section 20.2.5). We then pay special attention to the properties and effects of 'keystone' species – those with particularly profound and far-reaching consequences elsewhere in the food web (Section 20.2.6).

Second, we consider interrelationships between food web structure and stability (Sections 20.3 and 20.4). Ecologists are interested in community stability for two reasons. The first is practical – and pressing. The stability of a community measures its sensitivity to disturbance, and natural and agricultural communities are being disturbed at an ever-increasing rate. It is essential to know how communities react to such disturbances and how they are likely to respond in the future. The second reason is less practical but more fundamental. The communities we actually see are, inevitably, those that have persisted. Persistent communities are likely to possess properties conferring stability. The most fundamental question in community ecology is: 'Why are communities the way they are?' Part of the answer is therefore likely to be: 'Because they possess certain stabilizing properties'.

20.2 Indirect effects in food webs

20.2.1 'Unexpected' effects

The removal of a species (experimentally, managerially or naturally) can be a powerful tool in unraveling the workings of a food web. If a predator species is removed, we expect an increase in the density of its prey. If a competitor species is removed, we expect an increase in the success of species with which it competes. Not surprisingly, there are plenty of examples of such expected results.

Sometimes, however, removing a species may lead to a *de*crease in competitor abundance, or the removal of a predator may lead to a decrease in prey abundance. Such unexpected effects arise when direct effects are less important than the effects that occur through indirect pathways. Thus, the removal of a species might increase the density of one competitor, which in turn causes another competitor to decline. Or the removal of a predator might increase the abundance of a prey species that is competitively superior to another, leading to a decrease in the density of the latter. In a survey of more than 100 experimental studies of predation, more than 90% demonstrated statistically significant results, and of these about one in three showed unexpected effects (Sih *et al.*, 1985).

These indirect effects are brought especially into focus when the initial removal is carried out for some managerial reason – either the biological control of a pest (Cory & Myers, 2000) or the eradication of an exotic, invader species (Zavaleta *et al.*, 2001) – since the deliberate aim is to solve a problem, not create further, unexpected problems.

mesopredators

For example, there are many islands on which feral cats have been allowed to escape domestication and now threaten native prey, especially birds, with extinction. The 'obvious' response is to eliminate the cats (and conserve their island prey), but as a simple model developed by Courchamp *et al.* (1999) explains, the programs may not have the desired effect, especially where, as is often the case, rats have also been allowed to colonize the island (Figure 20.1). The rats ('mesopredators') typically both compete with and prey upon the birds. Hence, removal of the cats ('superpredators'), which normally prey upon the rats as well as the birds, is likely to increase not decrease the threat to the birds once predation pressure on the mesopredators is removed. Thus, introduced cats on Stewart Island, New Zealand preyed upon an endangered flightless parrot, the kakapo, *Strigops habroptilus* (Karl & Best, 1982);

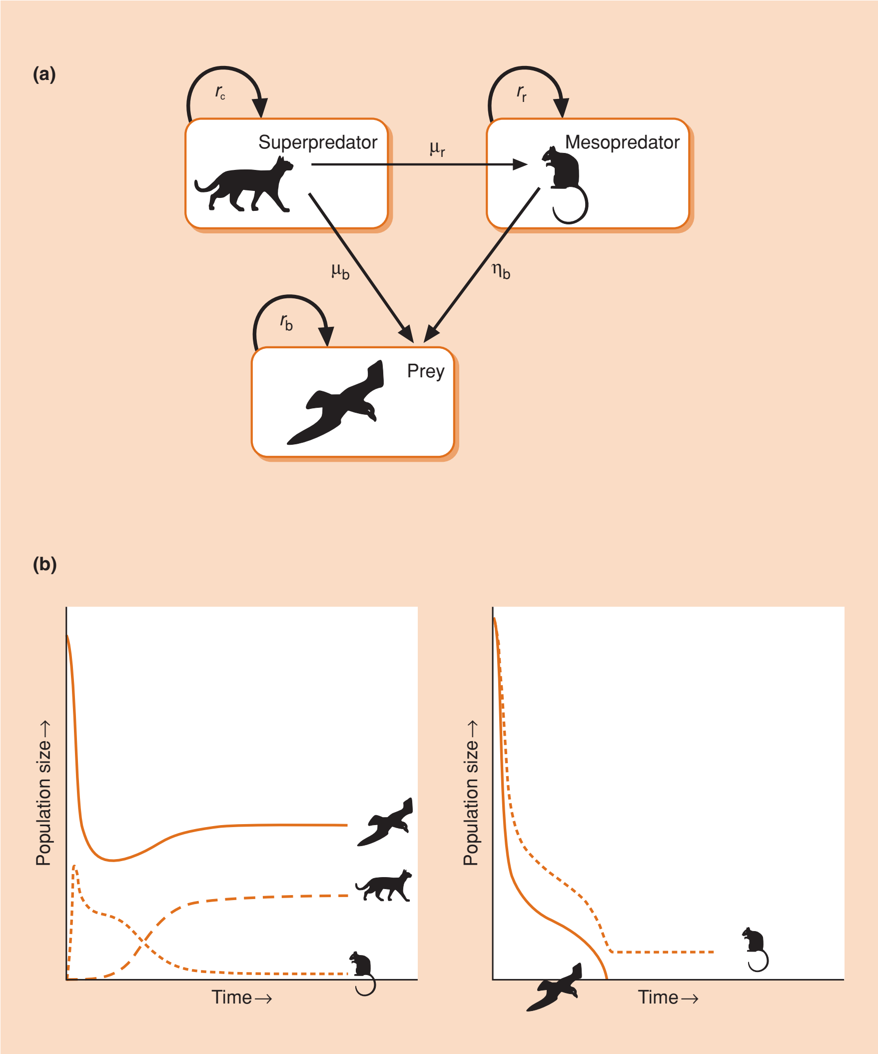


Figure 20.1 (a) Schematic representation of a model of an interaction in which a 'superpredator' (such as a cat) preys both on 'mesopredators' (such as rats, for which it shows a preference) at a per capita rate μ_r, and on prey (such as birds) at a per capita rate μ_b, while the mesopredator also attacks prey at a per capita rate η_b. Each species also recruits to its own population at net per capita rates r_c, r_r and r_b. (b) The output of the model with realistic parameter values: with all three species present, the superpredator keeps the mesopredator in check and all three species coexist (left); but in the absence of the superpredator, the mesopredator drives the prey to extinction (right). (After Courchamp *et al.*, 1999.)

but controlling cats alone would have been risky, since their preferred prey are three species of introduced rats, which, unchecked, could pose far more of a threat to the kakapo. In fact, Stewart Island's kakapo population was translocated to smaller offshore islands where exotic mammalian predators (like rats) were absent or had been eradicated.

Further indirect effects, though not really 'unexpected', have occurred following the release of the weevil, *Rhinocyllus conicus*, as a biological control agent of exotic thistles, *Carduus* spp., in the USA (Louda *et al.*, 1997). The beetle also attacks native thistles in the genus *Cirsium* and reduces the abundance of a native picture-winged fly, *Paracantha culta*, which feeds on thistle seeds – the weevil indirectly harms species that were never its intended target.

20.2.2 Trophic cascades

The indirect effect within a food web that has probably received most attention is the so-called trophic cascade (Paine, 1980; Polis *et al.*, 2000). It occurs when a predator reduces the abundance of its prey, and this cascades down to the trophic level below, such that the prey's own resources (typically plants) increase in abundance. Of course, it need not stop there. In a food chain with four links, a top predator may reduce the abundance of an intermediate predator, which may allow the abundance of a herbivore to increase, leading to a decrease in plant abundance.

The Great Salt Lake of Utah in the USA provides a natural experiment that illustrates a trophic cascade. There, what is essentially a two-level trophic system (zooplankton–phytoplankton) is augmented by a third trophic level (a predatory insect, *Trichocorixa verticalis*) in unusually wet years when salinity is lowered (Wurtsbaugh, 1992). Normally, the zooplankton, dominated by a brine shrimp (*Artemia franciscana*), are capable of keeping phytoplankton biomass at a low level, producing high water clarity. But when salinity declined from above 100 g l^{-1} to 50 g l^{-1} in 1985, *Trichochorixa* invaded and *Artemia* biomass was reduced from 720 to 2 mg m^{-3}, leading to a massive increase in the abundance of phytoplankton, a 20-fold increase in chlorophyll *a* concentration and a fourfold decrease in water clarity (Figure 20.2).

Another example of a trophic cascade, but also of the complexity of indirect effects, is provided by a 2-year experiment in which bird predation pressure was manipulated in an intertidal community on the northwest coast of the USA, in order to determine the effects of the birds on three limpet species (prey) and their algal food (Wootton, 1992). Glaucous-winged gulls (*Larus glaucescens*) and oystercatchers (*Haematopus bachmani*) were excluded by means of wire cages from large areas (each 10 m^2) in which limpets were common. Overall, limpet biomass was much lower in the presence of birds, and the effects of bird predation cascaded down to the plant trophic level, because grazing pressure on the fleshy algae was reduced. In addition, the birds freed up space for algal colonization through the removal of barnacles (Figure 20.3).

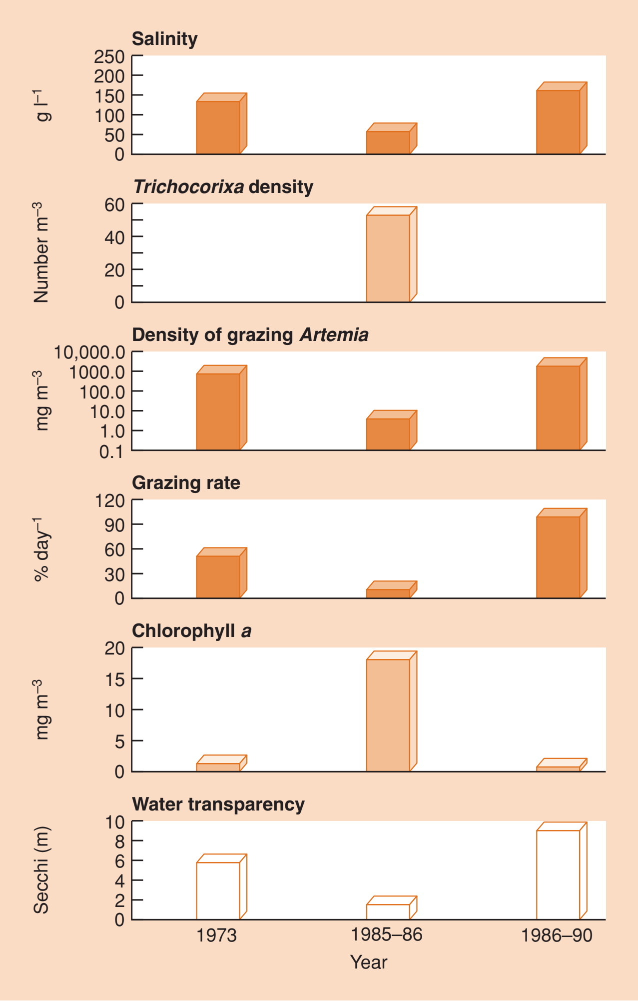


Figure 20.2 Variation in the pelagic ecosystem of the Great Salt Lake during three periods that differed in salinity. (After Wurtsbaugh, 1992.)

It also became evident, however, that while birds reduced the abundance of one of the limpet species, *Lottia digitalis*, as might have been expected, they increased the abundance of a second limpet species (*L. strigatella*) and had no effect on the third, *L. pelta*. The reasons are complex and go well beyond the direct effects of consumption of limpets. *L. digitalis*, a light-colored limpet, tends to occur on light-colored goose barnacles (*Pollicipes polymerus*), whilst dark *L. pelta* occurs primarily on dark Californian mussels (*Mytilus californianus*). Both limpets show strong habitat selection for these cryptic locations. Predation by gulls reduced the area covered by goose barnacles (to the detriment of *L. digitalis*), leading through competitive release to an increase in the area covered by mussels (benefiting *L. pelta*). The third species, *L. strigatella*, is competitively inferior to the others and increased in density because of competitive release.

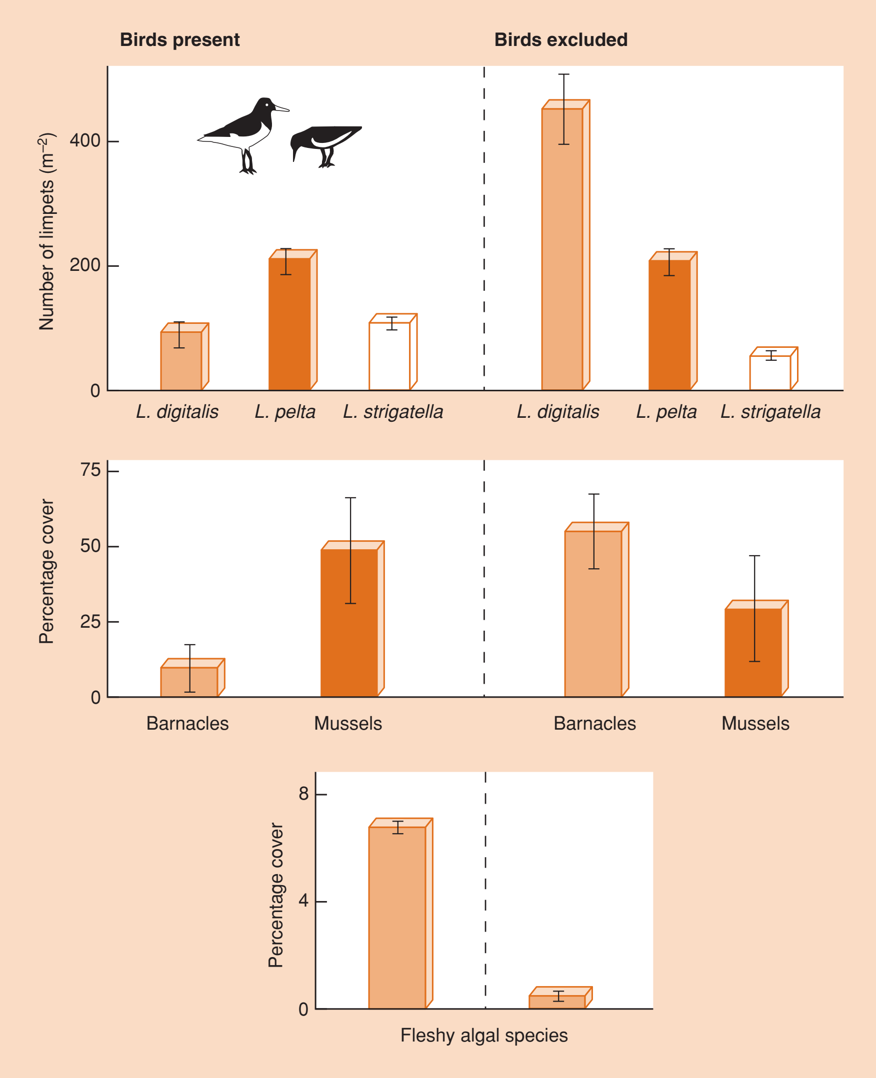


Figure 20.3 When birds are excluded from the intertidal community, barnacles increase in abundance at the expense of mussels, and three limpet species show marked changes in density, reflecting changes in the availability of cryptic habitat and competitive interactions as well as the easing of direct predation. Algal cover is much reduced in the absence of effects of birds on intertidal animals (means ± SE are shown). (After Wootton, 1992.)

20.2.3 Four trophic levels

In a four-level trophic system, if it is subject to trophic cascade, we might expect that the abundances of the top carnivores and the herbivores are positively correlated, as are those of the primary carnivores and the plants. This is precisely what was found in an experimental study of the food web in Eel River, northern California (Figure 20.4a) (Power, 1990). Large fish (roach, *Hesperoleucas symmetricus*, and steelhead trout, *Oncorhynchus mykiss*) reduced the abundance of fish fry and invertebrate predators, allowing their prey, tuft-weaving midge larvae (*Pseudochironomus richardsoni*) to attain high density and to exert intense grazing pressure on filamentous algae (*Cladophora*), whose biomass was thus kept low.

Support for the expected pattern also comes from the tropical lowland forests of Costa Rica and a study of *Tarsobaenus* beetles preying on *Pheidole* ants that prey on a variety of herbivores that attack ant-plants, *Piper cenocladum* (though the detailed trophic interactions are slightly more complex than this – Figure 20.5a). A descriptive study at a number of sites showed precisely the alternation of abundances expected in a four-level trophic cascade: relatively high abundances of plants and ants associated with low levels of herbivory and beetle abundance at three sites, but low abundances of plants and ants associated with high levels of herbivory and beetle abundance at a fourth (Figure 20.5b). Moreover, when beetle abundance was manipulated experimentally at one of the sites, ant and plant abundance were significantly higher, and levels of herbivory lower, in the absence of beetles than in their presence (Figure 20.5c).

four levels can act like three

On the other hand, in a four-level trophic stream community in New Zealand (brown trout (*Salmo trutta*),

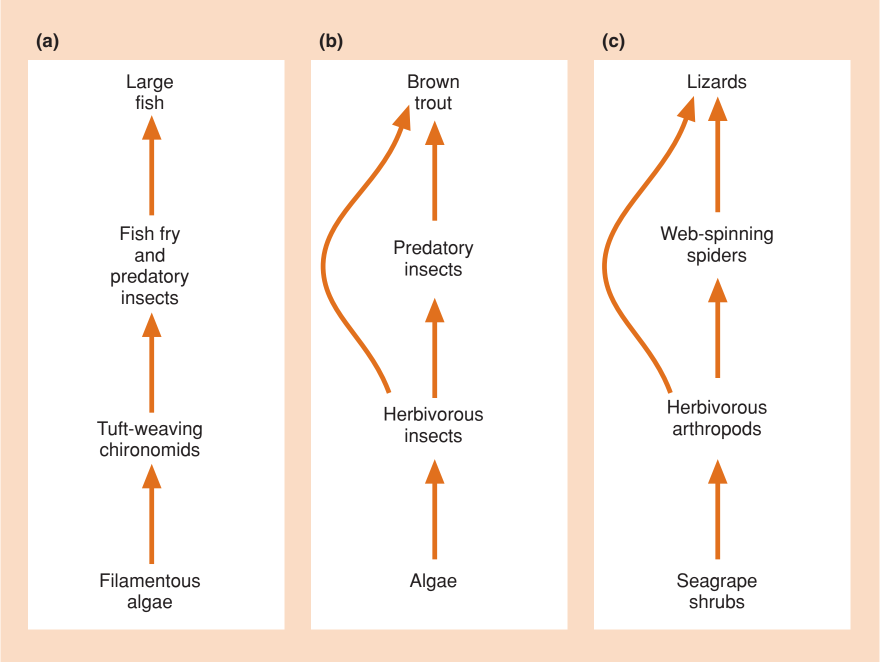


Figure 20.4 Three examples of food webs, each with four trophic levels. (a) The absence of omnivory (feeding at more than one trophic level) in this North American stream community means it functions as a four-level trophic system. On the other hand, web (b) from a New Zealand stream community and web (c) from a terrestrial Bahamanian community both function as three-level trophic webs. This is because of the strong direct effects of omnivorous top predators on herbivores and their less influential effects on intermediate predators. (After Power, 1990; Flecker & Townsend, 1994; Spiller & Schoener, 1994, respectively.)

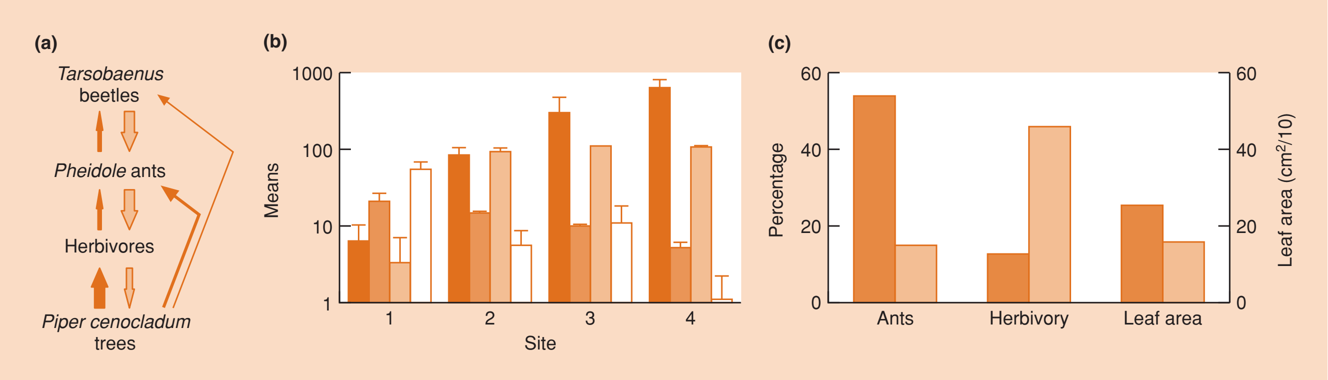


Figure 20.5 (a) Schematic representation of a four-level food chain in Costa Rica. Pale arrows denote mortality and dark arrows a contribution to the consumer's biomass; arrow breadth denotes their relative importance. Both (b) and (c) show evidence of a trophic cascade flowing down from the beetles: with positive correlations between the beetles and herbivores and between the ants and trees. (b) The relative abundance of ant-plants (■), abundance of ants (■) and of beetles (■), and strength of herbivory (□) at four sites. Means and standard errors are shown; the units of measurement are various and are given in the original references. (c) The results of an experiment at site 4 when replicate enclosures were established without beetles (■) and with beetles (■). Units are: ants, % of plant petioles occupied; herbivory, % of leaf area eaten; leaf area, cm^2 per 10 leaves. (After Letourneau & Dyer, 1998a, 1998b; Pace *et al.*, 1999.)

predatory invertebrates, grazing invertebrates and algae), the presence of the top predator did not lead to reduced algal biomass, because the fish influenced not only the predatory invertebrates but also directly affected the activity of the herbivorous species at the next trophic level down (Figure 20.4b) (Flecker & Townsend, 1994). They did this both by consuming grazers and by con-straining the foraging behavior of the survivors (McIntosh & Townsend, 1994). A similar situation has been reported for a four-level trophic terrestrial community in the Bahamas, consisting of lizards, web spiders, herbivorous arthropods and seagrape shrubs (*Coccoloba uvifera*) (Figure 20.4c) (Spiller & Schoener, 1994). The results of experimental manipulations indicated a strong interaction between top predators (lizards) and herbivores, but a weak effect of lizards on spiders. Consequently, the net effect of top predators on plants was positive and there was less leaf damage in the presence of lizards. These four-level trophic communities have a trophic cascade, but it functions as if they had only three levels.

20.2.4 Cascades in all habitats? Community- or species-level cascades?

are trophic cascades all wet?

So much of the discussion of trophic cascades, including their original identification, has been based on aquatic (either marine or freshwater) examples that the question has seriously been asked 'are trophic cascades all wet?' (Strong, 1992). As pointed out by Polis *et al.* (2000), however, in order to answer this question we should recognize a distinction between community- and species-level cascades (Polis, 1999). In the former, the predators in a community, as a whole, control the abundance of the herbivores, such that the plants, as a whole, are released from control by the herbivores. But in a species-level cascade, increases in a particular predator give rise to decreases in particular herbivores and increases in particular plants, without this affecting the whole community. Thus, Schmitz *et al.* (2000), in apparent contradiction of the 'all cascades are wet' proposition, reviewed a total of 41 studies in terrestrial habitats demonstrating trophic cascades; but Polis *et al.* (2000) pointed out that all of these referred only to subsets of the communities of which they were part – that is, they were essentially species-level cascades. Moreover, the measures of plant performance in these studies were typically short term and small scale (for instance, 'leaf damage' as in the lizard–spider–herbivore–seagrape example above) rather than broader scale responses of significance to the whole community, such as plant biomass or productivity.

Polis *et al.* (2000) proposed, then, that community-level cascades are most likely to occur in systems with the following characteristics: (i) the habitats are relatively discrete and homogeneous; (ii) the prey population dynamics (including those of the primary producers) are uniformly fast relative to those of their consumers; (iii) the common prey tend to be uniformly edible; and (iv) the trophic levels tend to be discrete and species interactions strong, such that the system is dominated by discrete trophic chains.

If this proposition is correct, then community-level cascades are most likely in pelagic communities of lakes and in benthic communities of streams and rocky shores (all 'wet') and perhaps in agricultural communities. These tend to be discrete, relatively simple communities, based on fast-growing plants often dominated by a single taxon (phytoplankton, kelp or an agricultural crop). This is not to say (as the Schmitz *et al.* (2000) review confirms) that such forces are absent in more diffuse, species-rich systems, but rather that patterns of consumption are so differentiated that their overall effects are buffered. From the point of view of the whole community, such effects may be represented as trophic trickles rather than cascades.

Certainly, the accumulating evidence seems to support a pattern of overt community-level cascades in simple, especially wet, communities, and much more limited cascades embedded within a broader web in more diverse, especially terrestrial, communities. It remains to be seen, however, whether this reflects some underlying realities or simply differences in the practical difficulties of manipulating and studying cascades in different habitats. An attempt to decide whether there are real differences between aquatic and terrestrial food webs was forced to conclude that there is little evidence, either empirical or theoretical, to either support or refute the idea (Chase, 2000).

20.2.5 Top-down or bottom-up control of food webs? Why is the world green?

We have seen that trophic cascades are normally viewed 'from the top', starting at the highest trophic level. So, in a three-level trophic community, we think of the predators controlling the abundance of the grazers and say that the grazers are subject to 'top-down control'. Reciprocally, the predators are subject to bottom-up control (abundance determined by their resources): a standard predator–prey interaction. In turn, the plants are also subject to bottom-up control, having been released from top-down control by the effects of the predators on the grazers. Thus, in a trophic cascade, top-down and bottom-up control alternate as we move from one trophic level to the next.

But suppose instead that we start at the other end of the food chain, and assume that the plants are controlled bottom-up by competition for their resources. It is still possible for the herbivores to be limited by competition for plants – *their* resources – and for the predators to be limited by competition for herbivores. In this scenario, all trophic levels are subject to bottom-up control (also called 'donor control'), because the resource controls the abundance of the consumer but the consumer does not control the abundance of the resource. The question has therefore arisen: 'Are food webs – or are particular *types* of food web – dominated by either top-down or bottom-up control?' (Note again, though, that even when top-down control 'dominates', top-down and bottom-up control are expected to alternate from trophic level to trophic level.)

top-down, bottom-up and cascades

Clearly, this is linked to the issues we have just been dealing with. Top-down control should dominate in systems with powerful community-level trophic cascades. But in systems where trophic cascades, if they exist at all, are limited to the species level, the community as a whole could be dominated by top-down or bottom-up control. Also, there are some communities that tend, inevitably, to be dominated by bottom-up control, because consumers have little or no influence on the supply of their food resource. The most obvious group of organisms to which this applies is the detritivores (see Chapter 11), but consumers of nectar and seeds are also likely to come into this category (Odum & Biever, 1984) and few of the multitude of rare phytophagous insects are likely to have any impact upon the abundance of their host plants (Lawton, 1989).

why is the world green? . . .

The widespread importance of top-down control, foreshadowing the idea of the trophic cascade, was first advocated in a famous paper by Hairston *et al.* (1960), which asked 'Why is the world green?' They answered, in effect, that the world is green because top-down control predominates: green plant biomass accumulates because predators keep herbivores in check. The argument was later extended to systems with fewer or more than three trophic levels (Fretwell, 1977; Oksanen *et al.*, 1981).

. . . or is it prickly and bad tasting?

Murdoch (1966), in particular, challenged these ideas. His view, described by Pimm (1991) as 'the world is prickly and tastes bad', emphasized that even if the world is green (assuming it is), it does not necessarily follow that the herbivores are failing to capitalize on this because they are limited, top-down, by their predators. Many plants have evolved physical and chemical defenses that make life difficult for herbivores (see Chapter 3). The herbivores may therefore be competing fiercely for a limited amount of palatable and unprotected plant material; and their predators may, in turn, compete for scarce herbivores. A world controlled from the bottom-up may still be green.

Oksanen (1988), moreover, has argued that the world is not always green – particularly if the observer is standing in the middle of a desert or on the northern coast of Greenland. Oksanen's contention (see also Oksanen *et al.*, 1981) is that: (i) in extremely unproductive or 'white' ecosystems, grazing will be light because there is not enough food to support effective populations of herbivores: both the plants and the herbivores will be limited bottom-up; (ii) at the highest levels of plant productivity, in 'green' ecosystems, there will also be light grazing because of top-down limitation by predators (as argued by Hairston *et al.*, 1960); but (iii) between these extremes, ecosystems may be 'yellow', where plants are top-down limited by grazers because there are insufficient herbivores to support effective populations of predators. The suggestion, then, is that productivity shifts the balance between top-down and bottom-up control by altering the lengths of food chains. This still remains to be critically tested.

an influence of primary productivity?

There are also suggestions that the level of primary productivity may be influential in other ways in determining whether top-down or bottom-up control is predominant. Chase (2003) examined the effect of nutrient concentrations on a freshwater web comprising an insect predator, *Belostoma flumineum*, feeding on two species of herbivorous snails, *Physella girina* and *Helisoma trivolvis*, in turn feeding on macrophytes and algae within a larger food web including zooplankton and phytoplankton. At the lowest nutrient concentrations, the snails were dominated by the smaller *P. gyrina*, vulnerable to predation, and the predator gave rise to a trophic cascade extending to the primary producers. But at the highest concentrations, the snails were dominated by the larger *H. trivolvis*, relatively invulnerable to predation, and no trophic cascade was apparent (Figure 20.6). This study, therefore, also lends support to Murdoch's proposition that the 'world tastes bad', in that invulnerable herbivores gave rise to a web with a relative dominance of bottom-up control. Overall, though, we see again that the elucidation of clear patterns in the predominance of top-down or bottom-up control remains a challenge for the future.

20.2.6 Strong interactors and keystone species

Some species are more intimately and tightly woven into the fabric of the food web than others. A species whose removal would produce a significant effect (extinction or a large change in density) in at least one other species may be thought of as a strong interactor. Some strong interactors would lead, through their removal, to significant changes spreading throughout the food web – we refer to these as *keystone species*.

A keystone is the wedge-shaped block at the highest point of an arch that locks the other pieces together. Its early use in food web architecture referred to a top predator (the starfish *Pisaster* on a rocky shore; see Paine (1966) and Section 19.4.2) that has an indirect beneficial effect on a suite of inferior competitors by depressing the abundance of a superior competitor. Removal of the keystone predator, just like the removal of the keystone in an arch, leads to a collapse of the structure. More precisely, it leads to extinction or large changes in abundance of several species, producing a community with a very different species composition and, to our eyes, an obviously different physical appearance.

what is a keystone species?

It is now usually accepted that keystone species can occur at other trophic levels (Hunter & Price, 1992). Use of the term has certainly broadened since it was first coined (Piraino *et al.*, 2002), leading some to question whether it has any value at all. Others have defined it more narrowly – in particular, as a species whose impact is 'disproportionately large relative to its abundance' (Power *et al.*, 1996). This has the advantage of excluding from keystone status what would otherwise be rather trivial examples, especially 'ecological dominants' at lower trophic levels, where one species may provide the resource on which a whole myriad of other species depend – for example, a coral, or the oak trees in an oak woodland. It is certainly more challenging and more useful to identify species with disproportionate effects.

Semantic quibbles aside, it remains important to acknowledge that while all species no doubt influence the structure of their communities to a degree, some are far more influential than

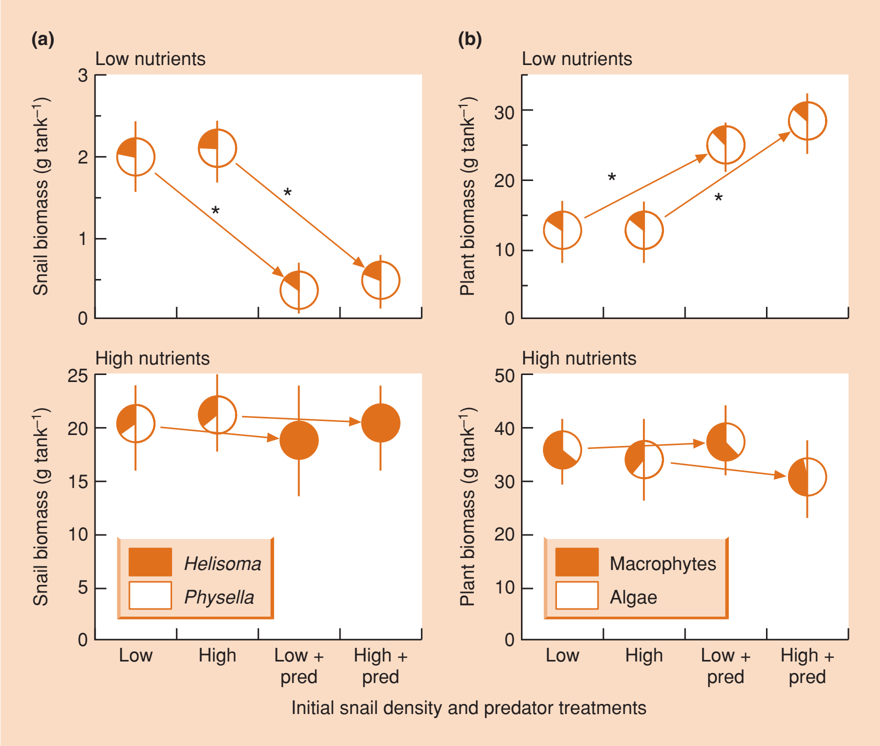


Figure 20.6 Top-down control, but only with low productivity. (a) Snail biomass and (b) plant biomass in experimental ponds with low or high nutrient treatments (vertical bars are standard errors). With low nutrients, the snails were dominated by *Physella* (vulnerable to predation) and the addition of predators led to a significant decline (indicated by *) in snail biomass and a consequent increase in plant biomass (dominated by algae). But with high nutrients, *Helisoma* snails (less vulnerable to predation) increased their relative abundance, and the addition of predators led neither to a decline in snail biomass nor to an increase in plant biomass (often dominated by macrophytes). (After Chase, 2003.)

others. Indeed, various indices have been proposed to measure this influence (Piraino *et al.*, 2002); for example, the 'community importance' of a species is the percentage of other species lost from the community after its removal (Mills *et al.*, 1993). Also, recognizing the concept of keystone species and attempting to identify them are both important from a practical point of view because keystone species are likely to have a crucial role in conservation: changes in their abundance will, by definition, have significant repercussions for a whole range of other species. Inevitably, though, the dividing line between keystone species and the rest is not clear cut.

keystone species can occur throughout the food web

In principle, keystone species can occur throughout the food web. Jones *et al.* (1997) point out that it need not even be their trophic role that makes them important, but rather that they act as 'ecological engineers' (see Section 13.1). Beavers, for example, in cutting down a tree and building a dam, create a habitat on which hundreds of species rely. Keystone mutualists (Mills *et al.*, 1993) may also exert influence out of proportion to their abundance: examples include a pollinating insect on which an ecologically dominant plant relies, or a nitrogen-fixing bacterium supporting a legume and hence the whole structure of a plant community and the animals reliant on it. Certainly, keystone species are limited neither to top predators nor consumers mediating coexistence amongst their prey. For example, lesser snow geese (*Chen caerulescens caerulescens*) are herbivores that breed in large colonies in coastal brackish and freshwater marshes along the west coast of Hudson Bay in Canada. At their nesting sites in spring, before the onset of above-ground growth of vegetation, adult geese grub for the roots and rhizomes of graminoid plants in dry areas and eat the swollen bases of sedge shoots in wet areas. Their activity creates bare patches (1–5 m^2) of peat and sediment. Since there are few pioneer plant species able to recolonize these patches, recovery is very slow. Furthermore, in ungrubbed brackish marshes, intense grazing by high densities of geese later in the summer is essential in establishing and maintaining grazing 'lawns' of *Carex* and *Puccinellia* (Kerbes *et al.*, 1990). It seems reasonable to consider the lesser snow goose as a keystone (herbivore) species.

20.3 Food web structure, productivity and stability

Any ecological community can be characterized by its *structure* (number of species, interaction strength within the food web, average length of food chains, etc.), by certain *quantities* (especially biomass and the rate of production of biomass, which we can summarize as '*productivity*') and by its temporal *stability* (Worm & Duffy, 2003). In the remainder of this chapter, we examine some of the interrelationships between these three.

Much of the very considerable recent interest in this area has been generated by the understandable concern to know what might be the consequences of the inexorable decline in biodiversity (a key aspect of structure) for the stability and productivity of biological communities.

We will be particularly concerned with the effects of food web structure (food web complexity in this section; food chain length and a number of other measures in Section 20.4) on the stability of the structure itself and the stability of community productivity. It should be emphasized at the outset, however, that progress in our understanding of food webs depends critically on the quality of data that are gathered from natural communities. Recently, several authors have called this into doubt, particularly for earlier studies, pointing out that organisms have often been grouped into taxa extremely unevenly and sometimes at the grossest of levels. For example, even in the same web, different taxa may have been grouped at the level of kingdom (plants), family (Diptera) and species (polar bear). Some of the most thoroughly described food webs have been examined for the effects of such an uneven resolution by progressively lumping web elements into coarser and coarser taxa (Martinez, 1991; Hall & Raffaelli, 1993, Thompson & Townsend, 2000). The uncomfortable conclusion is that most food web properties seem to be sensitive to the level of taxonomic resolution that is achieved. These limitations should be borne in mind as we explore the evidence for food web patterns in the following sections.

First, however, it is necessary to define 'stability', or rather to identify the various different types of stability.

20.3.1 What do we mean by 'stability'?

resilience and resistance

Of the various aspects of stability, an initial distinction can be made between the resilience of a community (or any other system) and its resistance. *Resilience* describes the speed with which a community returns to its former state after it has been perturbed and displaced from that state. *Resistance* describes the ability of the community to avoid displacement in the first place. (Figure 20.7 provides a figurative illustration of these and other aspects of stability.)

local and global stability

The second distinction is between local stability and global stability. *Local stability* describes the tendency of a community to return to its original state (or something close to it) when subjected to a small perturbation. *Global stability* describes this tendency when the community is subjected to a large perturbation.

dynamic fragility and robustness

A third aspect is related to the local/global distinction but concentrates more on the environment of the community. The stability of any community depends on the environment in which it exists, as well as on the densities and characteristics of the component species. A community that is stable only within a narrow range of environmental conditions, or for only a very limited range of species' characteristics, is said to be *dynamically fragile*. Conversely, one that is stable within a wide range of conditions and characteristics is said to be *dynamically robust*.

Lastly, it remains for us to specify the aspect of the community on which we will focus. Ecologists have often taken a demographic approach. They have concentrated on the *structure* of a community. However, it is also possible to focus on the stability of ecosystem processes, especially *productivity*.

20.3.2 Community complexity and the 'conventional wisdom'

The connections between food web structure and food web stability have preoccupied ecologists for at least half a century. Initially, the 'conventional wisdom' was that increased complexity within a community leads to increased stability; that is, more complex communities are better able to remain structurally the same in the face of a disturbance such as the loss of one or more species. Increased complexity, then as now, was variously taken to mean more species, more interactions between species, greater average strength of interaction, or some combination of all of these things. Elton (1958) brought together a variety of empirical and theoretical observations in support of the view that more complex communities are more stable (simple mathematical models are inherently unstable, species-poor island communities are liable to invasion, etc.). Now, however, it is clear his assertions were mostly either untrue or else liable to some other plausible interpretation. (Indeed, Elton himself pointed out that more extensive analysis was necessary.) At about the same time, MacArthur (1955) proposed a more theoretical argument in favor of the conventional wisdom. He suggested that the more possible pathways there were by which energy passed through a community, the less likely it was that the densities of constituent species would change in response to an abnormally raised or lowered density of one of the other species.

20.3.3 Complexity and stability in model communities: populations

The conventional wisdom, however, has by no means always received support, and has been undermined in particular by the analysis of mathematical models. A watershed study was that by May (1972). He constructed model food webs comprising a number of species, and examined the way in which the population size of each species changed in the neighborhood of its equilibrium abundance (i.e. the *local* stability of *individual populations*).

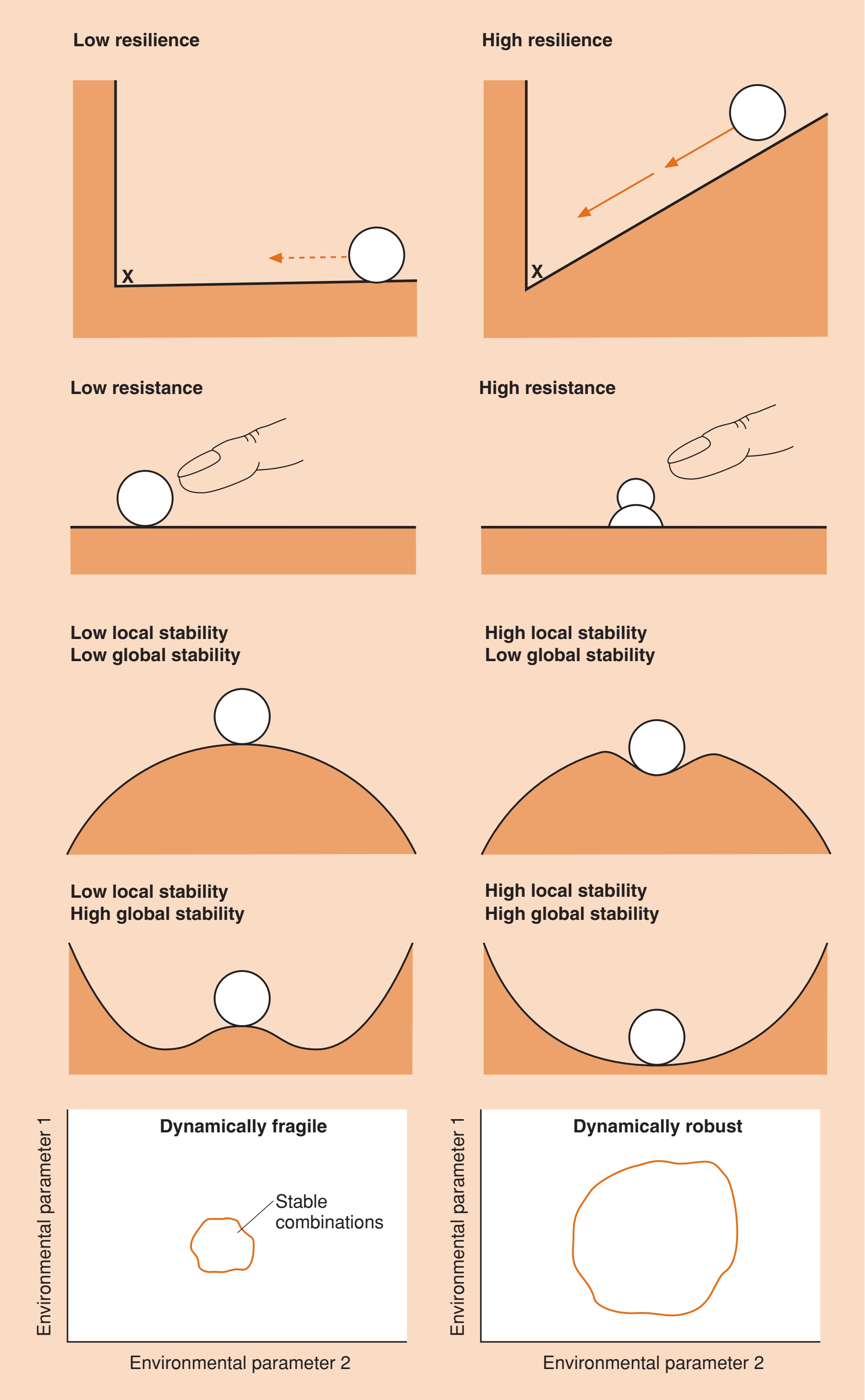


Figure 20.7 Various aspects of stability, used in this chapter to describe communities, illustrated here in a figurative way. In the resilience diagrams, X marks the spot from which the community has been displaced.

Each species was influenced by its interaction with all other species, and the term β_{ij} was used to measure the effect of species *j*'s density on species *i*'s rate of increase. The food webs were 'randomly assembled', with all self-regulatory terms (β_{ii}, β_{jj}, etc.) set at –1, but all other β values distributed at random, including a certain number of zeros. The webs could then be described by three parameters: *S*, the number of species; *C*, the 'connectance' of the web (the fraction of all possible pairs of species that interacted directly, i.e. with β_{ij} non-zero); and β, the average 'interaction strength' (i.e. the average of the non-zero β values, disregarding sign). May found that these food webs were only likely to be stable (i.e. the populations would return to equilibrium after a small disturbance) if:

$$\beta(SC)^{1/2} < 1. \tag{20.1}$$

Otherwise, they tended to be unstable.

In other words, increases in the number of species, in connectance and in interaction strength all tend to increase instability (because they increase the left-hand side of the inequality above). Yet each of these represents an increase in complexity. Thus, this model (along with others) suggests that complexity leads to *instability*, and it certainly indicates that there is no necessary, unavoidable connection linking stability to complexity.

many models defy the conventional wisdom

Other studies, however, have suggested that this connection between complexity and instability may be an artefact arising out of the particular characteristics of the model communities or the way they have been analyzed. In the first place, randomly assembled food webs often contain biologically unreasonable elements (e.g. loops of the type: A eats B eats C eats A). Analyses of food webs that are constrained to be reasonable (Lawlor, 1978; Pimm, 1979) show that whilst stability still declines with complexity, there is no sharp transition from stability to instability (compared with the inequality in Equation 20.1). Second, if systems are 'donor controlled' (i.e. $\beta_{ij} > 0$, $\beta_{ji} = 0$), stability is unaffected by or actually increases with complexity (DeAngelis, 1975). And the relationship between complexity and stability in models becomes more complicated if attention is focused on the resilience of those communities that *are* stable. While the proportion of stable communities may decrease with increased complexity, resilience *within* this subset (a crucial aspect of stability) may increase (Pimm, 1979).

Finally, though, the relationship between species richness and the variability of populations appears to be affected in a very general way by the relationship between the mean (m) and variance (s^2) of abundance of individual populations over time (Tilman, 1999). This relationship can be denoted as:

$$s^2 = cm^z, \tag{20.2}$$

where c is a constant and z is the so-called scaling coefficient. There are grounds for expecting values of z to lie between 1 and 2 (Murdoch & Stewart-Oaten, 1989) and most observed values seem to do so (Cottingham *et al.*, 2001). In this range, population variability increases with species richness (Figure 20.8) – a connection between complexity and population instability, as found in May's original model.

Overall, therefore, most models indicate that population stability tends to decrease as complexity increases. This is sufficient to undermine the conventional wisdom prior to 1970. However, the conflicting results amongst the models at least suggest that no single relationship will be appropriate in all communities. It would be wrong to replace one sweeping generalization with another.

20.3.4 Complexity and stability in model communities: whole communities

The effects of complexity, especially species richness, on the stability of aggregate properties of whole communities, such as their biomass or productivity, seem rather more straightforward, at least from a theoretical point of view (Cottingham *et al.*, 2001). Broadly, in richer communities, the dynamics of these aggregate properties are *more* stable. In the first place, as long as the fluctuations in different populations are not perfectly correlated, there is an inevitable 'statistical averaging' effect when populations are added together – when one goes up, another is going down – and this tends to increase in effectiveness as richness (the number of populations) increases.

aggregate properties are more stable in richer communities

This effect interacts in turn with the variance to mean relationship of Equation 20.2. As richness increases, average abundance tends to decrease, and the value of z in Equation 20.2 determines how the variance in abundance changes with this. Specifically, the greater the value of z, the greater the proportionate decrease in variance, and the greater the increase in stability with increasing richness (Figure 20.8). Only in the rare and probably unrealistic case of z being less than 1 (variance *increases* proportionately as mean abundance declines) is the statistical averaging effect absent.

Note that the related topic of the relationship between richness and productivity – in so far as this is different from the relationship between richness and the *stability* of productivity – is picked up in the next chapter (see Section 21.7), which is devoted to species richness.

20.3.5 Complexity and stability in practice: populations

what should we expect to see in nature?

Even if complexity and population instability are connected in models, this does not mean that we should necessarily expect to see the same association in real communities. For one thing, the range and predictability of environmental conditions will vary from place to place. In a stable and predictable environment, a community that is dynamically fragile may still persist. However, in a variable and unpredictable environment, only a community that is dynamically robust will be able to persist. Hence, we might expect to see: (i) complex and fragile communities in stable and predictable environments, and simple and robust communities in variable and unpredictable

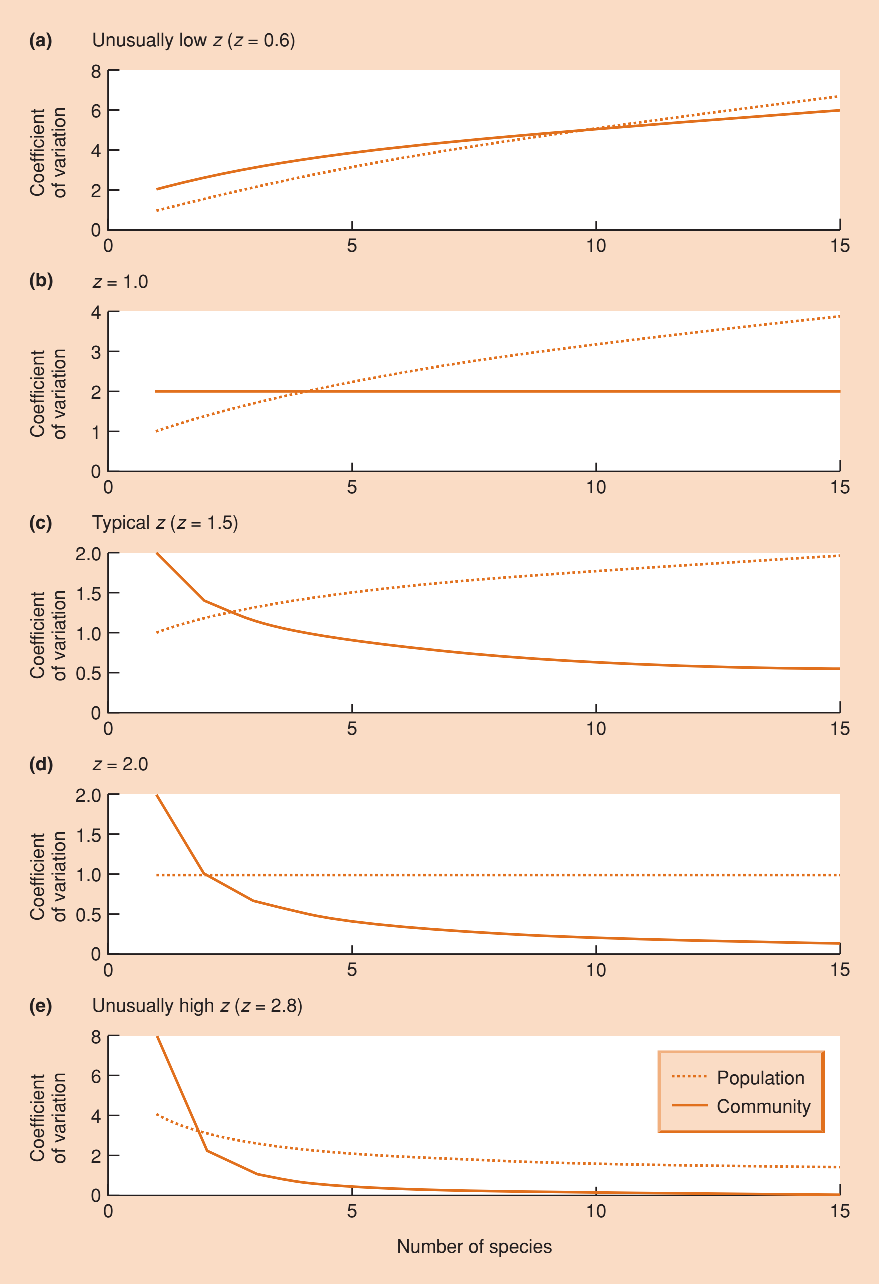


Figure 20.8 The effect of species richness (number of species) on the temporal variability (coefficient of variation, CV) of population size and aggregate community abundance, in model communities in which all species are equally abundant and have the same CV, for various values of the scaling coefficient, z, in the relationship between the mean and variance of abundance (Equation 20.2). (a) $z = 0.6$, an unusually low value. (b) $z = 1.0$, the lower end of typical values. (c) $z = 1.5$, a typical value. (d) $z = 2.0$, the upper end of typical values. (e) $z = 2.8$, an unusually high value. (After Cottingham *et al.*, 2001.)

environments; but (ii) approximately the same recorded stability (in terms of population fluctuations, etc.) in all communities, since this will depend on the inherent stability of the community combined with the variability of the environment. Moreover, we might expect manmade perturbations to have their most profound effects on the dynamically fragile, complex communities of stable environments, which are relatively unused to perturbations, but least effect on the simple, robust communities of variable environments, which have previously been subjected to natural perturbations.

connections to *r* and *K*

It is also worth noting that there is likely to be an important parallel between the properties of a community and the properties of its constituent populations. In stable environments, populations will be subject to a relatively high degree of *K* selection (see Section 4.12); in variable environments they will be subject to a relatively high degree of *r* selection. The *K*-selected populations (high competitive ability, high inherent survivorship but low reproductive output) will be *resistant* to perturbations, but once perturbed will have little capacity to recover (low resilience). The *r*-selected populations, by contrast, will have little resistance but a higher resilience. The forces acting on the component populations will therefore reinforce the properties of their communities, namely fragility (low resilience) in stable environments and robustness in variable ones.

what is the evidence from real communities?

A number of studies have examined the relationship between S, C and β in real communities, following the prediction summarized in Equation 20.1. The argument they use runs as follows. The communities we observe must be stable – otherwise we would not be able to observe them. If communities are only stable for $\beta(SC)^{1/2} < 1$ (or at least when the left-hand side of the inequality is low), then increases in S will lead to decreased stability unless there are compensatory decreases in C and/or β. It is usually assumed, for want of evidence, that β is constant (though ecologists are rising to the challenge of quantifying interaction strengths – e.g. Benke *et al.*, 2001). Thus, communities with more species will only retain stability if there is an associated decline in average connectance, C. We should therefore observe a negative correlation between S and C. A group of 40 food webs was gleaned from the literature by Briand (1983), including terrestrial, freshwater and marine examples. For each community, a single value for connectance was calculated as the total number of identified interspecies links as a proportion of the total possible number. Connectance is plotted against S in Figure 20.9a. As predicted, connectance decreases with species number.

connectance decreases with species richness – except when it doesn't

However, the data in Briand's compilation were not collected for the purpose of quantitative study of food web properties. Moreover, the level of taxonomic resolution varied substantially from web to web. More recent studies, in which food webs have been much more rigorously documented, indicate that C may decrease with S (as predicted) (Figure 20.9b), that C may be independent of S (Figure 20.9c) or may even increase with S (Figure 20.9d). Thus, no single relationship between complexity and stability receives consistent support from food web analyses.

Might other hypotheses do better in accounting for the recorded patterns in connectance? Morphological, physiological and behavioral features restrict the number of types of prey that a consumer can exploit. If each species is adapted to feed on a fixed number of other species, then SC turns out to be constant (Warren, 1994), and C should decrease with increasing S. But if each species feeds on anything whose characteristics fall within

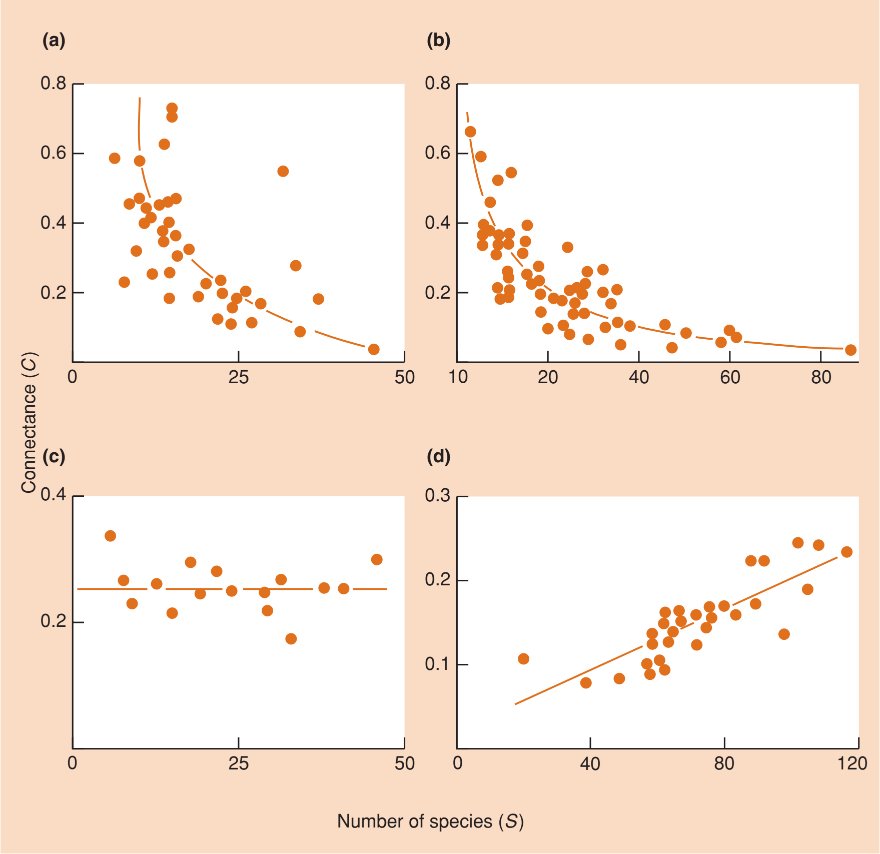


Figure 20.9 The relationships between connectance (C) and species richness (S). (a) For a compilation from the literature of 40 food webs from terrestrial, freshwater and marine environments. (After Briand, 1983.) (b) For a compilation of 95 insect-dominated webs from various habitats. (After Schoenly *et al.*, 1991.) (c) For seasonal versions of a food web for a large pond in northern England, varying in species richness from 12 to 32. (After Warren, 1989.) (d) For food webs from swamps and streams in Costa Rica and Venezuela. (After Winemiller, 1990.) ((a–d) after Hall & Raffaelli, 1993.)

Table 20.1 The influence of nutrient addition on species richness, equitability ($H/\ln S$) and diversity (Shannon's index, H) in two fields; and grazing by African buffalo on species diversity in two areas of vegetation. (After McNaughton, 1977.)

	Control plots	*Experimental plots*	*Statistical significance*
Nutrient addition			
Species richness per 0.5 m^2 plot			
Species-poor plot	20.8	22.5	NS
Species-rich plot	31.0	30.8	NS
Equitability			
Species-poor plot	0.660	0.615	NS
Species-rich plot	0.793	0.740	$P < 0.05$
Diversity			
Species-poor plot	2.001	1.915	NS
Species-rich plot	2.722	2.532	$P < 0.05$
Grazing			
Species diversity			
Species-poor plot	1.069	1.357	NS
Species-rich plot	1.783	1.302	$P < 0.005$

NS, not significant.

the range to which it is adapted, then as richness increases, so too will the likely number within the acceptable range. In this more realistic case, connectance would be roughly constant. Moreover, if webs are made up of specialists, overall connectance will be low, whereas webs composed of generalists will have high connectance. The proportion of specialists may change with richness. Thus, the inconsistency of pattern may simply reflect a diversity of forces acting on different webs.

The prediction that populations in richer communities are less stable when disturbed can also be investigated experimentally. One classic study, for example, monitored the resistance in two grassland communities (McNaughton, 1978). In the first, plant nutrients were added to the soil of a community in New York State; in the second, the action of grazing animals was manipulated in the Serengeti. In both cases, the treatment was applied to species-rich and species-poor plant communities, and in both, disturbance reduced the diversity of the former but not the latter (Table 20.1). This was consistent with the prediction, but the effects, while significant, were relatively slight.

Similarly, Tilman (1996) pooled data for 39 common plant species from 207 grassland plots in Cedar Creek Natural History Area, Minnesota, over an 11-year period. He found that variation in the biomass of individual species increased significantly, but only very weakly, with the richness of the plots (Figure 20.10a).

Finally, there have been a number of studies directed at the question of whether the level of 'perceived stability' of natural populations (interannual variation in abundance) varies with the richness or complexity of the community. Leigh (1975) for herbivorous vertebrates, Bigger (1976) for crop pests and Wolda (1978) for insects, all failed to find evidence that it did so.

no consistent answers

Overall, therefore, like the theoretical studies, empirical studies hint at decreased population stability (increased variability) in more complex communities, but the effect seems to be weak and inconsistent.

20.3.6 Complexity and stability in practice: whole communities

Turning to the aggregate, whole community level, evidence is largely consistent in supporting the prediction that increased richness in a community increases stability (decreases variability), though a number of studies have failed to detect any consistent relationship (Cottingham *et al.*, 2001; Worm & Duffy, 2003).

data support the models: aggregates are more stable in richer communities

First, returning to McNaughton's (1978) studies of US and Serengeti grasslands, the effects of perturbations were quite different when viewed in ecosystem (as opposed to population) terms. The addition of fertilizer significantly increased primary productivity in the species-poor field in New York State (+53%), but only slightly and insignificantly changed productivity in the species-rich field (+16%); and grazing in the Serengeti significantly reduced the standing crop biomass in the species-poor grassland (−69%), but only slightly reduced that of the species-rich field (−11%). Similarly, in Tilman's (1996) Minnesota grasslands, in contrast to the weak negative effect found at the population level, there was a strong positive effect of richness on the stability of community biomass (Figure 20.10b).

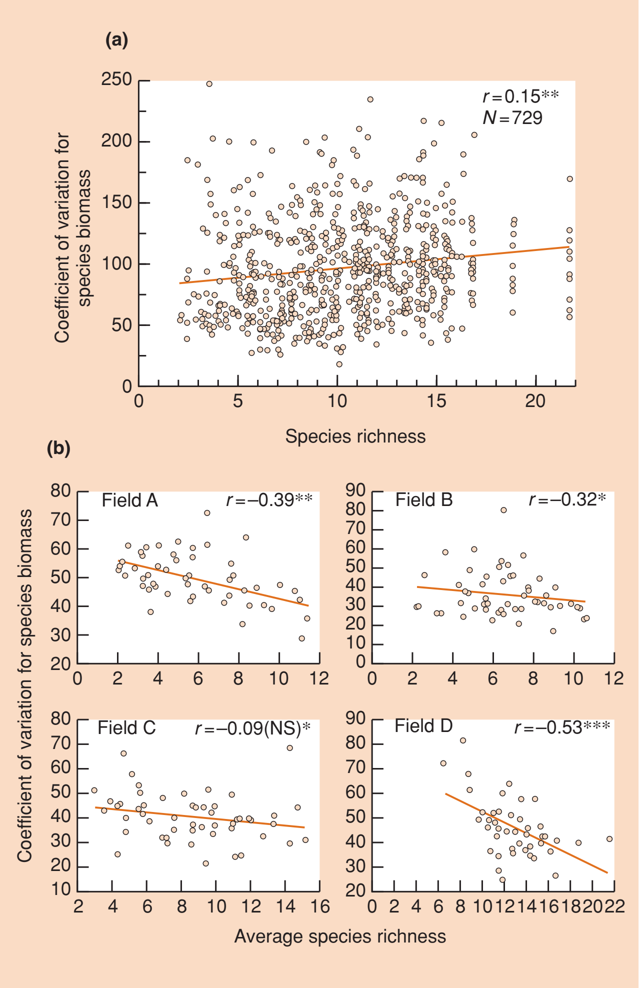


Figure 20.10 (a) The coefficient of variation of population biomass for 39 plant species from plots in four fields in Minnesota over 11 years (1984–94) plotted against species richness in the plots. Variation increased with richness but the slope was very shallow. (b) The coefficient of variation for community biomass in each plot plotted against species richness for each of the four fields. Variation consistently decreased with richness. In both cases, regression lines and correlation coefficients are shown. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. (After Tilman, 1996.)

McGrady-Steed *et al.* (1997) manipulated richness in aquatic microbial communities (producers, herbivores, bacterivores and predators) and found that variation in another ecosystem measure, carbon dioxide flux (a measure of community respiration) also declined with richness (Figure 20.11). On the other hand, in an experimental study of small grassland communities perturbed by an induced drought, Wardle *et al.* (2000) found detailed community composition to be a far better predictor of stability than overall richness.

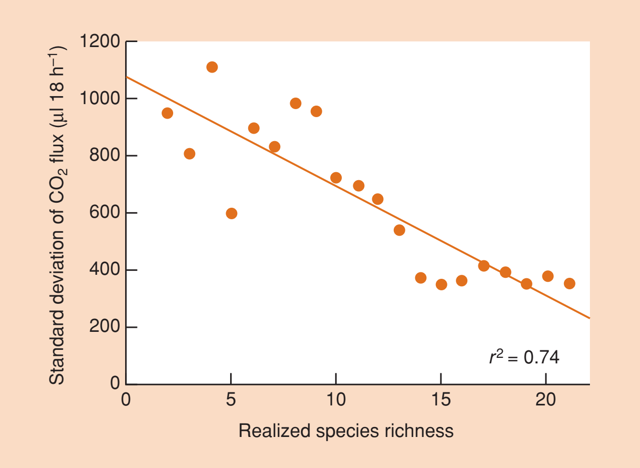


Figure 20.11 Variation (i.e. 'instability') in productivity (standard deviation of carbon dioxide flux) declined with species richness in microbial communities observed over a 6-week period. Richness is described as 'realized' because it refers to the number of species present at the time of the observation, irrespective of the number of species with which the community was initiated. (After McGrady-Steed *et al.*, 1997.)

Studies of the response of a community to a perturbation (e.g. McNaughton, 1978) or of variations in the community in response to year-to-year variations in the environment (e.g. Tilman, 1996), are focused largely on the resistance of communities to change. A quite different perspective examines the resilience of communities to perturbations in ecosystem characteristics such as the energy or nutrient levels contained within them. O'Neill (1976), for example, considered the community as a three-compartment system consisting of active plant tissue (*P*), heterotrophic organisms (*H*) and inactive dead organic matter (*D*). The rate of change in the standing crop in these compartments depends on transfers of energy between them (Figure 20.12a). Inserting real data from six communities representing tundra, tropical forest, temperate deciduous forest, a salt marsh, a freshwater spring and a pond, O'Neill subjected the *models* of these communities to a standard perturbation: a 10% decrease in the initial standing crop of active plant tissue. He then monitored the rates of recovery towards equilibrium, and plotted these as a function of the energy input per unit standing crop of living tissue (Figure 20.12b).

importance of the nature – not just the richness – of the community

The pond system, with a relatively low standing crop and a high rate of biomass turnover, was the most resilient. Most of its plant populations have short lives and rapid rates of population increase. The salt marsh and forests had intermediate values, whilst tundra had the lowest resilience. There is a clear relationship

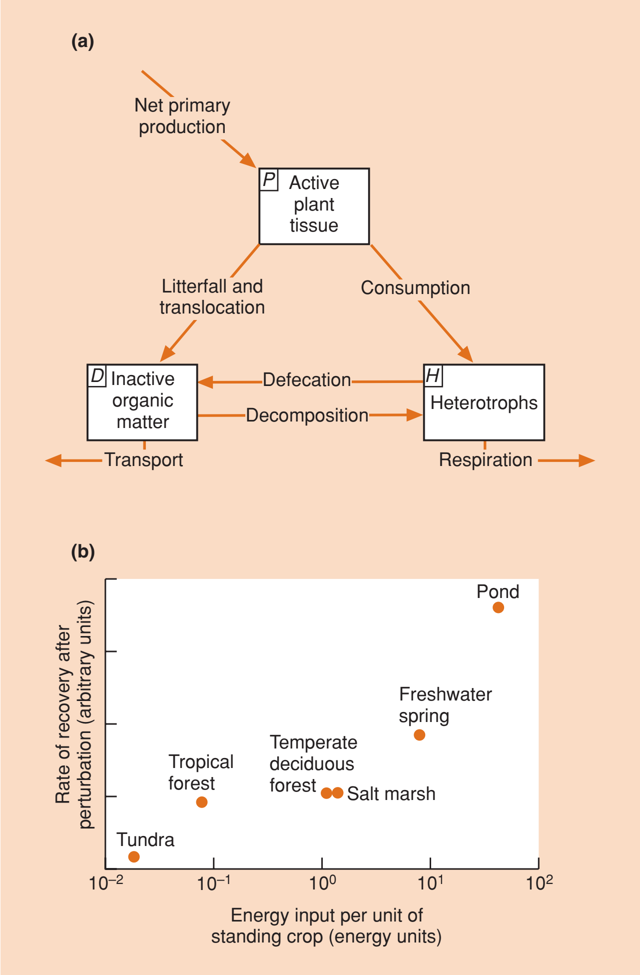


Figure 20.12 (a) A simple model of a community. The three boxes represent components of the system and arrows represent transfers of energy between the system components. (b) The rate of recovery (index of resilience) after perturbation (as a function of energy input per unit standing crop) for models of six contrasting communities. The pond community was most resilient to perturbation, tundra least so. (After O'Neill, 1976.)

between resilience and energy input per unit standing crop. This seems to depend in part on the relative importance of heterotrophs in the system. The most resilient system, the pond, had a biomass of heterotrophs 5.4 times that of autotrophs (reflecting the short life and rapid turnover of phytoplankton, the dominant plants in this system), whilst the least resilient tundra had a heterotroph : autotroph ratio of only 0.004. Thus, the flux of energy through the system has an important influence on resilience. The higher this flux, the more quickly will the effects of a perturbation be 'flushed' from the system. An exactly analogous conclusion has been reached by DeAngelis (1980), but for nutrient cycling rather than energy flow. Here too, then, stability seems more influenced by the nature of the species in the community than by simple measures such as overall richness.

20.3.7 The number of species or their identity? Keystones again

Indeed, it is clear that the whole concept of a keystone species (see Section 20.2.6) is itself a recognition of the fact that the effects of a disturbance on structure or function are likely to depend very much on the precise nature of the disturbance – that is, on *which* species are lost. Reinforcement of this idea is provided by a simulation study carried out by Dunne *et al.* (2002), in which they took 16 published food webs and subjected them to the sequential removal of species according to one of four criteria: (i) removing the most connected species first; (ii) randomly removing species; (iii) removing the most connected species first excluding basal species (those having predators but no prey); and (iv) removing the least connected species first. The stability of the webs was then judged by the number of secondary extinctions that resulted from the simulated removals, such extinctions occurring when species were left with no prey (and so basal species were subject to primary but not secondary extinction). In the first place, the robustness of community composition in the face of species loss increased with connectance of the communities – further support for an increase in community stability with complexity. Overall, however, it is also clear that secondary extinctions followed most rapidly when the most connected species were removed, and least rapidly when the least connected species were removed, with random removals lying between the two (Figure 20.13). There were, moreover, some interesting exceptions when, for example, the removal of a least connected species led to a rapid cascade of secondary extinctions because it was a basal species with a single predator, which was itself preyed upon by a wide variety of species. This, finally in this section, reminds us that the idiosyncrasies of individual webs are likely always to undermine the generality of any 'rules' even if such rules can be agreed on.

20.4 Empirical patterns in food webs: the number of trophic levels

In the previous section, we examined very general aspects of food web structure – richness, complexity – and related them to the stability of food webs. In this section, we examine some more specific aspects of structure and ask, first, if there are detectable repeated patterns in nature, and second whether we can account for them. We deal first, at greatest length, with the number of trophic levels, and then turn to omnivory and the extent to which food webs are compartmentalized.

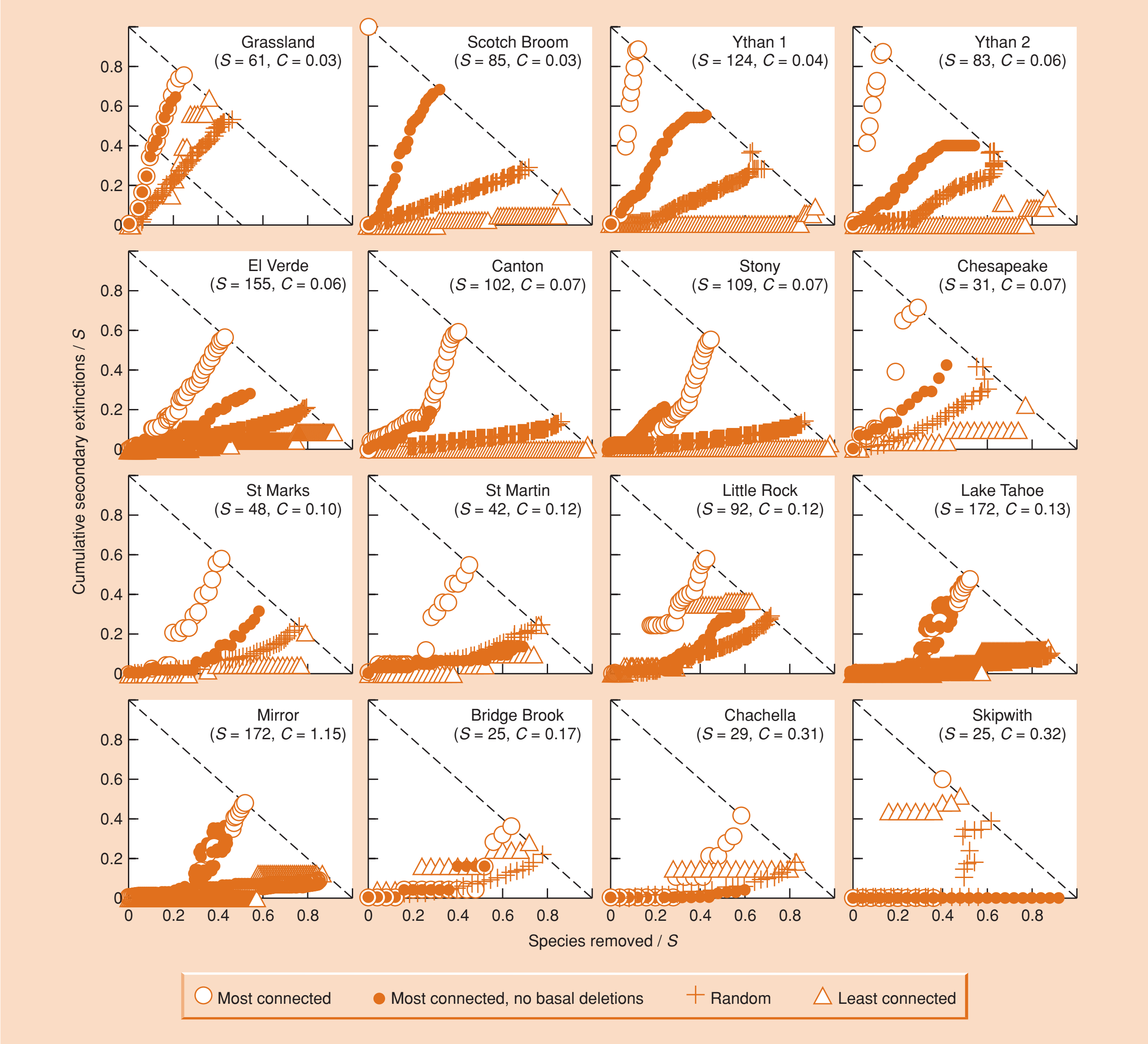
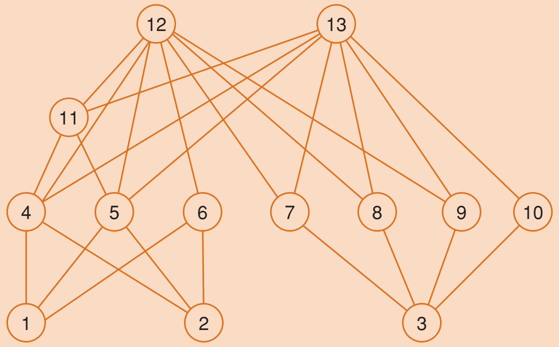


Figure 20.13 The effect of sequential species removal on the number of consequential ('secondary') species extinctions, as a proportion of the total number of species originally in the web, S, for each of 16 previously described food webs. The four different rules for species removal are described in the key. Robustness of the webs (the tendency *not* to suffer secondary extinctions) increased with the connectance of the webs, C (regression coefficients for the four rules: −0.62 (NS), 1.16 ($P < 0.001$), 1.01 ($P < 0.001$) and 0.47 ($P < 0.005$)). Overall, though, robustness was lowest when the most connected species were removed first and highest when the least connected were removed first. The origins of the webs are described in Dunne *et al.* (2002). (After Dunne *et al.*, 2002.)

food chain length

A fundamental feature of any food web is the number of trophic links in the pathways that run from basal species to top predators. Variations in the number of links have usually been investigated by examining *food chains*, defined as sequences of species running from a basal species to a species that feeds on it, to another species that feeds on the second, and so on up to a top predator (fed on by no other species). This does not imply a belief that communities are organized as linear chains (as opposed to more diffuse webs); rather, individual chains are identified purely as a means



Maximal food chains

1	4	11	12	2	4	11	12	3	7	12
1	4	11	13	2	4	11	13	3	7	13
1	4	12		2	4	12		3	8	12
1	4	13		2	4	13		3	8	13
1	5	11	12	2	5	11	12	3	9	12
1	5	11	13	2	5	11	13	3	9	13
1	5	12		2	5	12		3	10	13
1	5	13		2	5	13				
1	6	12		2	6	12				

Figure 20.14 Community matrix for an exposed intertidal rocky shore in Washington State, USA. The pathways of all possible maximal food chains are listed. 1, detritus; 2, plankton; 3, benthic algae; 4, acorn barnacles; 5, *Mytilus edulis*; 6, *Pollicipes*; 7, chitons; 8, limpets; 9, *Tegula*; 10, *Littorina*; 11, *Thais*; 12, *Pisaster*; 13, *Leptasterias*. (After Briand, 1983.)

of trying to quantify the number of links. Food chain length has been defined in various ways (Post, 2002), and in particular has sometimes been used to describe the number of species in the chain, and sometimes (as here) the number of links. For instance, starting with basal species 1 in Figure 20.14, we can trace four possible trophic pathways via species 4 to a top predator: 1–4–11–12, 1–4–11–13, 1–4–12 and 1–4–13. This provides four food chain lengths: 3, 3, 2 and 2. Figure 20.14 lists a total of 21 further chains, starting from basal species 1, 2 and 3. The average of all the possible food chain lengths is 2.32. Adding one to this gives us the number of trophic levels that can be assigned to the food web. Almost all communities described have consisted of between two and five trophic levels, and most of these have had three or four. What sets the limit on food chain length? And how can we account for variations in length?

parasites are usually ignored

In addressing these questions, we will conform to a bias that has pervaded investigations of food chain length – a bias in favor of predators and against parasites. Thus, when a food chain is described as having four trophic levels, these would typically be a plant, a herbivore, a predator that eats the herbivore, and a top predator that eats the intermediate predator. Assume the top predator is an eagle. Even without collecting the data, it is all but certain that the eagle is attacked by parasites (perhaps fleas), which are themselves attacked by pathogens. But the convention is to describe the chain as having four trophic levels. Indeed, descriptions of food webs generally have paid little attention to parasites. There is little doubt that this neglect will have to be rectified (Thompson *et al.*, 2005).

20.4.1 Productivity? Productive space? Or just space?

It has long been argued that energetic considerations set a limit to the number of trophic levels that an environment can support. Of the radiant energy that reaches the earth, only a small fraction is fixed by photosynthesis and made available as either live food for herbivores or dead food for detritivores. Indeed, the amount of energy available for consumption is considerably less than that fixed by the plants, because of work done by the plants (in growth and maintenance) and because of losses due to inefficiencies in all energy-conversion processes (see Chapter 17). Thereafter, each feeding link amongst heterotrophs is characterized by the same phenomenon: at most 50%, sometimes as little as 1%, and typically around 10% of energy consumed at one trophic level is available as food to the next. The observed pattern of just three or four trophic levels could arise, therefore, simply because a viable population of predators at a further trophic level could not be supported by the available energy.

greater primary productivity supports more trophic levels? . . .

The most obvious testable predictions stemming from this hypothesis are, first, systems with greater primary productivity (e.g. at lower latitudes) should be able to support a larger number of trophic levels; and second, systems where energy is transferred more efficiently (e.g. based on insects rather than vertebrates) should also have more trophic levels. However, these predictions have received little support from natural systems. For instance, an analysis of 32 published food webs in habitats ranging from desert and woodland to Arctic lakes and tropical seas found no difference in the length of food chains when 22 webs from low-productivity habitats (less than 100 g of carbon m^{-2} $year^{-1}$) were compared with 10 webs from high-productivity habitats (greater than 1000 g m^{-2} $year^{-1}$). The median food chain length was 2.0 in both cases (Briand & Cohen, 1987). Moreover, a survey of 95 insect-dominated webs revealed first that food chains in tropical webs were no longer than those from (presumably) less productive temperate and desert situations, but also that these food chains composed of insects were no longer than those involving vertebrates (Schoenly *et al.*, 1991).

On the other hand, a number of studies on a much smaller scale (e.g. in a group of streams; Townsend *et al.*, 1998) or where resource availability has been manipulated experimentally, have shown food chain length to decrease with decreased productivity, especially when the decreases take productivity below around 10 g carbon m^{-2} $year^{-1}$ (Post, 2002). For example, in an experiment using water-filled containers as analogs of natural tree-holes, a 10-fold or 100-fold reduction from a 'natural' level of energy input (leaf litter) reduced maximal food chain length by one link, because in this simple community of mosquitoes, midges, beetles and mites, the principal predator – a chironomid midge *Anatopynia pennipes* – was usually absent from the less productive habitats (Jenkins *et al.*, 1992). This suggests that the simple productivity argument may indeed apply in the least productive environments (the most unproductive deserts, the deepest reaches of caves). However, establishing this is likely to prove difficult, since there are other reasons for expecting top predators to be absent from such environments (their size, their isolation, etc.; Post, 2002).

. . . or should it be *total* available energy?

In fact, though, the simple productivity argument may have been misguided in the first place: what matters in an ecological community is not the energy available per unit area but the *total* available energy, that is, productivity per unit area multiplied by the space (or volume) occupied by the ecosystem – the 'productive space' hypothesis (Schoener, 1989). A very small and isolated habitat, for example, no matter how productive locally, is unlikely to provide enough energy for viable populations at higher trophic levels. A number of studies appear to support the productive space hypothesis, in that the number of trophic levels is positively correlated with the total available energy – an example is shown in Figure 20.15a. On the other hand, the rare attempts that have been made to determine the separate contributions of ecosystem size and local productivity have detected an effect from size but not from productivity (e.g. Figure 20.15b).

Results like these may indicate that total energy is indeed important but is far more dependent on ecosystem size than productivity per unit area. But they may mean, alternatively, that ecosystem size affects food chain length by some other means and available energy has no detectable effect (Post, 2002). One possibility is that ecosystem size affects species richness (it certainly does so – see Chapter 21) and richer webs tend to support longer chains. Unsurprisingly, richness and chain length tend to be associated. Untangling causation from correlation is an important challenge.

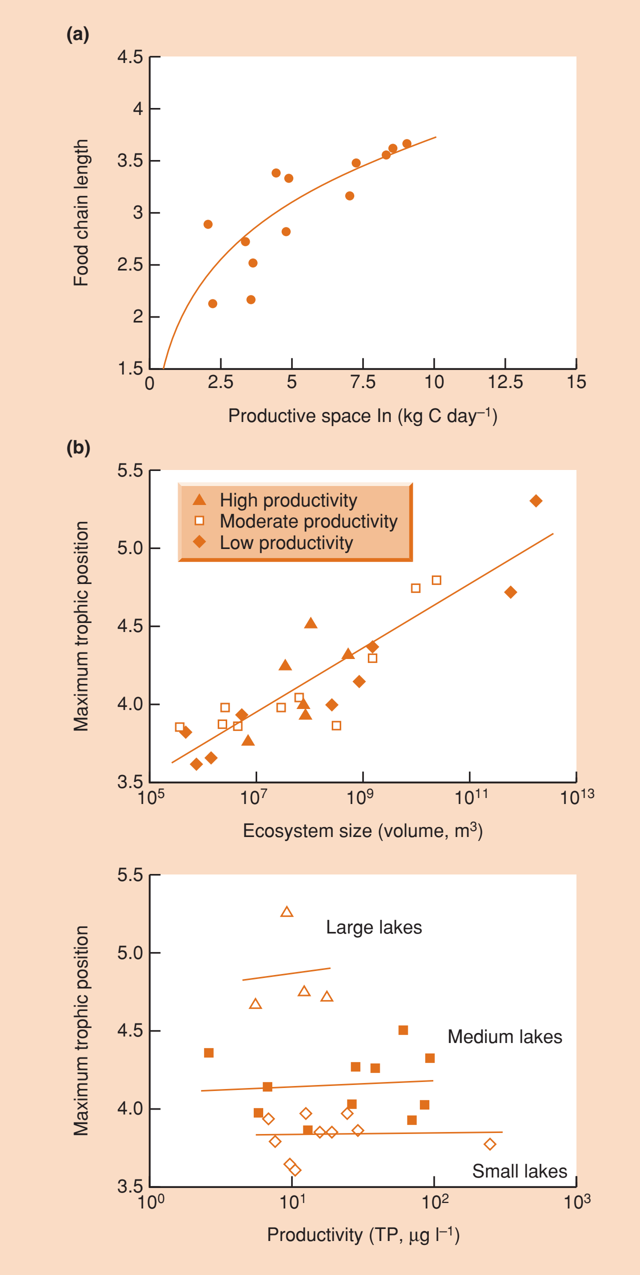


Figure 20.15 (*right*) (a) The food chain length (FCL) increases with productive space for the food webs of 14 lakes in Ontario and Quebec; productive space (PS) = productivity × lake area; $FCL = 2.94PS^{0.21}$, $r^2 = 0.48$. (After Vander Zanden *et al.*, 1999.) (b) Relationships between maximum trophic position and ecosystem size (above) or productivity (below) for 25 lakes in northeastern North America. The maximum trophic position increased with ecosystem size apparently independently of whether productivity was low (2–11 $\mu g\ l^{-1}$ total phosphorus (TP)), moderate (11–30 $\mu g\ l^{-1}$ TP) or high (30–250 $\mu g\ l^{-1}$ TP). However, when small (3×10^5 to 3×10^7 m^3), medium (3×10^7 to 3×10^9 m^3) and large lakes (3×10^9 to 3×10^{12} m^3) were examined separately, the maximum trophic position did not vary with productivity. The maximum trophic position is the trophic position (FCL + 1) of the species with the highest average trophic position in each of the lake food webs. (After Post *et al.*, 2000.)

If available energy is found ultimately to have no effect on food chain length, it should perhaps be borne in mind that species richness is usually significantly higher in productive regions (see Chapter 21), and that each consumer probably feeds on only a limited range of species at a lower trophic level. Hence, the amount of energy flowing up a single food chain in a productive region (a large amount of energy, but divided amongst many subsystems) may not be very different from that flowing up a single food chain in an unproductive region (having been divided amongst fewer subsystems).

20.4.2 Dynamic fragility of model food webs

Another popular idea has been that the length of food chains is limited by the lowered stability (especially resilience) of longer chains. In turn, we might then expect food chains to be shorter in environments subject to greater disturbance, where only the most stable food chains could persist. In particular, when Pimm and Lawton (1977) examined variously structured four-species Lotka–Volterra models (Figure 20.16a), webs with more trophic levels had return times after a perturbation that were substantially longer than those with fewer levels. Because less resilient systems are unlikely to persist in an inconstant environment, it was argued that only systems with few trophic levels will commonly be found in nature. However, these models had self-limitation (effectively, intraspecific competition) only at the lowest trophic level, and food chain length and the proportion of self-limited species was therefore confounded (Figure 20.16a). When a wider range of food webs was examined with self-limitation distributed more systematically (Figure 20.16b–e) (Sterner *et al*., 1997a), there was a weak but significant *increase* in stability in longer food chains when the number of species and the number of self-limited species were held constant. Overall, there is no convincing case for dynamic fragility affecting the length of food chains significantly.

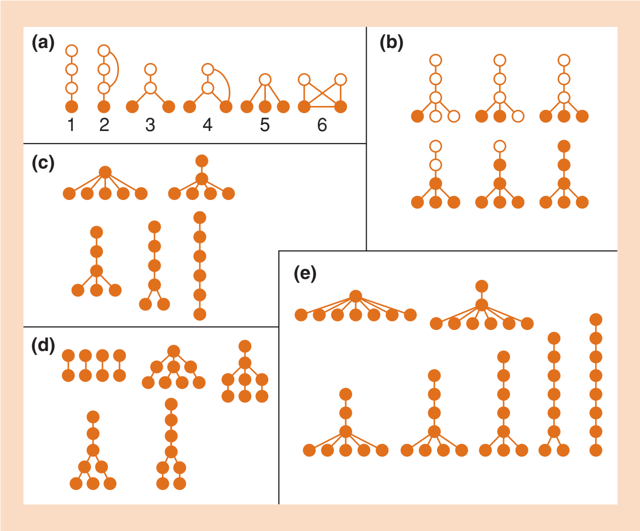


Figure 20.16 Sets of model food webs, the dynamics of which were examined to determine the effect of food chain length on stability having accounted for variations in the number of species and the number with self-limitation (●). (a) The original set examined by Pimm and Lawton (1997). (b) Six-species, four-level webs with varying degrees of self-limitation. (c) Six-species webs of self-limited species with varying numbers of trophic levels and species concentrated in the basal level. (d) Eight-species webs of self-limited species with varying numbers of trophic levels and species dispersed among the levels. (e) Eight-species webs of self-limited species with varying numbers of trophic levels and species concentrated in the basal level. (After Sterner *et al*., 1997a.)

20.4.3 Constraints on predator design and behavior

There may also be evolutionary constraints on the anatomy or behavior of predators that limit the lengths of food chains. To feed on prey at a given trophic level, a predator has to be large enough, maneuverable enough and fierce enough to effect a capture. In general, predators are larger than their prey (not true, though, of grazing insects and parasites), and body size tends to increase (and density to decrease) at successive trophic levels (Cohen *et al*., 2003). There may well be a limit above which design constraints rule out another link in the food chain. It may be impossible to design a predator that is both fast enough to catch an eagle and big and fierce enough to kill it.

Also, consider the arrival in a community of a new carnivore species. Would it do best to feed on the herbivores or the carnivores already there? The herbivores are more abundant and less well protected. The advantage to feeding low down in the food chain can readily be seen. Of course, if all species did this, competition would intensify, and feeding higher in the food chain could reduce competition. But it is difficult to imagine a top predator sticking religiously to a rule that it should prey only on the trophic level immediately below it, especially as the prey there are likely to be larger, fiercer and rarer than species at lower levels. Overall, theoretical explorations (Hastings & Conrad, 1979) suggest that an evolutionarily stable food chain length (one that would be optimal for predator fitness) would be around two (three trophic levels). Such arguments, however, have rather little to offer by way of explanation for the variations in food chain length.

Thus, there are complete answers to neither of our original questions (see p. 595). The constraints on predators are likely to set some general upper limit on the lengths of many food chains. Food chains are likely to be atypically short in especially unproductive environments. Food chain length seems to increase with increases in productive space, but it is unclear whether this is an association with the total energy available in an ecosystem or with ecosystem size alone – and if the latter, it is unclear precisely how size comes to determine food chain length. The two longest established hypotheses – energy per unit area and dynamic fragility – have, if anything, the least support.

are the data simply not good enough?

Finally, it is important to note that, as with connectance, estimates of food chain length are sensitive to the degree of taxonomic resolution. This may be why many of the more recently documented webs have longer than average chain lengths ranging from five to seven (Hall & Raffaelli, 1993). Moreover, if a well-resolved large web is progressively simplified by lumping taxa together (in a manner analogous to earlier studies), the estimate of food chain length declines (Martinez, 1993). There is clearly a need for rigorous studies of many more food webs before acceptable generalizations can be reached.

20.4.4 Omnivory

Technically, an omnivore is an animal that takes prey from more than one trophic level. Compilations of early descriptions of food webs indicated that omnivores are usually uncommon; this was taken to support expectations from simple model communities, where omnivory is destabilizing (Pimm, 1982). It was argued that in cases of omnivory, intermediate species both compete with and are preyed upon by top species and in consequence are unlikely to persist long. A more complex and realistic model incorporated 'life history omnivory', in which different life history stages of a species feed on different trophic levels, as when tadpoles are herbivores and adult frogs and toads are carnivores (Pimm & Rice, 1987). Life history omnivory also reduces stability, but much less than single life stage omnivory does. Intriguingly, omnivory is not destabilizing in donor-control models, and omnivores are common in decomposer food webs (Walter, 1987; Usio & Townsend, 2001; Woodward & Hildrew, 2002), to which donor-control dynamics can be applied.

In fact, an increasing number of studies indicate that omnivory is not uncommon at all, and that earlier indications of its rarity were an artefact of the webs being only poorly described (Polis & Strong, 1996; Winemiller, 1996). For example, Sprules and Bowerman (1988) found omnivory to be common in plankton food webs in North American glacial lakes, having identified all their zooplankton to species level and produced webs that were much more reliable as a result (Figure 20.17). Polis (1991) found similar results in his detailed study of a desert sand community. What is more, later modeling studies have undermined the whole suggestion that omnivory is inherently destabilizing. Dunne *et al.*'s (2002) simulation study detected no relationship between the level of omnivory and the stability of webs to species removal, while other models indicate that omnivory may in fact stabilize food webs (McCann & Hastings, 1997). It is sobering to note that theoretical and empirical studies have managed to march in step twice in quick succession, but to quite different tunes. It reminds us that both sorts of study can only ever be as good as the assumptions on which they are inevitably based.

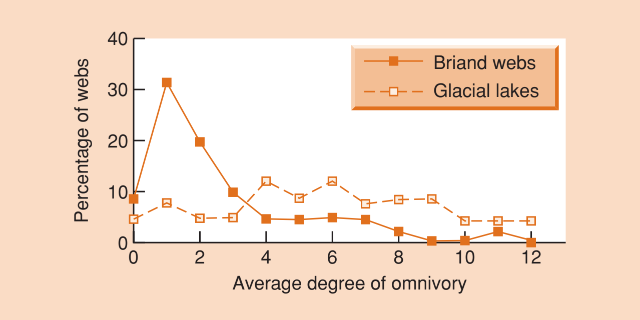


Figure 20.17 The prevalence of omnivory in glacial lakes in northeast North America (Sprules & Bowerman, 1988) is much greater than that observed in Briand's set of food webs (see Figure 20.9a). The degree of omnivory in a web is quantified as the number of closed omnivorous links divided by the number of top predators. A closed omnivorous link exists when a feeding path can be traced to a prey more than one trophic level away, and from that prey back to the predator through at least one other prey occupying an intermediate trophic level.

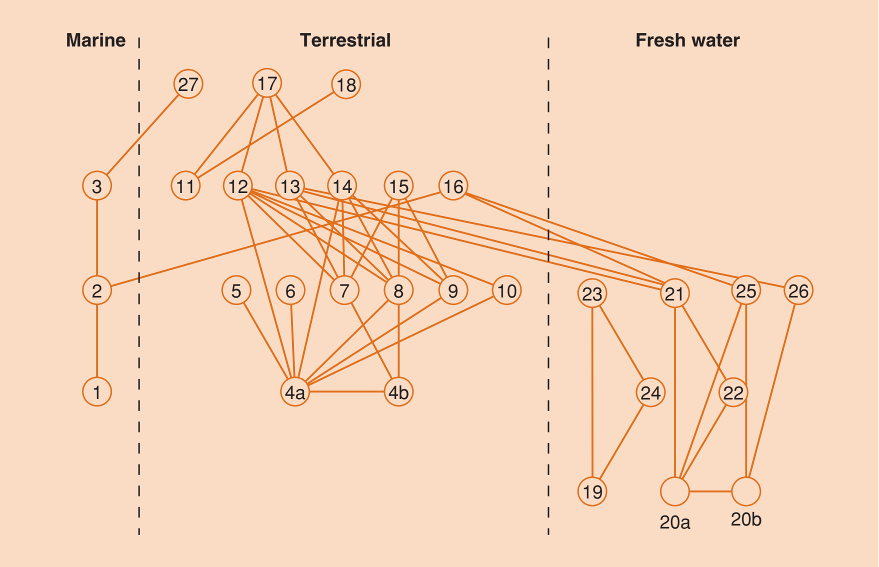
20.4.5 Compartmentalization

A food web is compartmentalized if it is organized into subunits within which interactions are strong, but between which interactions are weak. (The most perfectly compartmentalized community possesses only linear food chains.) Do food webs tend to be compartmentalized?

Not surprisingly, in studies where habitat divisions are major and unequivocal, there is a clear tendency for compartments to map onto habitats. For instance, Figure 20.18 shows the results of a classic study describing the major interactions within and between three interconnected habitats on Bear Island in the Arctic Ocean (Summerhayes & Elton, 1923). There is a significantly smaller number of interactions between habitats than would be expected by chance (Pimm & Lawton, 1980).

On the other hand, when habitat divisions are subtler, the evidence for compartments is typically poor, and there are even greater difficulties in providing a clear demonstration of compartments (or the lack of them) *within* habitats. Early analyses, certainly, suggested that food webs within habitats are only as compartmentalized as would be expected by chance alone (Pimm & Lawton, 1980; Pimm, 1982). More recently, though, promising methodological advances have been made that seem capable of identifying compartments within larger webs, especially when the

Figure 20.18 The major interactions within and between three interconnected habitats on Bear Island in the Arctic Ocean. 1, plankton; 2, marine animals; 3, seals; 4a, plants; 4b, dead plants; 5, worms; 6, geese; 7, Collembola; 8, Diptera; 9, mites; 10, Hymenoptera; 11, seabirds; 12, snow bunting; 13, purple sandpiper; 14, ptarmigan; 15, spiders; 16, ducks and divers; 17, Arctic fox; 18, skua and glaucous gull; 19, planktonic algae; 20a, benthic algae; 20b, decaying matter; 21, protozoa a; 22, protozoa b; 23, invertebrates a; 24, Diptera; 25, invertebrates b; 26, microcrustacean; 27, polar bear. (After Pimm & Lawton, 1980.)



taxonomic resolution within the web is high and the strengths of interactions between the species can be weighted (Krause *et al.*, 2002). Interestingly, the methods lean heavily on ideas from sociology, where the aim is to identify social cliques within a broader society. An example is shown in Figure 20.19. Also, an alternative perspective has been to emphasize that what have been described as distinct food webs in different habitats may often be linked by 'spatial subsidies' – crucial flows of energy and materials (Polis *et al.*, 1997) – as, for example, when lake fish that normally prey upon other fish in the pelagic (open water) food web, switch to quite different prey in the benthic food web when their preferred prey are scarce (Schindler & Scheuerell, 2002). That is, what might seem to be separate webs are in fact compartments within a larger web.

Since no clear consensus has emerged that food webs are more compartmentalized than would be expected by chance alone, it would be inappropriate to argue that compartmentalization has been 'favored' because compartmentalized webs persist. None the less, since the earliest theoretical studies (e.g. May, 1972), a consensus *has* emerged that communities will have increased stability if they are compartmentalized, and it is easy to see why this might be so. In the first place, a disturbance to a compartmentalized web tends to be contained within the disturbed compartment, limiting the overall extent of the effects in the wider web. In addition, though, spatial subsidies between compartments will tend to buffer individual compartments against the worst excesses of disturbances within them. For instance, in the example above, piscivorous fish, when their preferred prey are rare, may switch to the benthos rather than driving populations of those preferred prey to extinction. The apparent contradiction between these two justifications of the stabilizing properties of compartmentalization can be resolved if we emphasize the first where a seemingly unified web is in fact a series of semidetached compartments, and emphasize the second where seemingly separate webs are in fact coupled. Thus, it may be that an intermediate degree of compartmentalization is the most stable.

answers are uncertain – but it is important that we discover them

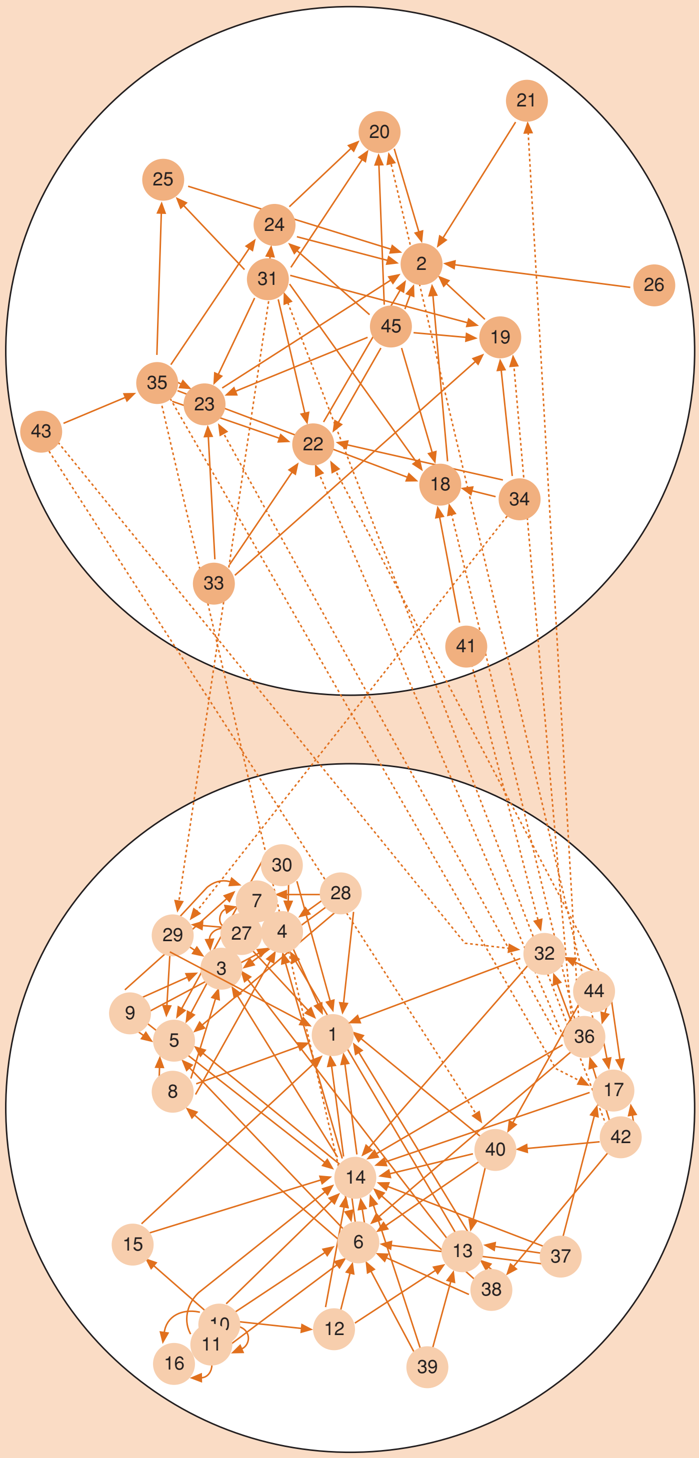
This chapter closes, then, with a tone that has pervaded much of it: suggestive but uncertain. Further progress, though, is essential. One standard answer of ecologists to the layman's question 'What does it matter if we lose *that* species?' is, quite rightly, 'But you must also consider the wider effects of that loss; losing that species may affect the whole food web of which it is part'. The need for further understanding of those wider effects is intense.

Summary

In this chapter, we shift the focus to systems that usually have at least three trophic levels and with 'many' species.

We describe 'unexpected' effects in food webs, where, for example, the removal of a predator may lead to a decrease in prey abundance.

The indirect effect within food webs that has received most attention is the trophic cascade. We discuss cascades in systems with three and four trophic levels, and address the question of whether cascades are equally common in all types of habitat, requiring a distinction to be made between community- and species-level cascades. We ask whether food webs, or particular types of food web, are dominated by either top-down (trophic cascade) or bottom-up control. We then define and discuss the importance of keystone species.



1	Phytoplankton
2	Benthic producers
3	Bacteria <1 µm (small)
4	Bacteria >1 <2 µm (medium)
5	Bacteria >2 µm (large)
6	*Acartia tonsa* (copepod)
7	Microciliates
8	Macrociliates
9	Predaceous ciliates
10	*Chrysaora quinquecirrha* (sea nettle)
11	*Mnemiopsis leidyi* (comb jelly)
12	*Nemopsis bachei* (jellyfish)
13	Cladocera
14	Other zooplankton
15	*Anchoa mitchilli* larvae (anchovy)
16	*Anchoa mitchilli* eggs
17	Fish larvae
18	*Marenzelleria viridis* (polychaete)
19	*Nereis succinea* (polychaete)
20	*Hetermastus filiformis* (oligochaete)
21	Other polychaetes
22	*Corophium lacustre* (amphipod)
23	*Leptocheirus plumulosus* (amphipod)
24	Other meiofauna
25	*Macoma baithica* (Baltic clam)
26	*Macoma mitchelli* (rosy clam)
27	*Rangia cuneata* (wedge clam)
28	*Mulinia lateralis* (coot clam)
29	*Mya arenaria* (soft-shelled clam)
30	*Crassostrea virginica* (oyster)
31	*Callinectes sapidus* (blue crab)
32	*Anchoa mitchilli* (bay anchovy)
33	*Micropogon undulatus* (croaker)
34	*Trinectes maculatus* (hogchoaker)
35	*Leiostomus xanthurus* (spot)
36	*Cynoscion regalis* (weakfish)
37	*Alosa sapidissima* (American shad)
38	*Alosa pseudoharengus* (alewife)
39	*Alosa aestivalis* (blue-back herring)
40	*Brevoctia tyranus* (menhaden)
41	*Morone americana* (white perch)
42	*Morone saxatilis* (striped bass)
43	*Pomatomas saltatrix* (bluefish)
44	*Paralichthys dentatus* (flounder)
45	*Arius felis* (catfish)

Figure 20.19 Pictorial representation of the results of an analysis of a food web from Chesapeake Bay (see also Figure 20.13) in which interactions between the 45 taxa were quantified and the taxa assigned to compartments (the number of which was not predetermined) in such a way as to maximize the differential between the connectance within compartments (in this case 0.0099) and that between compartments (in this case 0.000087, more than two orders of magnitude lower). Food webs may be considered compartmentalized if that differential is sufficiently large. Arrows represent interactions and point from predator to prey: solid color, within compartments; dashed lines, between compartments. (After Krause *et al.*, 2002.)

Any ecological community can be characterized by its structure, its productivity and its temporal stability. The variety of meanings of 'stability' is outlined, distinguishing resilience and resistance, local and global stability, and dynamic fragility and robustness.

For many years, the 'conventional wisdom' was that more complex communities were more stable. We describe the simple mathematical models that first undermined this view. We show how, in general, the effects of food web complexity on population stability in model systems has been equivocal, whereas for aggregate properties of whole model communities, such as their biomass or productivity, complexity (especially species richness) tends consistently to enhance stability.

In real communities, too, evidence is equivocal at the population level, including both studies that have examined the relationships between species richness and connectance and those that have manipulated richness experimentally. Again, turning to the aggregate, whole community level, evidence is largely consistent in supporting the prediction that increased richness increases stability (decreases variability). We stress, though, the importance of the nature, not just the richness, of a community in these regards, returning to the importance of keystone species.

Limitations and patterns in food chain length are discussed. We examine the evidence that food chain length is limited by productivity, by 'productive space' (productivity compounded by the extent of the community) or simply by 'space' – but that evidence is inconclusive. We examine, too, the arguments that food chain length is limited by dynamic fragility (ultimately unconvincing) or by constraints on predator design and behavior. There is a clear need for rigorous studies of many more food webs before acceptable generalizations can be reached.

We examine work linking the prevalence of omnivory and its effect on food web stability, noting that earlier work found omnivory to be rare and destabilizing, whereas later work found it common and with no consistent effect on stability.

Finally, we ask whether food webs tend to be more compartmentalized than would be expected by chance. As long as habitat divisions are subtle, the evidence for compartments is typically poor, and there are even greater difficulties in demonstrating compartments (or the lack of them) within habitats. There is, though, a clear consensus from theoretical studies that communities will have increased stability if they are compartmentalized.

Chapter 21

Patterns in Species Richness

21.1 Introduction

hot spots of species richness

Why the number of species varies from place to place, and from time to time, are questions that present themselves not only to ecologists but to anybody who observes and ponders the natural world. They are interesting questions in their own right – but they are also questions of practical importance. A remarkable 44% of the world's plant species and 35% of vertebrate species (other than fish) are endemic to just 25 separate 'hot spots' occupying a small proportion of the earth's surface (Myers *et al*., 2000). Knowledge of the spatial distribution of species richness is a prerequisite for prioritizing conservation efforts both at a large scale (setting global priorities) and at a regional and local scale (setting national priorities). This aspect of conservation planning will be discussed in Section 22.4.

biodiversity and species richness

It is important to distinguish between *species richness* (the number of species present in a defined geographical unit – see Section 16.2) and *biodiversity*. The term biodiversity makes frequent appearances in both the popular media and the scientific literature – but it often does so without an unambiguous definition. At its simplest, biodiversity is synonymous with species richness. Biodiversity, though, can also be viewed at scales smaller and larger than the species. For example, we may include genetic diversity within species, recognizing the value of conserving genetically distinct subpopulations and subspecies. Above the species level, we may wish to ensure that species without close relatives are afforded special protection, so that the overall evolutionary variety of the world's biota is maintained as large as possible. At a larger scale still, we may include in biodiversity the variety of community types present in a region – swamps, deserts, early and late stages in a woodland succession, and so on. Thus, 'biodiversity' may itself, quite reasonably, have a diversity of meanings. Yet it is necessary to be specific if the term is to be of any practical use.

In this chapter we restrict our attention to species richness, partly because of its fundamental nature but mainly because so many more data are available for this than for any other aspect of biodiversity. We will address several questions. Why do some communities contain more species than others? Are there patterns or gradients of species richness? If so, what are the reasons for these patterns? There are plausible answers to the questions we ask, but these answers are by no means conclusive. Yet this is not so much a disappointment as a challenge to ecologists of the future. Much of the fascination of ecology lies in the fact that many of the problems are blatant, whereas the solutions are not. We will see that a full understanding of patterns in species richness must draw on our knowledge of all the ecological topics dealt with so far in this book.

the question of scale: macroecology

As with other areas of ecology, scale is a paramount feature in discussions of species richness; explanations for patterns usually have both smaller and larger scale components. Thus, the number of species living on a boulder in a river will reflect local influences such as the range of microhabitats provided (on the surface, in crevices and beneath the boulder) and the consequences of species interactions taking place (competition, predation, parasitism). However, larger scale influences of both a spatial and temporal nature will also be important. Thus, species richness may be large on our boulder because the regional pool of species is itself large (in the river as a whole or, at a still larger scale, in the geographic region) or because there has been a long interlude since the boulder was last turned over by a flood (or since the region was last glaciated). Comparatively more emphasis has been placed on local as opposed to regional questions in ecology, prompting Brown and Maurer (1989) to designate a subdiscipline of ecology as *macroecology* – to deal explicitly with understanding distribution and abundance at large spatial and temporal scales. Geographic patterns in species richness are a principal focus of macroecology (e.g. Gaston & Blackburn, 2000; Blackburn & Gaston, 2003).

21.1.1 Four types of factor affecting species richness

geographic factors

There are a number of factors to which the species richness of a community can be related, and these are of several different types. First, there are factors that can be referred to broadly as 'geographic', notably latitude, altitude and, in aquatic environments, depth. These have often been correlated with species richness, as we shall discuss below, but presumably they cannot be causal agents in their own right. If species richness changes with latitude, then there must be some other factor changing with latitude, exerting a direct effect on the communities.

factors correlated with latitude

A second group of factors does indeed show a tendency to be correlated with latitude (or altitude or depth), but they are not perfectly correlated. To the extent that they are correlated at all, they may play a part in explaining latitudinal and other gradients. But because they are not perfectly correlated, they serve also to blur the relationships along these gradients. Such factors include climatic variability, the input of energy, the productivity of the environment, and possibly the 'age' of the environment and the 'harshness' of the environment.

factors that are independent of latitude

A further group of factors vary geographically but quite independently of latitude (or altitude, island location or depth). They therefore tend to blur or counteract relationships between species richness and other factors. This is true of the amount of physical disturbance a habitat experiences, the isolation of the habitat and the extent to which it is physically and chemically heterogeneous.

biotic factors

Finally, there is a group of factors that are biological attributes of a community, but are also important influences on the structure of the community of which they are part. Notable amongst these are the amount of predation or parasitism in a community, the amount of competition, the spatial or architectural heterogeneity generated by the organisms themselves and the successional status of a community. These should be thought of as 'secondary' factors in that they are themselves the consequences of influences outside the community. Nevertheless, they can all play powerful roles in the final shaping of community structure.

A number of these factors have been discussed in previous chapters (disturbance and successional status in Chapter 16, competition, predation and parasitism in Chapter 19). In this chapter we continue by examining the relationships between species richness and factors that can be thought of as exerting an influence in their own right. We do this first by considering factors whose variation is primarily spatial (productivity, spatial heterogeneity, environmental harshness – Section 21.3) and, second, those whose variation is primarily temporal (climatic variation and environmental age – Section 21.4). We will then be in a position to consider patterns in species richness related to habitat area and remoteness (island patterns – Section 21.5), before moving to gradients in species richness related to latitude, altitude, depth, succession and position in the fossil record (Section 21.6). In Section 21.7, we take a different tack by asking whether variations in species richness themselves have consequences for the functioning of ecosystems (e.g. productivity, decomposition rate and nutrient cycling). We begin, though, by constructing a simple theoretical framework (following MacArthur (1972), probably the greatest macroecologist, although he did not use the term) to help us think about variations in species richness.

21.2 A simple model of species richness

To try to understand the determinants of species richness, it will be useful to begin with a simple model. Assume, for simplicity, that the resources available to a community can be depicted as a one-dimensional continuum, R units long (Figure 21.1). Each species uses only a portion of this resource continuum, and these portions define the *niche breadths* (n) of the various species: the average niche breadth within the community is $\bar{n}$. Some of these niches overlap, and the overlap between adjacent species can be measured by a value o. The average niche overlap within the community is then $\bar{o}$. With this simple background, it is possible to consider why some communities should contain more species than others.

a model incorporating niche breadth, niche overlap and resource range

First, for given values of $\bar{n}$ and $\bar{o}$, a community will contain more species the larger the value of R, i.e. the greater the range of resources (Figure 21.1a). This is true when the community is dominated by competition and the species 'partition' the resources (see Section 19.2). But, it will also presumably be true when competition is relatively unimportant. Wider resource spectra provide the means for existence of a wider range of species, whether or not those species interact with one another.

Second, for a given range of resources, more species will be accommodated if $\bar{n}$ is smaller, i.e. if the species are more specialized in their use of resources (Figure 21.1b).

Alternatively, if species overlap to a greater extent in their use of resources (greater $\bar{o}$), then more may coexist along the same resource continuum (Figure 21.1c).

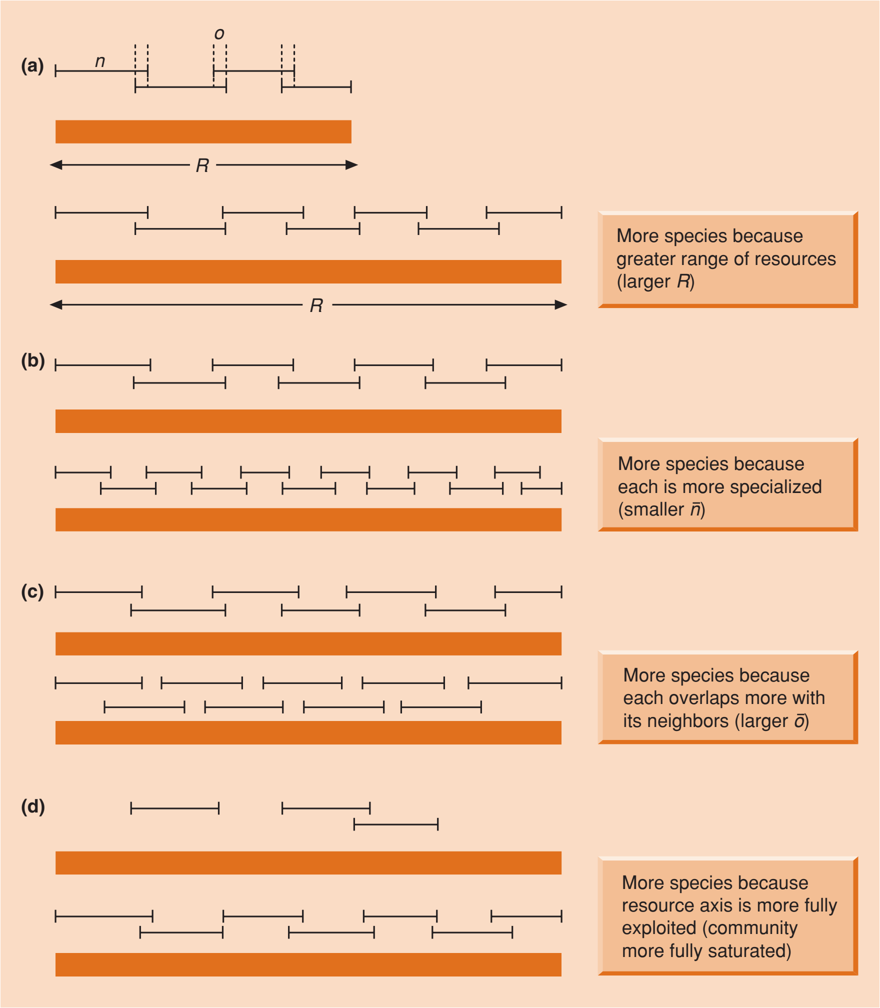


Figure 21.1 A simple model of species richness. Each species utilizes a portion *n* of the available resources (*R*), overlapping with adjacent species by an amount *o*. More species may occur in one community than in another (a) because a greater range of resources is present (larger *R*), (b) because each species is more specialized (smaller average *n*), (c) because each species overlaps more with its neighbors (larger average *o*), or (d) because the resource dimension is more fully exploited. (After MacArthur, 1972.)

Finally, a community will contain more species the more fully saturated it is; conversely, it will contain fewer species when more of the resource continuum is unexploited (Figure 21.1d).

21.2.1 The relationship between local and regional species richness

local vs regional richness – saturated or unsaturated communities?

One way to assess the degree to which communities are saturated with species is to plot the relationship between local species richness (assessed on a spatial scale where all the species could encounter each other in a community) and regional species richness (the number of species in the regional pool that could theoretically colonize the community). Local species richness is sometimes referred to as α richness (or α diversity) and regional species richness as γ richness. If communities are saturated with species (i.e. the niche space is fully utilized), local richness will reach an asymptote in its relationship with regional richness (Figure 21.2a). This appears to be the case for the Brazilian ground-dwelling ant communities studied by Soares *et al.* (2001) (Figure 21.2b). Similar patterns have been described for aquatic and terrestrial plant groups, fish, mammals and parasites, but nonsaturating patterns have just as often been described for a variety of taxa, including fish (Figure 21.2c), insects, birds, mammals, reptiles, molluscs and corals (reviewed by Srivastava, 1999). Local regional richness plots provide a useful tool for addressing the question of community saturation, but they must be used with caution. For example, Loreau (2000) points out that the nature of the relationship depends on the way that total richness (γ) is partitioned between within-community (α) and between-community richness (β), and this is a matter of the scale at which different communities are distinguished from one another. In other words, researchers might erroneously include within a single community several habitats that should be considered as different communities, or, alternatively,

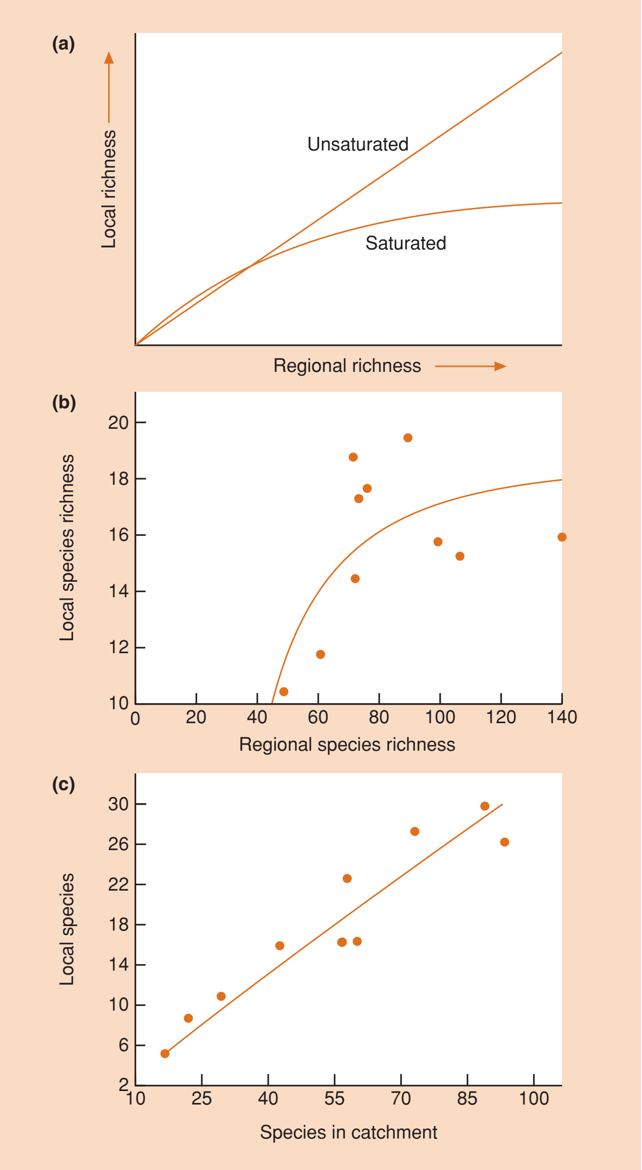


Figure 21.2 (a) In a saturated community, local richness is expected to increase with regional richness at very low levels of regional richness, but to quickly reach an upper limit. In an unsaturated community, on the other hand, local richness is expected to be a constant proportion of regional richness. (After Srivastava, 1999.) (b) Asymptotic relationship between local richness of litter-dwelling ant communities in 1 m^2 quadrats in 10 forest remnants in Brazil in relation to the size of the regional species pool (assumed to be the total number of species in the forest remnant concerned). (After Soares *et al.*, 2001.) (c) Nonasymptotic relationship between local species richness (number recorded over equal-sized areas of a river bed) and regional species pools (the number of species present in the entire drainage basin from which the local sample was drawn). (After Rosenzweig & Ziv, 1999.)

they may study local communities at an inappropriately small scale (e.g. 1 m^2 quadrats may have been too small to be ‘local’ communities in the ground-dwelling ant study of Soares *et al.*, 2001).

21.2.2 Species interactions and the simple model of species richness

the role of competition

We can also consider the relationship between the model in Figure 21.1 and two important kinds of species interactions described in previous chapters – interspecific competition and predation (see especially Chapter 19). If a community is dominated by interspecific competition, the resources are likely to be fully exploited. Species richness will then depend on the range of available resources, the extent to which species are specialists and the permitted extent of niche overlap (see Figure 21.1a–c).

the role of predation

Predation, on the other hand, is capable of exerting contrasting effects. First, we know that predators can exclude certain prey species; in the absence of these species the community may then be less than fully saturated, in the sense that some available resources may be unexploited (see Figure 21.1d). In this way, predation may reduce species richness. Second, though, predation may tend to keep species below their carrying capacities for much of the time, reducing the intensity and importance of direct interspecific competition for resources. This may then permit much more niche overlap and a greater richness of species than in a community dominated by competition (see Figure 21.1c). Finally, predation may generate richness patterns similar to those produced by competition when prey species compete for ‘enemy-free space’ (see Chapter 8). Such ‘apparent competition’ means that invasion and the stable coexistence of prey are favored by prey being sufficiently different from other prey species already present. In other words, there may be a limit to the similarity of prey that can coexist (equivalent to the presumed limits to similarity of coexisting competitors).

21.3 Spatially varying factors that influence species richness

21.3.1 Productivity and resource richness

variations in productivity

For plants, the productivity of the environment can depend on whichever nutrient or condition is most limiting to growth (dealt with in detail in Chapter 17). Broadly speaking, the productivity of the environment for animals follows the same trends as for plants, both as a result of the changes in resource levels at the base of the food chain, and as a result of the changes in critical conditions such as temperature.

If higher productivity is correlated with a wider *range* of available resources, then this is likely to lead to an increase in species richness (see Figure 21.1a). However, a more productive environment may have a higher rate of supply of resources but not a greater variety of resources. This might lead to more individuals per species rather than more species. Alternatively again, it is possible, even if the overall variety of resources is unaffected, that rare resources in an unproductive environment may become abundant enough in a productive environment for extra species to be added, because more specialized species can be accommodated (see Figure 21.1b).

increased productivity might lead to . . .
. . . increased richness . . .

In general, then, we might expect species richness to increase with productivity – a contention that is supported by an analysis of the species richness of trees in North America in relation to a crude measure of available environmental energy, *potential* evapotranspiration (PET). This is the amount of water that would evaporate or be transpired from a saturated surface (Figure 21.3a). However, while energy (heat and light) is necessary for tree functioning, plants also depend critically on actual water availability; energy and water availability inevitably interact, since higher energy inputs lead to more evapotranspiration and a greater requirement for water (Whittaker *et al.*, 2003). Thus, in a study of southern African trees, species richness increased with water availability (annual rainfall), but first increased and then decreased with available energy (PET) (Figure 21.3b). We present and discuss further hump-shaped relationships later in this section.

When the North American work (Figure 21.3a) was extended to four vertebrate groups, species richness was found to be correlated to some extent with tree species richness itself. However, the best correlations were consistently with PET (Figure 21.4). Why should animal species richness be positively correlated with crude atmospheric energy? The answer is not known with any certainty, but it may be because for an ectotherm, such as a reptile, extra atmospheric warmth would enhance the intake and utilization of food resources. While for an endotherm, such as a bird, the extra warmth would mean less expenditure of resources in maintaining body temperature and more available for growth and reproduction. In both cases, then, this could lead to faster individual and population growth and thus to larger populations. Warmer environments might therefore allow species with narrower niches to persist and such environments may therefore support more species in total (see Figure 21.1b) (Turner *et al.*, 1996).

Sometimes there seems to be a direct relationship between animal species richness and plant productivity. This was the case, for example, for the relationship between bird species richness and mean annual net primary productivity in South Africa (van Rensburg *et al.*, 2002). In the cases of seed-eating rodents and seed-eating ants in the southwestern deserts of the United States, Brown and Davidson (1977) recorded strong positive correlations between species richness and precipitation. In arid regions it is well established that mean annual precipitation is closely related to plant productivity and thus to the amount of seed resource

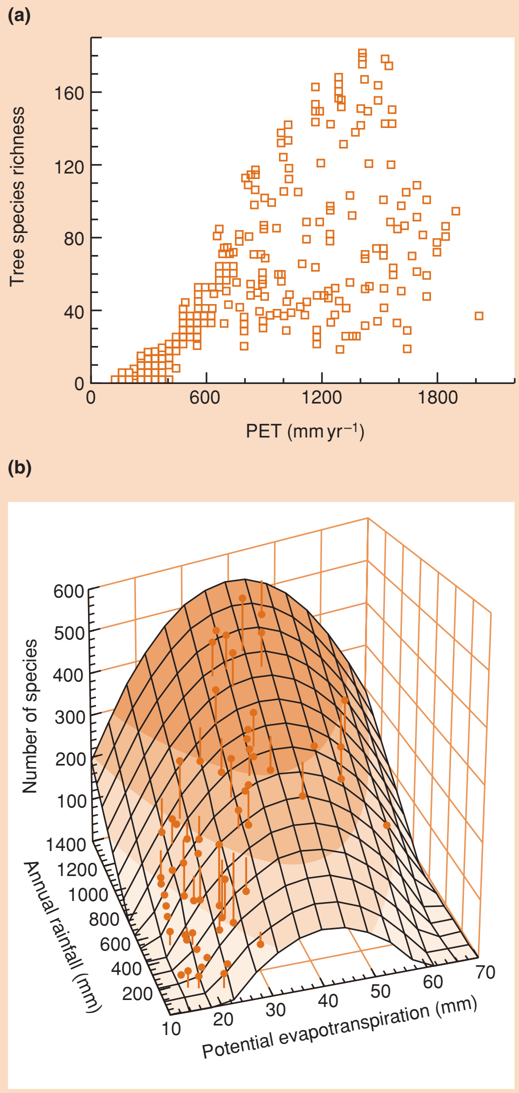


Figure 21.3 (a) Species richness of trees in North America, north of the Mexican border (in which the continent has been divided into 336 quadrats following lines of latitude and longitude) in relation to potential evapotranspiration (PET). (After Currie & Paquin, 1987; Currie, 1991.) (b) Species richness of southern African trees (in 25,000 km^2 cells) as a function of annual rainfall and PET. The surface describes the regression model between species richness, annual rainfall and PET, and the stalks show the residual variation associated with each data point. (After Whittaker *et al.*, 2003; data from O'Brien, 1993.)

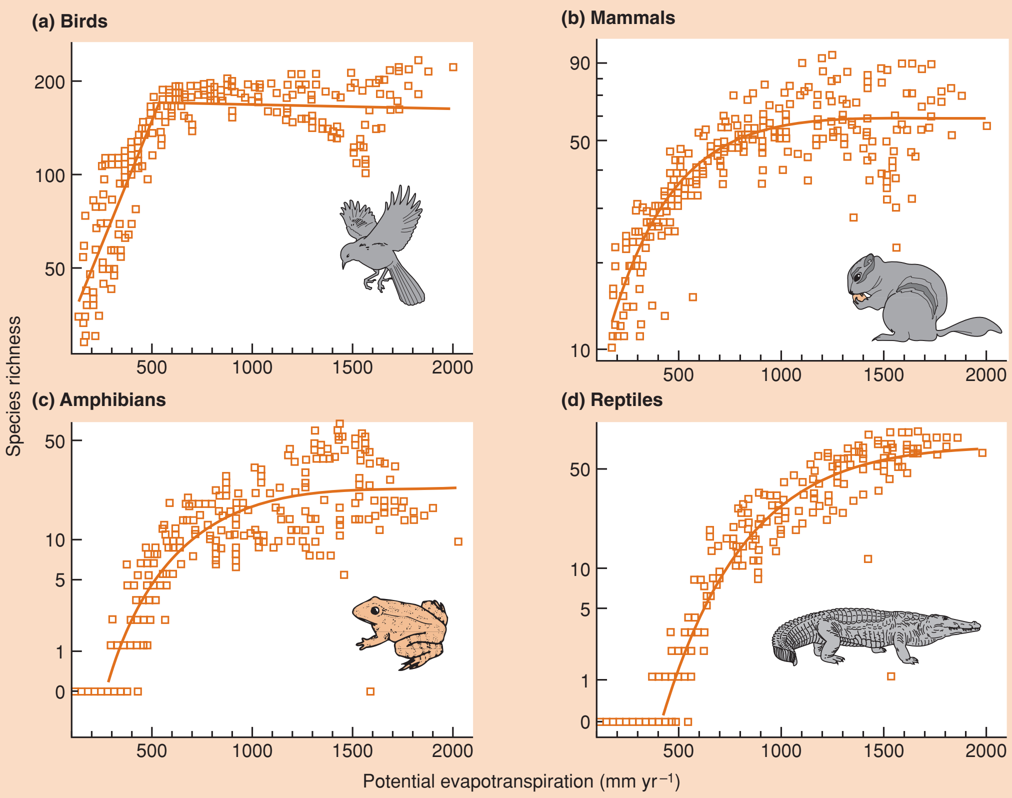


Figure 21.4 Species richness of (a) birds, (b) mammals, (c) amphibians, and (d) reptiles in North America in relation to potential evapotranspiration. (After Currie, 1991.)

available. It is particularly noteworthy that in species-rich sites, the communities contained more species of very large ants (which consume large seeds) and more species of very small ants (which take small seeds) (Davidson, 1977). It seems that either the range of sizes of seeds is greater in the more productive environments (see Figure 21.1a) or the abundance of seeds becomes sufficient to support extra consumer species with narrower niches (see Figure 21.1b).

. . . or decreased richness . . .

On the other hand, an increase in diversity with productivity is by no means universal, as noted in the unique Parkgrass experiment which started in 1856 at Rothamstead in England (see Section 16.2.1). A 3.2 ha (8-acre) pasture was divided into 20 plots, two serving as controls and the others receiving a fertilizer treatment once a year. While the unfertilized areas remained essentially unchanged, the fertilized areas showed a progressive decline in species richness (and diversity).

Such declines have long been recognized. Rosenzweig (1971) referred to them as illustrating the 'paradox of enrichment'. One possible resolution of the paradox is that high productivity leads to high rates of population growth, bringing about the extinction of some of the species present because of a speedy conclusion to any potential competitive exclusion. At lower productivity, the environment is more likely to have changed before competitive exclusion is achieved. An association between high productivity and low species richness has been found in several other studies of plant communities (reviewed by Cornwell & Grubb, 2003).

. . . or an increase then a decrease (hump-shaped relationships)

It is perhaps not surprising, then, that several studies have demonstrated both an increase and a decrease in richness with increasing productivity – that is, that species richness may be highest at intermediate levels of productivity. Species richness is low at the lowest productivities because of a shortage of resources, but also declines at the highest productivities where competitive exclusions speed rapidly to their conclusion. For instance, there are humped curves when the species richness of desert rodents is plotted against precipitation (and thus productivity) along a gradient in Israel (Abramsky & Rosenzweig, 1983), when the species richness of central European plants is plotted against soil nutrient supply (Cornwell & Grubb,

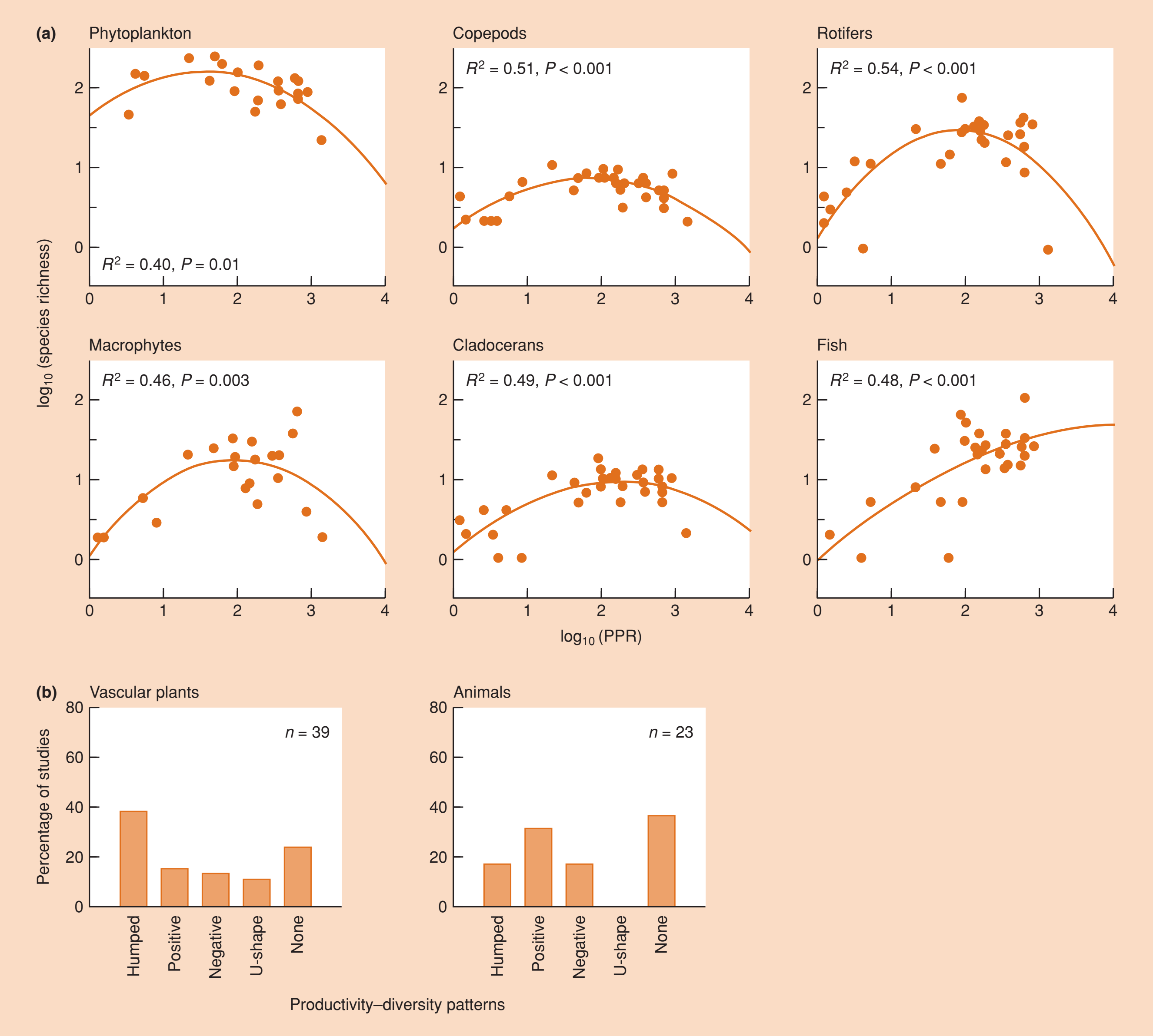


Figure 21.5 (a) Species richness of various taxonomic groups in lakes in North America plotted against gross primary productivity (PPR), with fitted quadratic regression lines (all significant at $P < 0.01$). (After Dodson *et al.*, 2000.) (b) Percentage of published studies on plants and animals showing various patterns of relationship between species richness and productivity. (After Mittelbach *et al.*, 2001.)

2003) and when the species richness of various taxonomic groups is plotted against gross primary productivity in the open water zones of lakes in North America (Figure 21.5a). An analysis of a wide range of such studies found that when communities of the same general type (e.g. tallgrass prairie) but differing in productivity were compared (Figure 21.5b), a positive relationship was the most common finding in animal studies (with fair numbers of humped and negative relationships), whereas with plants, humped relationships were the most common, with smaller numbers of positives and negatives (and even some unexplained U-shaped curves). When Venterink *et al.* (2003) assessed the relationship between plant species richness and plant productivity in 150 European wetland sites that differed in the nutrient that was limiting productivity (nitrogen, phosphorus or potassium), they found hump-shaped patterns for nitrogen- and phosphorus-limited sites but species richness declined monotonically with productivity in potassium-limited sites. Clearly, increased productivity can and does lead to increased or decreased species richness – or both.

productivity may affect species richness in combination with other factors

Productivity often, perhaps always, exerts its influence on species richness in combination with other factors. Thus, we saw earlier how grazer-mediated coexistence was most likely to occur in nutrient-rich situations where plant productivity is high, whereas grazing in nutrient-poor, unproductive settings was associated with a reduction in plant richness (see Section 19.4). Moreover, disturbance (dealt with in Chapter 16) can also interact with nutrient supply (productivity) to determine species richness patterns. Wilson and Tilman (2002) monitored for 8 years the effects of four levels each of disturbance (different amounts of annual tilling) and nitrogen addition (in a complete factorial design) on species richness in agricultural fields that had been abandoned 30 years previously. Species richness showed a hump-shaped relationship with disturbance in the zero nitrogen and lowest nitrogen addition treatments because over time, at intermediate disturbance levels, annual plants colonized plots that would otherwise have become dominated by perennials. However, there was no relationship between species richness and disturbance in the high nitrogen treatments, where clearly competitively dominant species emerged even in disturbed plots (Figure 21.6). The higher nutrient levels were presumably sufficient to support rapid growth of competitive dominants, and to lead to competitive exclusion of subordinates between disturbance episodes.

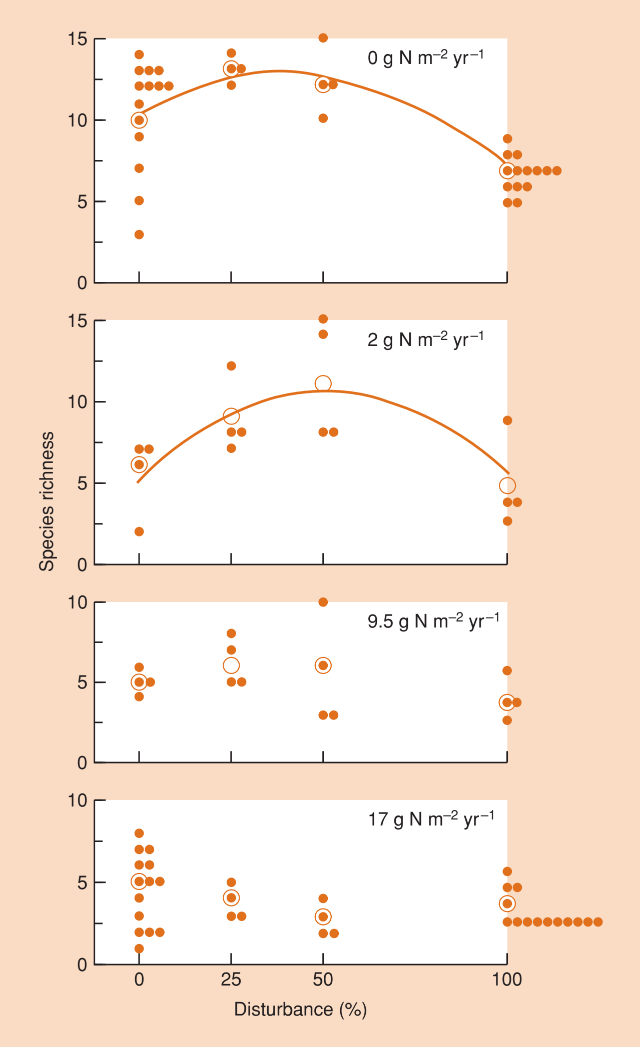


Figure 21.6 Species richness in old fields in Minnesota, USA, after 8 years across four levels of disturbance (quantified in terms of the percentage of bare ground produced by annual tilling) at four levels of nitrogen addition. Dots are values from replicate plots (1 m^2) and open circles are treatment means. Regression lines are shown only for significant relationships ($P < 0.05$). (After Wilson & Tilman, 2002.)

21.3.2 Spatial heterogeneity

We have already seen how the patchy nature of an environment, coupled with aggregative behavior, can lead to coexistence of competing species (see Section 8.5.5). In addition, environments that are more spatially heterogeneous can be expected to accommodate extra species because they provide a greater variety of microhabitats, a greater range of microclimates, more types of places to hide from predators and so on. In effect, the extent of the resource spectrum is increased (see Figure 21.1a).

richness and heterogeneity in an abiotic environment

In some cases, it has been possible to relate species richness to the spatial heterogeneity of the abiotic environment. For instance, a study of plant species growing in 51 plots alongside the Hood River, Canada, revealed a positive relationship between species richness and an index of spatial heterogeneity (based, among other things, on the number of categories of substrate, slope, drainage regimes and soil pH present) (Figure 21.7a).

animal richness related to plant spatial heterogeneity

Most studies of spatial heterogeneity, though, have related the species richness of animals to the structural diversity of the plants in their environment (Figure 21.7b–d), occasionally as a result of experimental manipulation of the plants, as with the spiders in Figure 21.7b, but more commonly through comparisons of different natural communities (Figure 21.7c, d). However, whether spatial heterogeneity arises intrinsically from the abiotic environment or is provided by other biological components of the community, it is capable of promoting an increase in species richness.

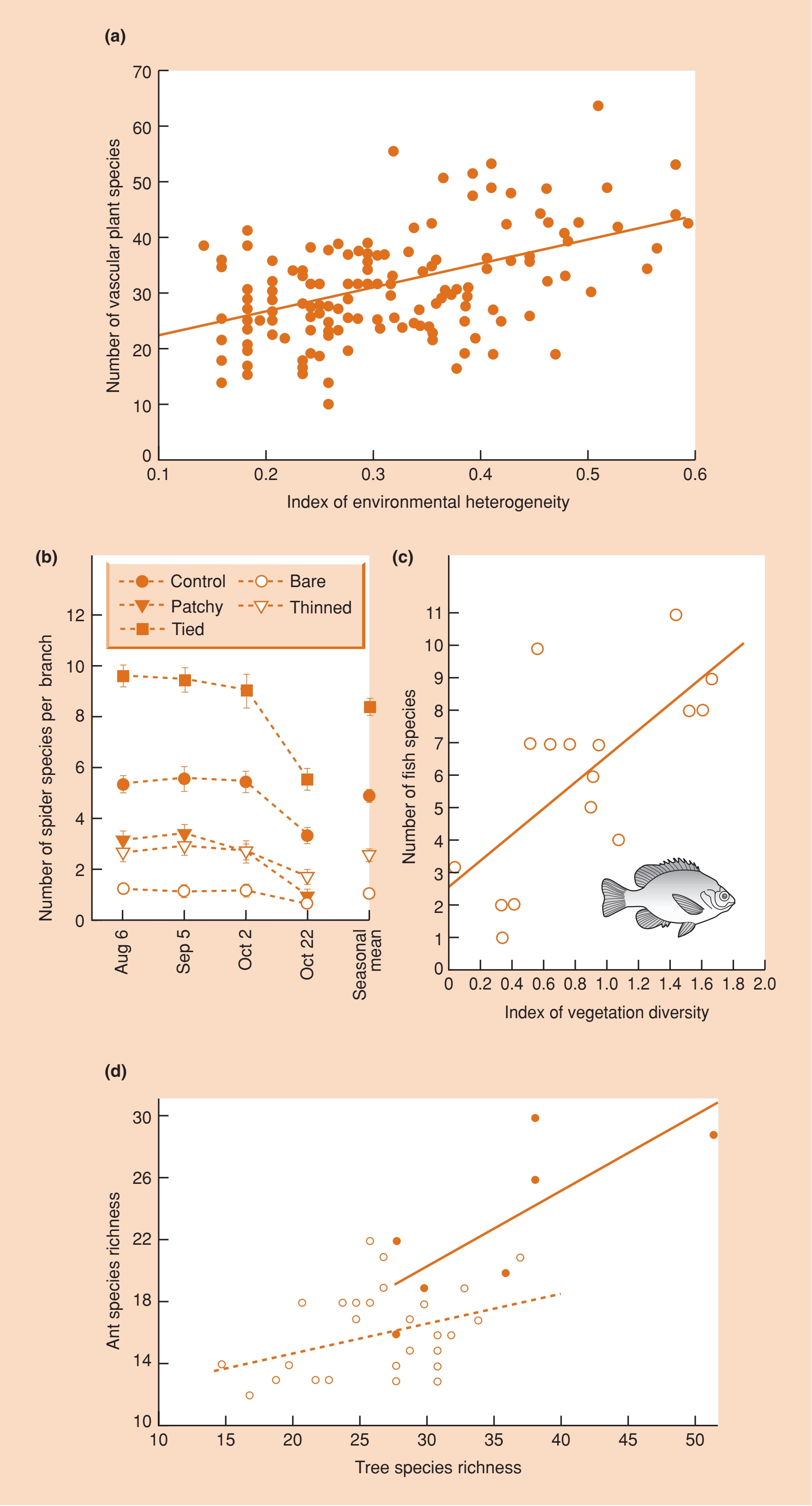


Figure 21.7 Relationship between the number of plants per 300 m^2 plot beside the Hood River, Northwest Territories, Canada, and an index (ranging from 0 to 1) of spatial heterogeneity in abiotic factors associated with topography and soil. (After Gould & Walker, 1997.) (b) In an experimental study, the number of spider species living on Douglas fir branches increases with their structural diversity. Those 'bare', 'patchy' or 'thinned' were less diverse than normal ('control') by virtue of having needles removed; those 'tied' were more diverse because their twigs were entwined together. (After Halaj *et al*., 2000.) (c) Relationships between animal species richness and an index of structural diversity of vegetation for freshwater fish in 18 Wisconsin lakes. (After Tonn & Magnuson, 1982.)
(d) Relationship between arboreal ant species richness in two regions of Brazilian savanna and the species richness of trees (a surrogate for spatial heterogeneity). ○, Distrito Federal; ●, Paraopeba region. (After Ribas *et al*., 2003.)

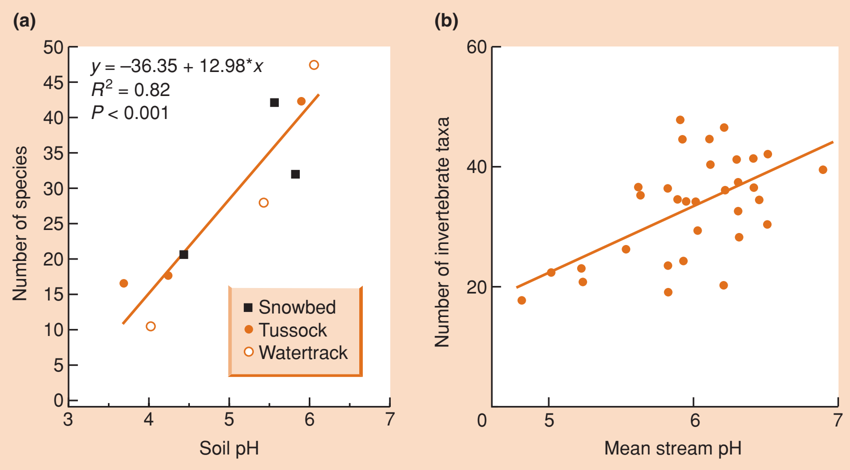


Figure 21.8 (a) The number of plant species per 72 m^2 sampling unit in the Alaskan Arctic tundra increases with pH. (After Gough *et al*., 2000.) (b) The number of taxa of invertebrates in streams in Ashdown Forest, southern England, increases with the pH of the streamwater. (After Townsend *et al*., 1983.)

21.3.3 Environmental harshness

what is harsh?

Environments dominated by an extreme abiotic factor – often called harsh environments – are more difficult to recognize than might be immediately apparent. An anthropocentric view might describe as extreme both very cold and very hot habitats, unusually alkaline lakes and grossly polluted rivers. However, species have evolved and live in all such environments, and what is very cold and extreme for us must seem benign and unremarkable to a penguin in the Antarctic.

We might try to get around the problem of defining environmental harshness by 'letting the organisms decide'. An environment may be classified as *extreme* if organisms, by their failure to live there, show it to be so. But if the claim is to be made – as it often is – that species richness is lower in extreme environments, then this definition is circular, and it is designed to prove the very claim we wish to test.

Perhaps the most reasonable definition of an extreme condition is one that requires, of any organism tolerating it, a morphological structure or biochemical mechanism that is not found in most related species and is costly, either in energetic terms or in terms of the compensatory changes in the organism's biological processes that are needed to accommodate it. For example, plants living in highly acidic soils (low pH) may be affected directly through injury by hydrogen ions or indirectly via deficiencies in the availability and uptake of important resources such as phosphorus, magnesium and calcium. In addition, aluminum, manganese and heavy metals may have their solubility increased to toxic levels, and mycorrhizal activity and nitrogen fixation may be impaired. Plants can only tolerate low pH if they have specific structures or mechanisms allowing them to avoid or counteract these effects.

are harsh environments the cause of low species richness?

Environments that experience a low pH can thus be considered harsh, and the mean number of plant species recorded per sampling unit in a study in the Alaskan Arctic tundra was indeed lowest in soils of low pH (Figure 21.8a). Similarly, the species richness of benthic stream invertebrates in the Ashdown Forest (southern UK) was markedly lower in the more acidic streams (Figure 21.8b). Further examples of extreme environments that are associated with low species richness include hot springs, caves and highly saline water bodies such as the Dead Sea. The problem with these examples, however, is that they are also characterized by other features associated with low species richness such as low productivity and low spatial heterogeneity. In addition, many occupy small areas (caves, hot springs) or areas that are rare compared to other types of habitat (only a small proportion of the streams in southern England are acidic). Hence extreme environments can often be seen as small and isolated islands. We will see in Section 21.5.1 that these features, too, are usually associated with low species richness. Although it appears reasonable that intrinsically extreme environments should as a consequence support few species, this has proved an extremely difficult proposition to establish.

21.4 Temporally varying factors that influence species richness

Temporal variation in conditions and resources may be predictable or unpredictable and operate on timescales from minutes through to centuries and millennia. All may influence species richness in profound ways.

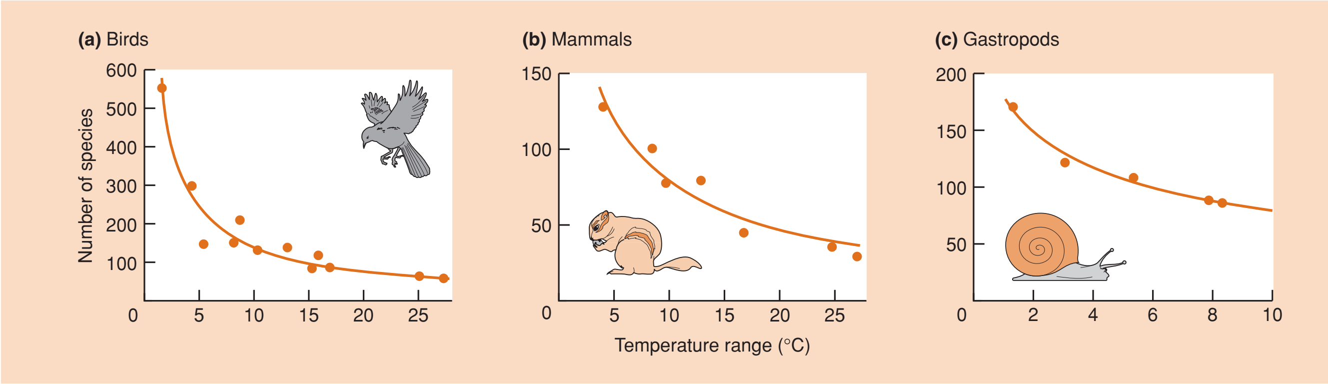


Figure 21.9 Relationships between species richness and the range of monthly mean temperatures at sites along the west coast of North America for (a) birds, (b) mammals and (c) gastropods. (After MacArthur, 1975.)

21.4.1 Climatic variation

temporal niche differentiation in seasonal environments

The effects of climatic variation on species richness depend on whether the variation is predictable or unpredictable (measured on timescales that matter to the organisms involved). In a predictable, seasonally changing environment, different species may be suited to conditions at different times of the year. More species might therefore be expected to coexist in a seasonal environment than in a completely constant one (see Figure 21.1a). Different annual plants in temperate regions, for instance, germinate, grow, flower and produce seeds at different times during a seasonal cycle; while phytoplankton and zooplankton pass through a seasonal succession in large, temperate lakes with a variety of species dominating in turn as changing conditions and resources become suitable for each.

specialization in nonseasonal environments

On the other hand, there are opportunities for specialization in nonseasonal environments that do not exist in seasonal environments. For example, it would be difficult for a long-lived obligate fruit-eater to exist in a seasonal environment when fruit is available for only a very limited portion of the year. But such specialization is found repeatedly in nonseasonal, tropical environments where fruit of one type or another is available continuously.

climatic instability may increase or decrease richness . . .

Unpredictable climatic variation (climatic instability) could have a number of effects on species richness: (i) stable environments may be able to support specialized species that would be unlikely to persist where conditions or resources fluctuated dramatically (see Figure 21.1b); (ii) stable environments are more likely to be saturated with species (see Figure 21.1d); and (iii) theory suggests that a higher degree of niche overlap will be found in more stable environments (see Figure 21.1c). All these processes could increase species richness. On the other hand, populations in a stable environment are more likely to reach their carrying capacities, the community is more likely to be dominated by competition, and species are therefore more likely to be excluded by competition (where $\bar{o}$ is smaller, see Figure 21.1c).

. . . but there is no good evidence either way

Some studies have seemed to support the notion that species richness increases as climatic variation decreases. For example, there is a significant negative relationship between species richness and the range of monthly mean temperatures for birds, mammals and gastropods that inhabit the west coast of North America (from Panama in the south to Alaska in the north) (Figure 21.9). However, this correlation does not prove causation, since there are many other things that change between Panama and Alaska. There is no established relationship between climatic instability and species richness.

21.4.2 Environmental age: evolutionary time

variable recovery from an ancient disturbance?

It has also often been suggested that communities that are 'disturbed' even on very extended timescales may none the less lack species because they have yet to reach an ecological or an evolutionary equilibrium. Thus communities may differ in species richness because some are closer to equilibrium and are therefore more saturated than others (see Figure 21.1d).

unchanging tropics and recovering temperate zones?

For example, many have argued that the tropics are richer in species than are more temperate regions at least in part because the tropics have existed over long and uninterrupted periods of evolutionary time, whereas the temperate regions are still recovering from the Pleistocene glaciations. It seems, however, that the long-term stability of the tropics has in the past been greatly exaggerated by ecologists. Whereas the climatic and biotic zones of the temperate region moved toward the equator during the glaciations, the tropical forest appears to have contracted to a limited number of small refuges surrounded by grasslands. A simplistic contrast between the unchanging tropics and the disturbed and recovering temperate regions is therefore untenable.

A comparison between the two polar regions may be more instructive. Both Arctic and Antarctic marine environments are cold, seasonal and strongly influenced by ice but their histories are quite different. The Arctic basin lost its fauna when covered by thick permanent ice at the height of the last glaciation and recolonization is underway; whereas a shallow water fauna has existed around the Antarctic since the mid-Palaeozoic (Clarke & Crame, 2003). Today the two polar faunas contrast markedly, the Arctic being depauperate and the Antarctic rich, most likely reflecting the importance of their histories.

21.5 Habitat area and remoteness: island biogeography

larger islands contain more species: contrasting explanations

It is well established that the number of species on islands decreases as island area decreases. Such a *species–area* relationship is shown in Figure 21.10a for terrestrial vascular plants on islands in the Stockholm Archipelago, Sweden.

'Islands', however, need not be islands of land in a sea of water. Lakes are islands in a 'sea' of land, mountain tops are high-altitude islands in a low-altitude ocean, gaps in a forest canopy where tree have fallen are islands in a sea of trees, and there can be islands of particular geological types, soil types or vegetation types surrounded by dissimilar types of rock, soil or vegetation. Species–area relationships can be equally apparent for these types of islands (Figure 21.10b–d).

The relationship between species richness and habitat area is one of the most consistent of all ecological patterns. However, the pattern raises an important question: 'Is the impoverishment of species on islands more than would be expected in comparably small areas of mainland?' In other words, does the characteristic isolation of islands contribute to their impoverishment of species? These are important questions for an understanding of community structure since there are many oceanic islands, many lakes, many mountaintops, many woodlands surrounded by fields, many isolated trees, and so on.

21.5.1 MacArthur and Wilson's 'equilibrium' theory

Probably the most obvious reason why larger areas should contain more species is that larger areas typically encompass more

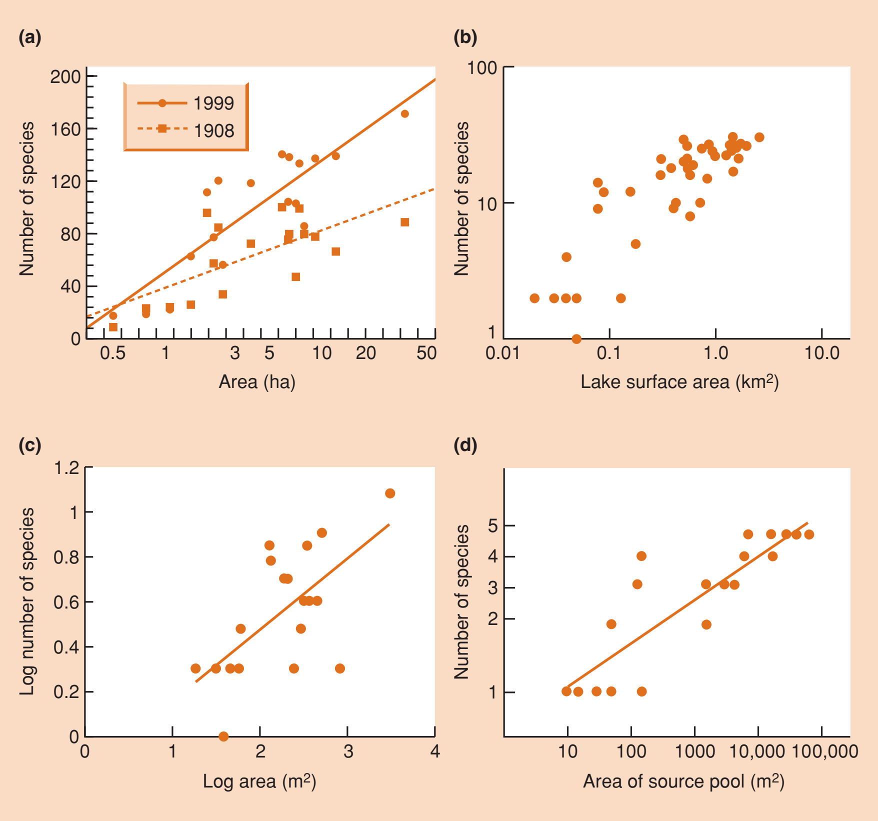


Figure 21.10 Species–area relationships. (a) Plants on islands east of Stockholm, Sweden: ●, survey completed in 1999 after grazing and hay-making had ceased; ■ survey completed in 1908 when intensive agriculture was practised. (After Lofgren & Jerling, 2002.) (b) Birds inhabiting lakes in Florida. (After Hoyer & Canfield, 1994.) (c) Bats inhabiting different-sized caves in Mexico. (After Brunet & Medellin, 2001.) (d) Fish living in Australian desert springs that have source pools of different sizes. (After Kodric-Brown & Brown, 1993.)

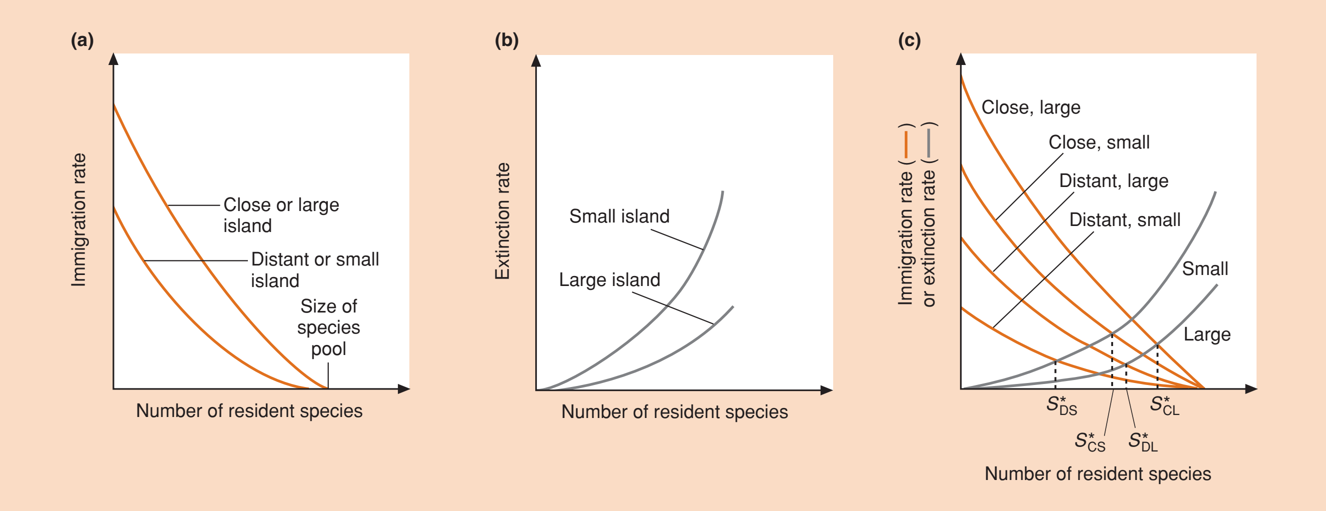


Figure 21.11 MacArthur and Wilson's (1976) equilibrium theory of island biogeography. (a) The rate of species immigration on to an island, plotted against the number of resident species on the island, for large and small islands and for close and distant islands. (b) The rate of species extinction on an island, plotted against the number of resident species on the island, for large and small islands. (c) The balance between immigration and extinction on small and large and on close and distant islands. In each case, S^* is the equilibrium species richness; C, close; D, distant; L, large; S, small.

different types of habitat. However, MacArthur and Wilson (1967) believed this explanation to be too simple. In their *equilibrium theory of island biogeography*, they argued: (i) that island size and isolation themselves played important roles – that the number of species on an island is determined by a balance between immigration and extinction; (ii) that this balance is dynamic, with species continually going extinct and being replaced (through immigration) by the same or by different species; and (iii) that immigration and extinction rates may vary with island size and isolation.

MacArthur and Wilson's immigration curves . . .

Taking immigration first, imagine an island that as yet contains no species at all. The rate of immigration of *species* will be high, because any colonizing individual represents a species new to that island. However, as the number of resident species rises, the rate of immigration of new, unrepresented species diminishes. The immigration rate reaches zero when all species from the source pool (i.e. from the mainland or from other nearby islands) are present on the island in question (Figure 21.11a).

The immigration graph is drawn as a curve, because immigration rate is likely to be particularly high when there are low numbers of residents and many of the species with the greatest powers of dispersal are yet to arrive. In fact, the curve should really be a blur rather than a single line, since the precise curve will depend on the exact sequence in which species arrive, and this will vary by chance. In this sense, the immigration curve can be thought of as the *most probable curve*.

The exact immigration curve will depend on the degree of remoteness of the island from its pool of potential colonizers (Figure 21.11a). The curve will always reach zero at the same point (when all members of the pool are resident), but it will generally have higher values on islands close to the source of immigration than on more remote islands, since colonizers have a greater chance of reaching an island the closer it is to the source. It is also likely that immigration rates will generally be higher on a large island than on a small island, since the larger island represents a larger target for the colonizers (Figure 21.11a).

. . . and extinction curves

The rate of species extinction on an island (Figure 21.11b) is bound to be zero when there are no species there, and it will generally be low when there are few species. However, as the number of resident species rises, the extinction rate is assumed by the theory to increase, probably at a more than proportionate rate. This is thought to occur because with more species, competitive exclusion becomes more likely, and the population size of each species is on average smaller, making it more vulnerable to chance extinction. Similar reasoning suggests that extinction rates should be higher on small than on large islands as population sizes will typically be smaller on small islands (Figure 21.11b). As with immigration, the extinction curves are best seen as 'most probable' curves.

the balance between immigration and extinction

In order to see the net effect of immigration and extinction, their two curves can be superimposed (Figure 21.11c). The number of species where the curves cross (S^*) is a dynamic equilibrium and should be the characteristic species richness for the island in question. Below S^*, richness increases (immigration rate exceeds extinction rate); above S^*, richness decreases (extinction exceeds immigration). The theory, then, makes a number of predictions:

1. The number of species on an island should eventually become roughly constant through time.
2. This should be a result of a continual *turnover* of species, with some becoming extinct and others immigrating.
3. Large islands should support more species than small islands.
4. Species number should decline with the increasing remoteness of an island.

predictions of equilibrium theory are not all exclusive to this theory

Note, though, that several of these predictions could also be made without any reference to the equilibrium theory. An approximate constancy of species number would be expected if richness were determined simply by island type. Similarly, a higher richness on larger islands would be expected as a consequence of larger islands having more habitat types. One test of the equilibrium theory, therefore, would be whether richness increases with area at a rate greater than could be accounted for by increases in habitat diversity alone (see Section 21.5.2).

The effect of island remoteness can be considered quite separately from the equilibrium theory. Merely recognizing that many species are limited in their dispersal ability, and have not yet colonized all islands, leads to the prediction that more remote islands are less likely to be saturated with potential colonizers (see Section 21.5.3). However, the final prediction arising from the equilibrium theory – constancy as a result of turnover – is truly characteristic of the equilibrium theory (see Section 21.5.4).

21.5.2 Habitat diversity alone – or a separate effect of area?

an example where habitat diversity is paramount

The most fundamental question in island biogeography, then, is whether there is an 'island effect' as such, or whether islands simply support few species because they are small areas containing few habitats. Does richness increase with area at a rate *greater* than could be accounted for by increases in habitat diversity alone? Some studies have attempted to partition species–area variation on islands into that which can be entirely accounted for in terms of habitat diversity, and that which remains and must be accounted for by island area in its own right. For beetles on the Canary Islands, the relationship between species richness and habitat diversity (as measured by plant species richness) is much stronger than that with island area, and this is particularly marked for the herbivorous beetles, presumably because of their particular food plant requirements (Figure 21.12a).

partitioning variation between habitat diversity and island area itself

On the other hand, in a study of a variety of animal groups living on the Lesser Antilles island in the West Indies, the variation in species richness from island to island was partitioned, statistically, into that attributable to island area alone, that attributable to habitat diversity alone, that attributable to correlated variation between area and habitat diversity (and hence not attributable to either alone), and that attributable to neither. For reptiles and amphibians (Figure 21.12b), like the beetles of the Canary Islands, habitat diversity was far more important than island area. But for bats, the reverse was the case, and for birds and butterflies, both area itself and habitat diversity had important parts to play.

experimental reductions in mangrove island area

An experiment was carried out to try to separate the effects of habitat diversity and area on some small mangrove islands in the Bay of Florida (Simberloff, 1976). These islands consist of pure stands of the mangrove species *Rhizophora mangle*, which support communities of insects, spiders, scorpions and isopods. After a preliminary faunal survey, some islands were reduced in size – by means of a power saw. Habitat diversity was not affected, but arthropod species richness on three islands none the less diminished over a period of 2 years (Figure 21.13). A control island, the size of which was unchanged, showed a slight *increase* in richness over the same period, presumably as a result of random events.

species–area graphs for islands and comparable mainland areas

Another way of trying to distinguish a separate effect of island area is to compare species–area graphs for islands with those for arbitrarily defined areas of mainland. The species–area relationships for mainland areas should be due almost entirely to habitat diversity (together with any 'sampling' effect involving increased probabilities of detecting rare species in larger areas). All species will be well able to 'disperse' between mainland areas, and the continual flow of individuals across the arbitrary boundaries will therefore mask local extinctions (i.e. what would be an extinction on an island is soon reversed by the exchange of individuals between local areas). An arbitrarily defined area of mainland should thus contain more species than an otherwise equivalent island, and this is usually interpreted as meaning that the slopes of the species–area graphs for islands should be steeper than those for mainland areas (since the effect of island isolation should be most marked on small islands, where extinctions are most likely). The difference between the two types of graph would then be attributable to the island effect in its own right. Table 21.1 shows that despite considerable variation, the island graphs do typically have steeper slopes.

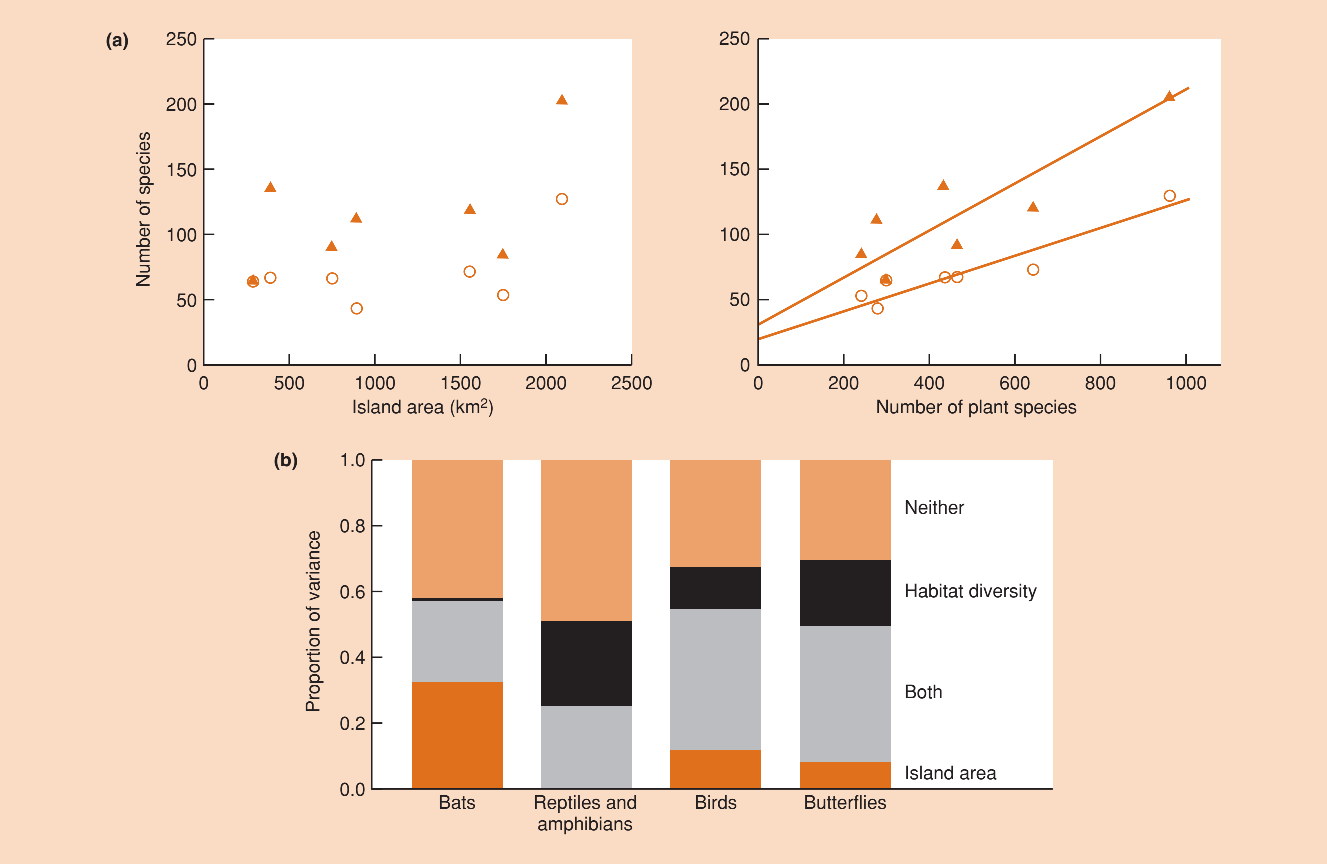


Figure 21.12 (a) The relationships between species richness of herbivorous (○) and carnivorous (▲) beetles of the Canary Islands and both island area and plant species richness. (After Becker, 1992.) (b) Proportion of variance, for four animal groups, in species richness among islands in the Lesser Antilles related uniquely to island area, uniquely to habitat diversity, to correlated variation between area and habitat diversity and unexplained by either. (After Ricklefs & Lovette, 1999.)

Note that a reduced number of species per unit area on islands should also lead to a lower value for the intercept on the *S*-axis of the species–area graph. Figure 21.14a illustrates both an increased slope and a reduced value for the intercept for the species–area graph for ant species on isolated Pacific islands, compared with the graph for progressively smaller areas of the very large island of New Guinea. Figure 21.14b gives a similar relationship for reptiles on islands off the coast of South Australia.

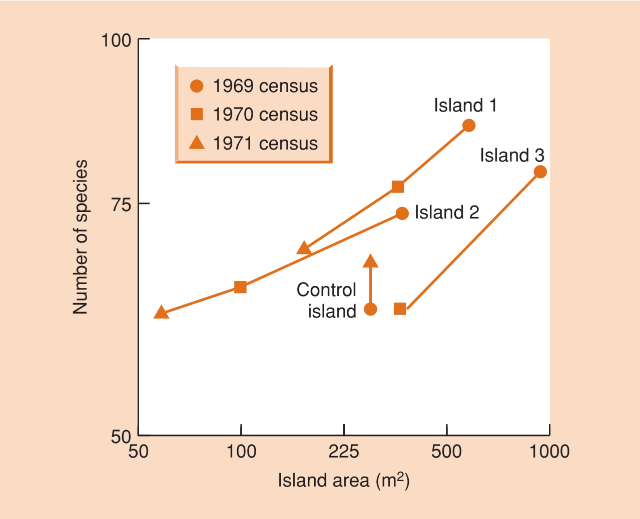


Figure 21.13 (*left*) The effect on the number of arthropod species of artificially reducing the size of mangrove islands. Islands 1 and 2 were reduced in size after both the 1969 and 1970 censuses. Island 3 was reduced only after the 1969 census. The control island was not reduced, and the change in its species richness was attributable to random fluctuations. (After Simberloff, 1976.)

Table 21.1 Values of the slope z, of species–area curves ($\log S = \log C + z \log A$, where S is species richness, A is area and C is a constant giving the number of species when A has a value of 1), for arbitrary areas of mainland, oceanic islands and habitat islands. (After Preston, 1962; May, 1975b; Gorman, 1979; Browne, 1981; Matter *et al.*, 2002; Barrett *et al.*, 2003; Storch *et al.*, 2003.)

Taxonomic group	*Location*	z
Arbitrary areas of mainland		
Birds	Central Europe	0.09
Flowering plants	England	0.10
Birds	Neoarctic	0.12
Savanna vegetation	Brazil	0.14
Land plants	Britain	0.16
Birds	Neotropics	0.16
Oceanic islands		
Birds	New Zealand islands	0.18
Lizards	Californian islands	0.20
Birds	West Indies	0.24
Birds	East Indies	0.28
Birds	East Central Pacific	0.30
Ants	Melanesia	0.30
Land plants	Galápagos	0.31
Beetles	West Indies	0.34
Mammals	Scandinavian islands	0.35
Habitat islands		
Zooplankton (lakes)	New York State	0.17
Snails (lakes)	New York State	0.23
Fish (lakes)	New York State	0.24
Birds (Paramo vegetation)	Andes	0.29
Mammals (mountains)	Great Basin, USA	0.43
Terrestrial invertebrates (caves)	West Virginia	0.72

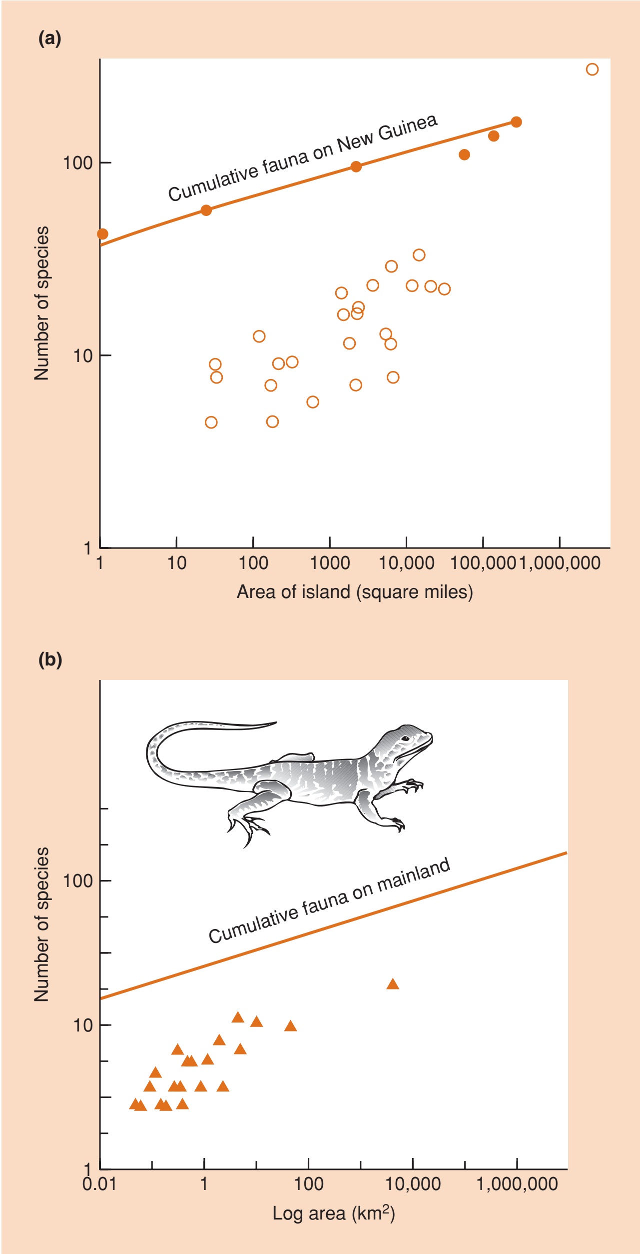


Figure 21.14 (a) The species–area graph for ponerine ants on various Moluccan and Melanesian islands compared with a graph for different-sized sample areas on the very large island of New Guinea. (After Wilson, 1961.) (b) The species–area graph for reptiles on islands off the coast of South Australia compared with the mainland species–area relationship. In this case, the islands were formed within the last 10,000 years as a result of rising sea level. (After Richman *et al.*, 1988.)

plant extinction and immigration rates in relation to island size

Overall, therefore, studies like this suggest a separate area effect (larger islands are larger targets for colonization; populations on larger islands have a lower risk of extinction) beyond a simple correlation between area and habitat diversity. Lofgren and Jerling (2002) were able to quantify plant extinction rates and immigration rates on islands of different sizes in the Stockholm Archipelago (see Figure 21.10a) by comparing species lists in their survey (1996–99) with those reported by J. W. Hamner from the period 1884–1908. In the intervening time, 93 new species appeared while 20 species disappeared from the islands. Many of the newcomers were trees, bushes and shade-tolerant shrubs, reflecting succession after the cessation of cattle grazing and hay-making in the 1960s. Despite the confounding effect of succession, and as predicted, extinction rate was negatively correlated and immigration rate positively correlated with island size.

21.5.3 Remoteness

It follows from the above argument that the island effect and the species impoverishment of an island should be greater for more remote islands. (Indeed, the comparison of islands with mainland areas is only an extreme example of a comparison of islands varying in remoteness, since local mainland areas can be thought of as having minimal remoteness.) Remoteness, however, can mean two things. First, it can simply refer to the degree of physical isolation. Alternatively, a single island can also itself vary in remoteness, depending on the type of organism being considered: the same island may be remote from the point of view of land mammals but not from the point of view of birds.

bird species richness on islands decreases with 'remoteness'

The effects of remoteness can be demonstrated either by plotting species richness against remoteness itself, or by comparing the species–area graphs of groups of islands (or for groups of organisms) that differ in their remoteness (or powers of colonization). In either case, there can be considerable difficulty in extricating the effects of remoteness from all the other characteristics by which two islands may differ. Nevertheless, the direct effect of remoteness can be seen in Figure 21.15 for nonmarine, lowland birds on tropical islands in the southwest Pacific. With increasing distance from the large source island of New Guinea, there is a decline in the number of species, expressed as a percentage of the number present on an island of similar area but close to New Guinea. Species richness decreases exponentially with distance, approximately halving every 2600 km. The species–area graph in Figure 21.16a also shows that remote islands of a given size possess fewer species than their counterparts close to a land mass. In addition, Figure 21.16b contrasts the species–area graphs of two classes of organisms in two regions: the relatively remote Azores (in the Atlantic, far to the west of Portugal) and the Channel Islands (close to the north coast of France). Whereas the Azores are indeed far more remote than the Channel Islands from the point of view of the birds, the two island groups are apparently equally remote for ferns, which are particularly good dispersers because of their light, wind-blown spores. Thus, on the basis of all these examples, the species impoverishment caused by the island effect does indeed appear to increase as the degree of isolation of the island increases. Note, also, that a multiple regression analysis of Lofgren and Jerling's 1999 Stockholm Archipelago database (see Figure 21.10a) demonstrated the overriding effect of island area on plant species richness (73% of variation explained), but distance to the nearest island also contributed significantly, explaining a further 17% of variation.

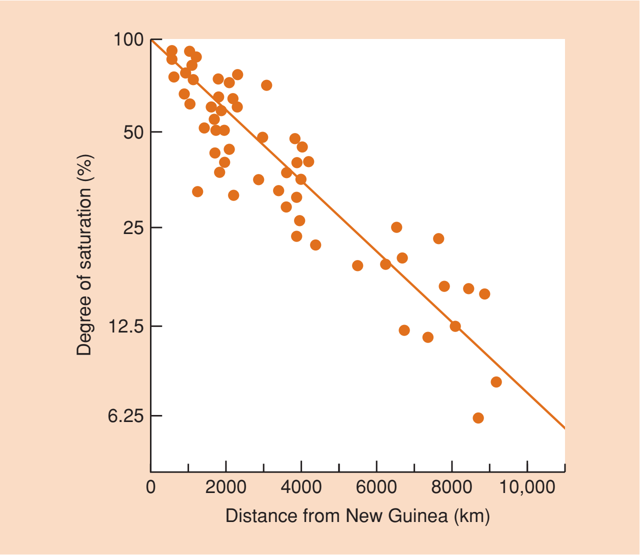


Figure 21.15 The number of resident, nonmarine, lowland bird species on islands more than 500 km from the larger source island of New Guinea expressed as a proportion of the number of species on an island of equivalent area but close to New Guinea, and plotted as a function of island distance from New Guinea. (After Diamond, 1972.)

A more transient but none the less important reason for the species impoverishment of islands, especially remote islands, is the fact that many lack species that they could potentially support, simply because there has been insufficient time for the species to colonize. An example is the island of Surtsey, which emerged in 1963 as a result of a volcanic eruption (Fridriksson, 1975). The new island, 40 km southwest of Iceland, was reached by bacteria and fungi, some seabirds, a fly and the seeds of several beach plants within 6 months of the start of the eruption. Its first established vascular plant was recorded in 1965, and the first moss colony in 1967. By 1973, 13 species of vascular plant and more than 66 mosses had become established (Figure 21.17). Colonization is continuing still. The general importance of this example is that the communities of many islands can be understood *neither* in terms of simple habitat suitability *nor* as a characteristic equilibrium richness. Rather, they stress that many island communities have not reached equilibrium and are certainly not fully 'saturated' with species.

21.5.4 Which species? Turnover

species turnover . . .

MacArthur and Wilson's equilibrium theory predicts not only a characteristic species richness for an island, but also a *turnover* of species in which new species continually colonize whilst others become extinct. This implies a significant degree of chance regarding precisely which species are present at any one time. However, studies of turnover itself are rare, because communities have to be followed over a period of time (usually difficult and costly). Good studies of turnover are rarer still, because it is necessary to count every species on every occasion so as to avoid 'pseudo-immigrations'

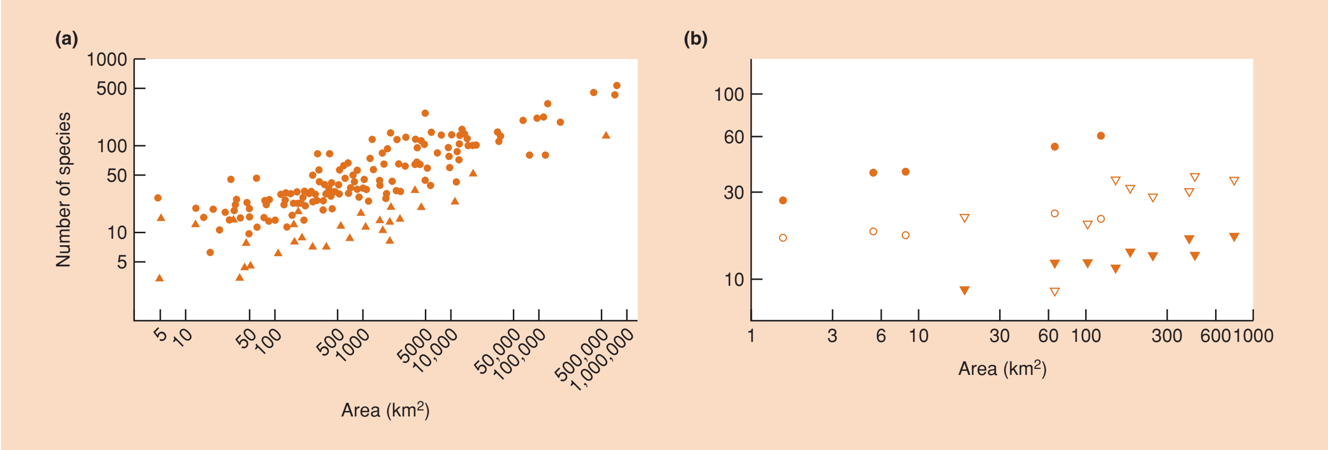


Figure 21.16 Remoteness increases the species impoverishment of islands. (a) A species–area plot for the land birds of individual islands in tropical and subtropical seas. ▲, islands more than 300 km from the next largest land mass or the very remote Hawaiian and Galápagos archipelagos; ●, islands less than 300 km from source. (b) Species–area plots in the Azores and the Channel Islands for land and freshwater breeding birds (▼, Azores; ●, Channel Islands) and for native ferns (▽, Azores; ○, Channel Islands). The Azores are more remote for birds but not for ferns. (After Williamson, 1981.)

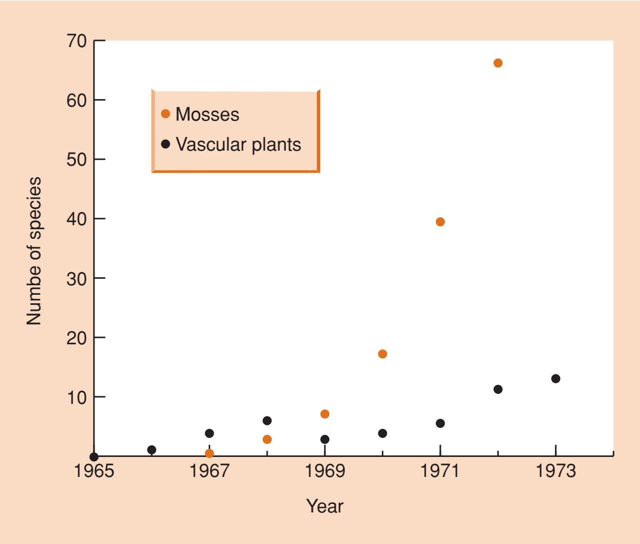


Figure 21.17 The number of species of mosses and vascular plants recorded on the new island of Surtsey from 1965 to 1973. (After Fridriksson, 1975.)

and 'pseudo-extinctions'. Indeed, any results are bound to be underestimates of actual turnover, because an observer cannot be everywhere all the time.

. . . is relatively high for temperate woodland birds . . .

One revealing study involved censuses from 1949 to 1975 of the breeding birds in a small oak wood (Eastern Wood) in southern England. In all, 44 species bred in the wood over this period, and 16 of them bred every year. The number breeding in any one year varied between 27 and 36, with an average of 32 species. The immigration and extinction 'curves' are shown in Figure 21.18. Their most obvious feature is the scattering of points as compared with the assumed simplicity of the MacArthur–Wilson model. Nevertheless, whilst the positive correlation in the extinction graph is statistically insignificant, the negative correlation in the immigration graph is highly significant; and the two lines do seem to cross at roughly 32 species, with three new immigrants and three extinctions each year. There is clearly a considerable turnover of species, and consequently considerable year-to-year variation in the bird community of Eastern Wood despite its approximately constant species richness.

. . . but not for birds on a tropical island

In contrast, a long-term study (surveys in 1954, 1976 and annually from 1984 to 1990) of the 15-strong bird community on tropical Guana Island, revealed no such turnover – no new species established and only one went extinct, as a result of habitat destruction (Mayer & Chipley, 1992). The position of Guana Island within an archipelago of numerous small islands may reduce the likelihood of local extinctions if there is continuous dispersal from island to island. On the other hand, it is conceivable that tropical birds really do have lower turnover rates – because they are more often sedentary, have lower adult mortality and are more often resident, as opposed to migratory (Mayer & Chipley, 1992).

Experimental evidence of turnover and indeterminacy is provided by the work of Simberloff and Wilson (1969), who exterminated the invertebrate fauna on a series of small mangrove islands in the Florida Keys and monitored recolonization. Within about 200 days, species richness had stabilized around the level

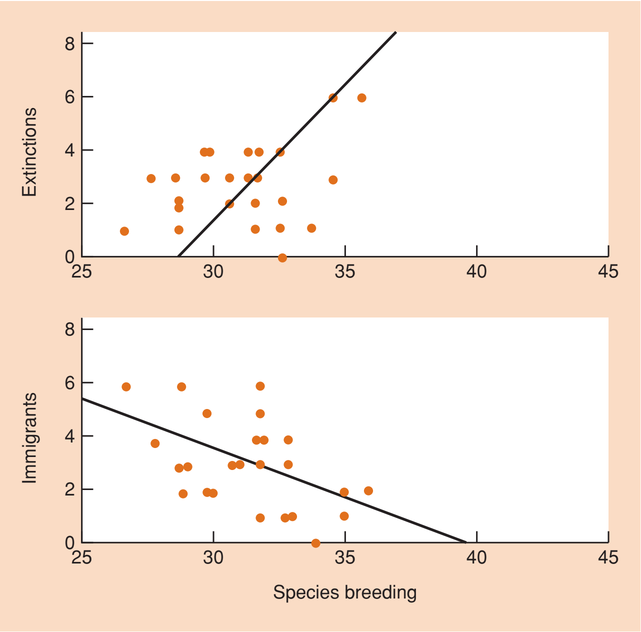


Figure 21.18 Immigration and extinction of breeding birds at Eastern Wood, UK. The line in the extinction diagram is at 45°. The line in the immigration diagram is the calculated regression line with a slope of −0.38. (After Beven, 1976; from Williamson, 1981.)

prior to defaunation, but with many differences in species composition. Since then, the rate of turnover of species on the islands has been estimated as 1.5 extinctions and colonizations per year (Simberloff, 1976).

Thus, the idea that there is a turnover of species leading to a characteristic equilibrium richness on islands, but an indeterminacy regarding particular species, appears to be correct – at least approximately.

21.5.5 Which species? Disharmony

some taxa are better suited to reach islands and persist there . . .

It has long been recognized – for example by Hooker in 1866 – that one of the main characteristics of island biotas is 'disharmony', that is, the relative proportions of different taxa are not the same on islands as they are on the mainland. We have already seen from the species–area relationships in Figure 21.16 that groups of organisms with good powers of dispersal (like ferns and, to a lesser extent, birds) are more likely to colonize remote islands than are groups with relatively poor powers of dispersal (most mammals).

. . . or vary in their risk of extinction

However, variation in dispersal ability is not the only factor leading to disharmony. Species may vary in their risk of extinction. Thus, species that naturally have low densities per unit area are bound to have only small populations on islands, and a chance fluctuation in a small population is quite likely to eliminate it altogether. Vertebrate predators, which generally have relatively small populations, are notable for their absence on many islands. For example, the birds on the Atlantic island of Tristan da Cunha have no bird, mammal or reptile predators apart from those released by humans. Specialist predators are also liable to be absent from islands because their immigration can only lead to colonization if their prey have arrived first. Similar arguments apply to parasites, mutualists and so on. In other words, for many species an island is only suitable if some other species is present, and disharmony arises because some types of organism are more 'dependent' than others.

incidence functions and assembly rules

The development by Diamond (1975) of *incidence functions* and *assembly rules* for the birds of the Bismark Archipelago is probably the fullest attempt to understand island communities by combining ideas on dispersal and extinction differentials with those on sequences of arrival and habitat suitability. Constructing such incidence functions (Figure 21.19) allowed Diamond to contrast 'supertramp' species (high rates of dispersal but a poorly developed ability to persist in communities with many other species), with 'high *S*' species (only able to persist on large islands with many other species), and to contrast these in turn with intermediate categories. Such work illustrates particularly clearly that it takes far more than a count of the number of species present to characterize the community of an island. Island communities are not merely impoverished – the impoverishment affects particular types of organism disproportionately.

21.5.6 Which species? Evolution

evolution rate on islands may be faster than colonization rate

No aspect of ecology can be fully understood without reference to evolutionary processes taking place over evolutionary timescales, and this is particularly true for an understanding of island communities. On isolated islands, the rate at which new species evolve may be comparable with or even faster than the rate at which they arrive as new colonists. Clearly, the communities of many islands will be incompletely understood by reference only to ecological processes.

endemism – more likely on remote islands (and for poor dispersers) . . .

One widespread illustration of this is the very common occurrence, especially on 'oceanic' islands, of *endemic* species (i.e. species that are found nowhere else). Almost all the species of *Drosophila* on Hawaii, for example (see Section 1.4.1), are endemics (apart from cosmopolitan urban 'pests') as are most of the species

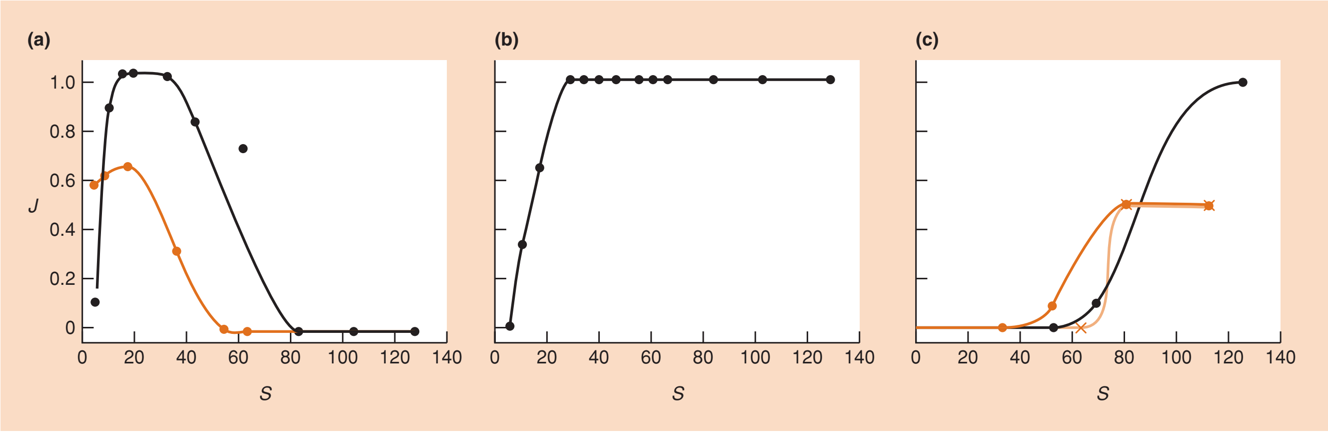


Figure 21.19 Incidence functions for various species in the Bismarcks in which *J*, the proportion of islands occupied by a given species, is plotted against *S*, a measure of island 'size' (actually the total number of bird species present). (a) Incidence functions for two 'supertramps': ●, flycatcher *Monarcha cinerascens*; ●, honeyeater *Myzomela pammelaena*. (b) Incidence function for the pigeon *Chalcophaps stephani*, a competent colonizer and, apparently, an effective competitor. (c) Incidence functions for three species that are restricted to larger islands: ●, hawk *Henicopernis longicauda*; ●, rail *Rallina tricolor*; ×, heron *Butorides striatus*. (After Diamond, 1975.)

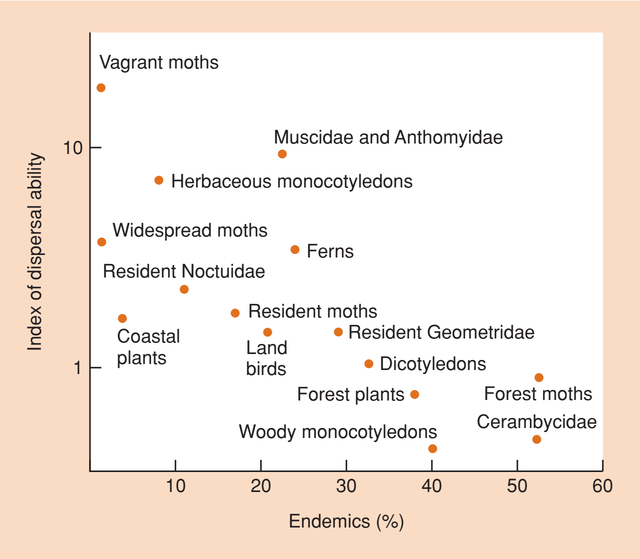


Figure 21.20 Poorly dispersing groups on Norfolk Island have a higher proportion of endemic species, and are more likely to contain species that have reached Norfolk Island from either New Caledonia or New Zealand than species from Australia, which is further away. The converse holds for good dispersers. (After Holloway, 1977.)

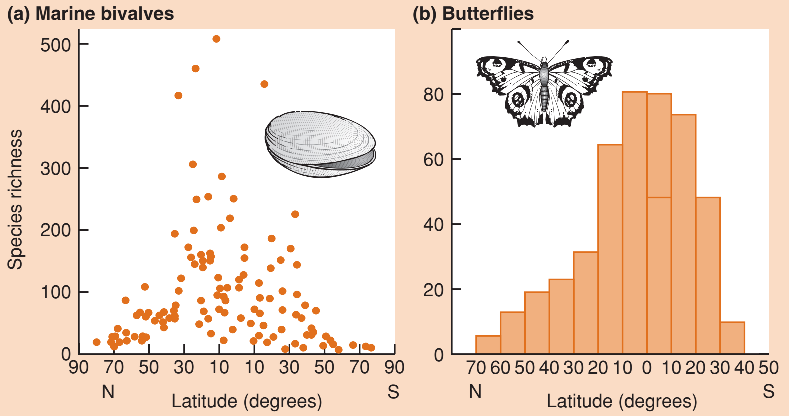
of land birds on the island of Tristan da Cunha. A more complete illustration of the balance between colonization and the evolution of endemics is provided by the animals and plants of Norfolk Island (Figure 21.20). This small island (about 70 km^2) is approximately 700 km from New Caledonia and New Zealand, but about 1200 km from Australia, and the ratio of Australian species to New Zealand and New Caledonian species within a group can therefore be used as a measure of that group's dispersal ability. As Figure 21.20 shows, the proportion of endemics on Norfolk Island is highest in groups with poor dispersal ability and lowest in groups with good dispersal ability.

. . . and in more ancient ecosystems

In a similar vein, Lake Tanganyika, one of the ancient and deep Great Rift lakes of Africa, contains 214 species of cichlid fish, many of which show exquisite specializations in the manner and location of their feeding. Of these 214 species, 80% are endemic. With an estimated age of the lake of 9–12 million years, together with evidence that the various endemic groups diverged some 3.5–5 million years ago, it is likely that this uniquely diverse, endemic fish fauna evolved within the lake from a single ancestral lineage (Meyer, 1993). By contrast, Lake Rudolph, which has only been an isolated water body for 5000 years, since its connection to the Nile system was broken, contains only 37 species of cichlid of which only 16% are endemic (Fryer & Iles, 1972).

21.6 Gradients of species richness

Sections 21.3–21.5 demonstrated how difficult explanations for variations in species richness are to formulate and test. It is easier to describe patterns, especially gradients, in species richness. These are discussed next. Explanations for these, too, however, are often very uncertain.



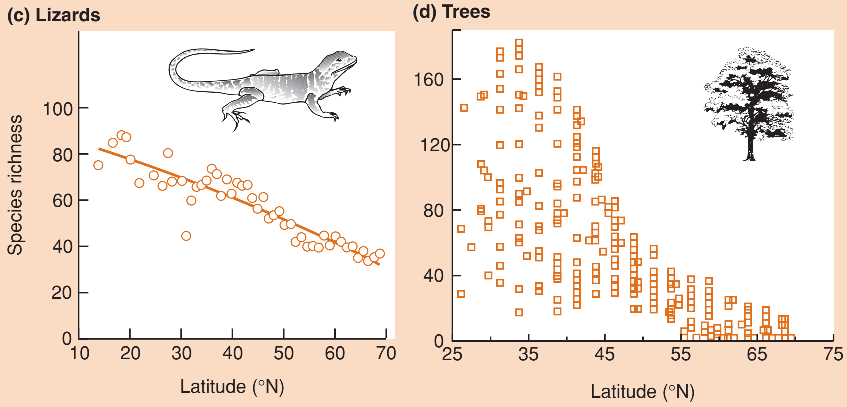


Figure 21.21 Latitudinal patterns in species richness in: (a) marine bivalves (after Flessa & Jablonski, 1995); (b) swallowtail butterflies (after Sutton & Collins, 1991); (c) quadruped mammals in North America (after Rosenzweig & Sandlin 1997); and (d) trees in North America (after Currie & Paquin, 1987.)

21.6.1 Latitudinal gradients

richness decreases with latitude

One of the most widely recognized patterns in species richness is the increase that occurs from the poles to the tropics. This can be seen in a wide variety of groups, including trees, marine invertebrates, mammals and lizards (Figure 21.21). The pattern can be seen, moreover, in terrestrial, marine and freshwater habitats.

a diversity of explanations: predation, . . .

A number of explanations related to our discussions in Section 21.3 and 21.4 have been put forward for the general latitudinal trend in species richness, but not one of these is without problems. In the first place, the richness of tropical communities has been attributed to a greater intensity of predation and to more specialized predators (Janzen, 1970; Connell, 1971; Clark & Clark, 1984). More intense predation could reduce the importance of competition, permitting greater niche overlap and promoting higher richness (see Figure 21.1c). However, even if predation is more intense in the tropics, which is far from certain, it cannot readily be forwarded as the root cause of tropical richness, since this begs the question of what gives rise to the richness of the predators themselves.

. . . productivity, . . .

Second, increasing species richness may be related to an increase in productivity as one moves from the poles to the equator. The length of the growing season increases from the poles to the tropics and, on average, there is certainly more heat and more light energy in more tropical regions. As discussed in Section 21.3.1, this can be associated with greater species richness, although increased productivity in at least some cases has been associated with reduced richness.

. . . nutrient supply, . . .

Moreover, light and heat are not the only determinants of plant productivity. Tropical soils often have lower concentrations of plant nutrients than temperate soils. The species-rich tropics might therefore be seen, in this sense, as reflecting their *low* productivity. In fact, tropical soils are poor in nutrients because most of the nutrients are locked up in the large tropical biomass. A productivity argument might therefore have to run as follows. The light, temperature and water regimes of the tropics lead to high biomass communities but not necessarily to diverse communities. This, though, leads to nutrient-poor soils and perhaps a wide range of light regimes from the forest floor to the canopy far above. These in turn lead to high plant species richness and thus to high animal species richness. There is certainly no *simple* 'productivity explanation' for the latitudinal trend in richness.

. . . climate . . .

Some ecologists have invoked the climate of low latitudes as a reason for their high species richness. Specifically, equatorial regions are generally less seasonal than temperate regions, and this may allow species to be more specialized (i.e. have narrower niches, see Figure 21.1b). The greater evolutionary 'age' of the tropics has also been proposed as a reason for their greater species richness (Flenley, 1993), and another line of argument suggests that the repeated fragmentation and coalescence of tropical forest refugia promoted genetic differentiation and speciation, accounting for much of the high richness in tropical regions (Connor, 1986). These ideas, too, are plausible but very far from proven.

. . . or area?

A final idea, the area hypothesis of Terborgh (1973), is worth highlighting. The area of the tropical zone is much greater than that of the other latitudinal zones, and Rosenzweig (2003) has claimed that more area means more species. Note that in such enormous geographic areas the focus is not on a balance between immigration and extinction (as it was for islands in Section 21.5.1) but between speciation and extinction. Species inhabiting more extensive regions (i.e. tropical species) can, in consequence, have larger geographic ranges. Rosenzweig (2003) argues that species with larger ranges (and consequently larger population sizes) are both less likely to go extinct (see Section 7.5) and more likely to speciate (allopatrically, because of a greater likelihood that their range will be bisected by a barrier). If it is true that extinction rates are lower and speciation rates are higher in regions of greater spatial extent, such regions should also have higher equilibrium species richnesses. However, the evidence for the underlying assumptions is scant.

Overall, therefore, the latitudinal gradient lacks an unambiguous explanation. This is hardly surprising. The components of a possible explanation – trends with area, productivity, climatic stability and so on – are themselves understood only in an incomplete and rudimentary way, and the latitudinal gradient intertwines these components with one another, and with other, often opposing forces: isolation, harshness and so on.

21.6.2 Gradients with altitude and depth

decreasing, increasing or hump-shaped richness relationships with altitude

A decrease in species richness with altitude, analogous to that observed with latitude, has frequently been reported in terrestrial environments (e.g. Figure 21.22a, b). On the other hand, some have reported a monotonic increase with altitude (e.g. Figure 21.22c) while about half the studies of altitudinal species richness have described hump-shaped patterns (e.g. Figure 21.22d) (Rahbek, 1995).

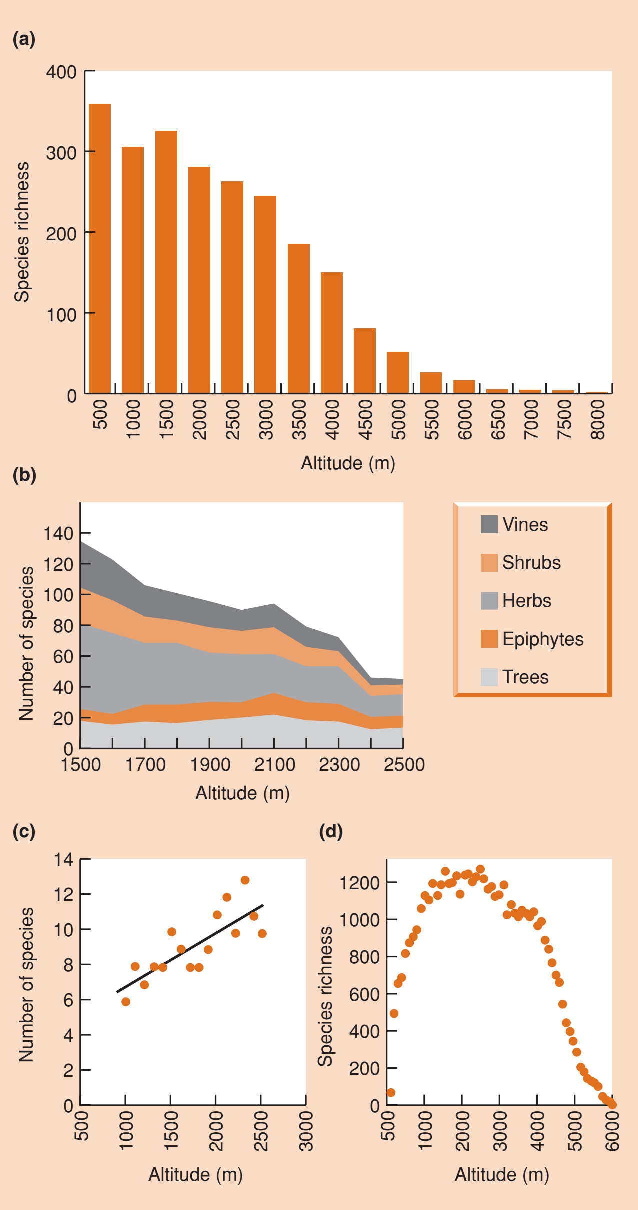


Figure 21.22 Relationships between species richness and altitude for: (a) breeding birds in the Nepalese Himalayas (after Hunter & Yonzon, 1992); (b) plants in the Sierra Manantlán, Mexico (after Vázquez & Givnish, 1998); (c) ants in Lee Canyon in the Spring Mountains of Nevada, USA (after Sanders *et al.*, 2003); and (d) flowering plants in the Nepalese Himalayas (after Grytnes & Vetaas, 2002).

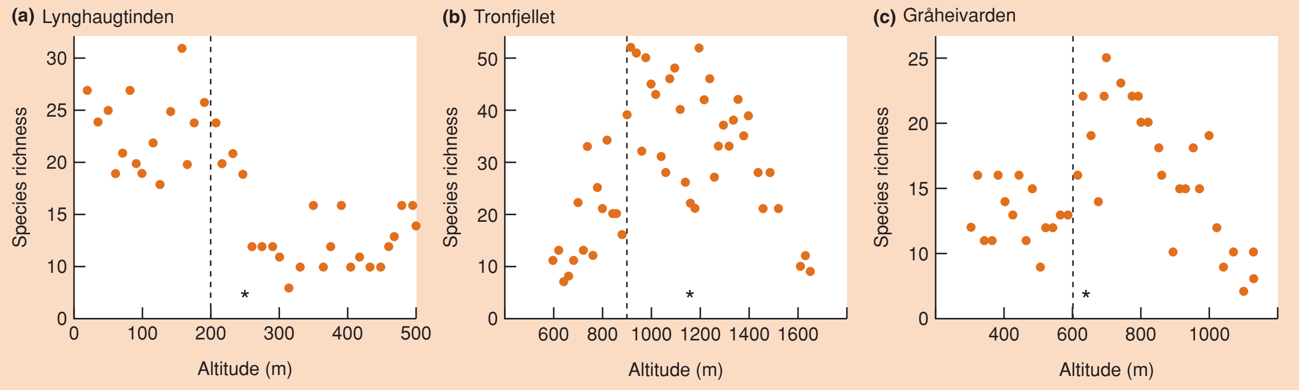


Figure 21.23 Scatter plots of species richness in relation to altitude for three transects in Norway. In each case the treeline is shown as a dashed line and the midpoint of the transect as an asterisk. (a) Lynghaugtinden shows a monotonic decline in richness with altitude. (b) Tronfjellet shows a hump-shaped pattern with its peak near the midpoint of the transect. (c) Gråheivarden shows an increase in richness just above the treeline followed by a decline towards the mountain top. (After Grytnes, 2003.)

again, a diversity of potential explanations

At least some of the factors instrumental in the latitudinal trend in richness are also likely to be important as explanations for altitudinal trends (although the problems in explaining the latitudinal trend apply equally to altitude). Thus, high-altitude communities almost invariably occupy smaller areas than those in lowlands at equivalent latitudes, and they will usually be more isolated from similar communities than in lowland sites. Therefore the effects of area and isolation are likely to contribute to observed decreases in species richness with altitude. In addition, declines in species richness have often been explained in terms of decreasing productivity associated with lower temperatures and shorter growing seasons at higher altitude, or physiological stress associated with climatic extremes near mountain tops. Indeed, the explanation for the converse, positive relationship between ant diversity and altitude in Figure 21.22c, is that precipitation increased with altitude in this case, resulting in higher productivity and less physiologically extreme conditions at higher altitude.

'hard boundaries' and hump-shaped relationships

The concept of 'hard boundaries' provides the basis for a hypothesis to explain hump-shaped relationships (Colwell & Hurtt, 1994). This null model approach assumes the random placement of species between an upper hard boundary (mountain top) and a lower hard boundary (valley bottom) and predicts a symmetric humped relationship in the middle of the gradient (which tapers most steeply as the boundaries are approached). Grytnes and Vetaas (2002) modeled the altitudinal pattern in Himalayan flowering plants and found that the actual distribution (Figure 21.22d) fitted best to a model combining hard boundaries with an underlying monotonic decline in richness with altitude.

In a revealing study of altitudinal transects in Norway, Grytnes (2003) reported a variety of patterns in vascular plant richness. The most northerly of the transects, at Lynghaugtinden, showed a monotonic decline, conforming best to the hypothesis relating declining area to increasing altitude (Figure 21.23a). Tronfjellet, on the other hand, had a pattern broadly consistent with the hard boundary hypothesis, peaking in richness in the middle of the altitudinal range and with steep declines near the boundaries (Figure 21.23b). Enriching the picture even further, Gråheivarden, the most southerly transect, revealed a pattern consistent with a third, 'mass effect' hypothesis. This concerns the establishment of species in sites where a self-maintaining population could not exist, via a spilling over of taxa from an adjacent biotic zone. The Gråheivarden transect supported the mass effect prediction of increased species richness near the treeline, where forest and alpine communities abut (Figure 21.23c).

patterns with depth in aquatic environments

In aquatic environments, the change in species richness with depth shows strong similarities to the terrestrial gradient with altitude. In larger lakes, the cold, dark, oxygen-poor abyssal depths contain fewer species than the shallow surface waters. Likewise, in marine habitats, plants are confined to the photic zone (where they can photosynthesize), which rarely extends below 30 m. In the open ocean, therefore, there is a rapid decrease in richness with depth, reversed only by the variety of often bizarre animals living on the ocean floor. Interestingly, however, in coastal regions the effect of depth on the species richness of benthic (bottom-dwelling) animals produces a peak of richness at about 1000 m, possibly reflecting higher environmental predictability there (Figure 21.24). At greater depths, beyond the continental slope, species richness declines again, probably because of the extreme paucity of food resources in abyssal regions.

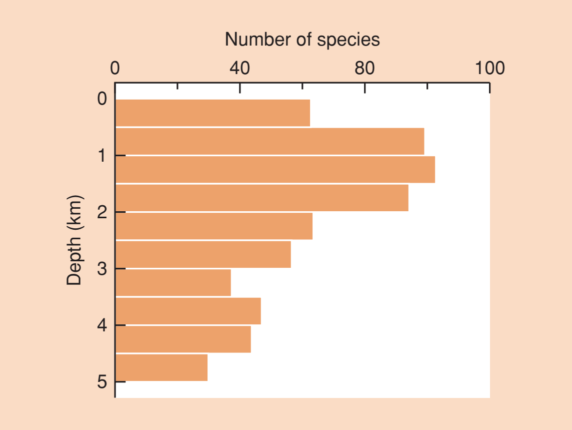


Figure 21.24 Depth gradient in species richness of the megabenthos (fish, decapods, holothurians and asteroids) in the ocean southwest of Ireland. (After Angel, 1994.)

21.6.3 Gradients during community succession

a hump-shaped richness relationship during succession . . .

We saw earlier (see, for example, Section 16.7.1) how, in community successions, if they run their full course, the number of species first increases (because of colonization) but eventually decreases (because of competition). This is most firmly established for plants, but the few studies that have been carried out on animals in successions indicate, at least, a parallel increase in species richness in the early stages of succession. Figure 21.25 illustrates this for birds following shifting cultivation in a tropical rainforest in northeast India, and for insects associated with old-field successions.

To a certain extent, the successional gradient is a necessary consequence of the gradual colonization of an area by species from surrounding communities that are at later successional stages; that is, later stages are more fully saturated with species (see Figure 21.1d). However, this is a small part of the story, since succession involves a process of replacement of species and not just the mere addition of new ones.

. . . caused by a cascade of effects?

Indeed, as with the other gradients in species richness, there is something of a cascade effect with succession: one process that increases richness kick-starts a second, which feeds into a third, and so on. The earliest species will be those that are the best colonizers and the best competitors for open space. They immediately provide resources (and introduce heterogeneity) that were not previously present. For example, the earliest plants generate resource-depletion zones in the soil that inevitably increase the spatial heterogeneity of plant nutrients. The plants themselves provide a new variety of microhabitats, and for the animals that might feed on them they provide a much greater range of food resources (see Figure 21.1a). The increase in herbivory and predation may then feed back to promote further increases in species richness (predator-mediated coexistence: see Figure 21.1c), which provides further resources and more heterogeneity, and so on. In addition, temperature, humidity and wind speed are much less variable (over time) within a forest than

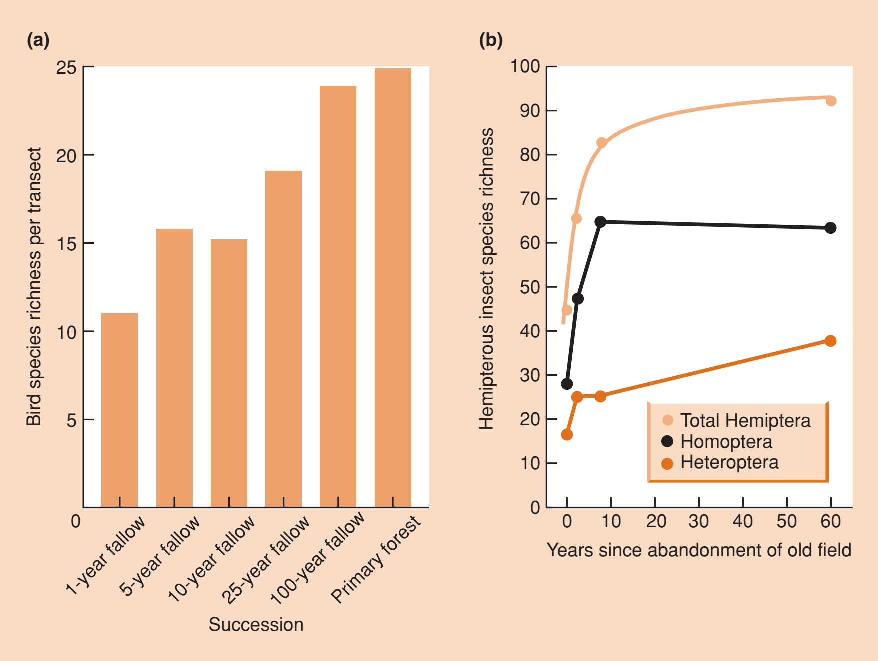


Figure 21.25 The increase in species richness during successions. (a) Birds following shifting cultivation in a tropical rainforest in northeast India. (After Shankar Raman *et al*., 1998.) (b) Hemipterous insects following an old-field succession. (After Brown & Southwood, 1983.)

in an exposed early successional stage, and the enhanced constancy of the environment may provide a stability of conditions and resources that permits specialist species to build up populations and persist (see Figure 21.1b). As with the other gradients, the interaction of many factors makes it difficult to disentangle cause from effect. But with the successional gradient of richness, the tangled web of cause and effect appears to be of the essence.

21.6.4 Patterns in taxon richness in the fossil record

Finally, it is of interest to take the processes that are believed to be instrumental in generating present-day gradients in richness and apply them to trends occurring over much longer timespans. The imperfection of the fossil record has always been the greatest impediment to the paleontological study of evolution. Nevertheless, some general patterns have emerged, and our knowledge of six important groups of organisms is summarized in Figure 21.26.

Cambrian explosion: exploiter-mediated coexistence?

Until about 600 million years ago, the world was populated virtually only by bacteria and algae, but then almost all the phyla of marine invertebrates entered the fossil record within the space of only a few million years (Figure 21.26a). Given that the introduction of a higher trophic level can increase richness at a lower level, it can be argued that the first single-celled herbivorous protist was probably instrumental in the Cambrian explosion in species richness. The opening up of space by cropping of the algal monoculture, coupled with the availability of recently evolved eukaryotic cells, may have caused the biggest burst of evolutionary diversification in earth's history. Since that time, taxonomic richness has increased steadily but erratically (Figure 21.26a), with five so-called mass extinctions and many smaller ones. Analysis of the pattern of 'recovery' peaks following extinction peaks indicates that the average recovery time is 10 million years (Kirchner & Weil, 2000).

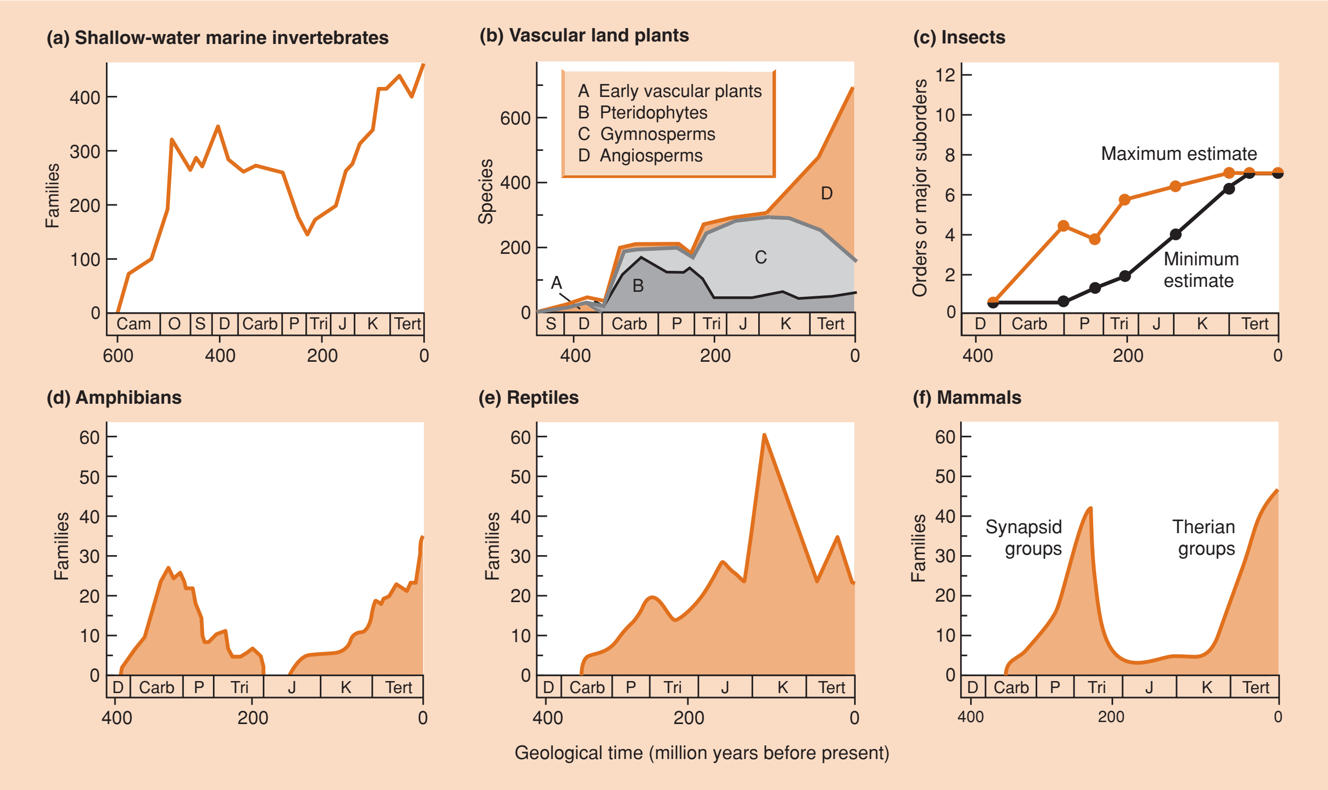


Figure 21.26 Curves showing patterns in taxon richness through the fossil record. (a) Families of shallow-water invertebrates. (After Valentine, 1970.) (b) Species of vascular land plants in four groups: early vascular plants, pteridophytes, gymnosperms and angiosperms. (After Niklas *et al.*, 1983.) (c) Major orders and suborders of insects. The minimum values are derived from definite fossil records; the maximum values include 'possible' records. (From Strong *et al.*, 1984.) (d–f) Vertebrate families of amphibians, reptiles and mammals, respectively. (After Webb, 1987.) Key to geological periods: Cam, Cambrian; O, Ordovician; S, Silurian; D, Devonian; Carb, Carboniferous; P, Permian; Tri, Triassic; J, Jurassic; K, Cretaceous; Tert, Tertiary.

Permian decline: a species–area relationship?

The dramatic decline in the number of families of shallow-water invertebrates as a result of the mass extinction at the end of the Permian (Figure 21.26a) could have been a result of the coalescence of the earth's continents to produce the single supercontinent of Pangaea. The joining of the continents produced a marked reduction in the area occupied by shallow seas (which occur around the periphery of continents) and thus a marked decline in the area of habitat available to shallow-water invertebrates. Moreover, at this time the world was subject to a prolonged period of global cooling in which huge quantities of water were locked up in enlarged polar caps and glaciers, causing a widespread reduction of warm shallow sea environments. Thus, a species–area relationship may be invoked to account for the reduction in richness of this fauna. In a related context, Rosenzweig (2003) reports a significant positive relationship when the number of fossil plant species of the northern hemisphere from various periods in the earth's history is plotted against the total area of the land mass during the period in question (11 periods with nonoverlapping lists of fossil species).

competitive displacement among the major plant groups?

The analysis of fossil remains of vascular land plants (Figure 21.26b) reveals four distinct evolutionary phases: (i) a Silurian–mid-Devonian proliferation of early vascular plants; (ii) a subsequent Late Devonian–Carboniferous radiation of fern-like lineages; (iii) the appearance of seed plants in the late Devonian and the adaptive radiation to a gymnosperm-dominated flora; and (iv) the appearance and rise of the flowering plants (angiosperms) in the Cretaceous and Tertiary. It seems that after an initial invasion of the land, made possible by the appearance of roots, the diversification of each plant group coincided with a decline in species numbers of the previously dominant group. In two of the transitions (early plants to gymnosperms, and gymnosperms to angiosperms), this pattern may reflect the competitive displacement of older, less specialized taxa by newer and presumably more specialized taxa.

coevolution as a driver of richness increase?

The first undoubtedly phytophagous insects are known from the Carboniferous. Thereafter, modern orders appeared steadily (Figure 21.26c) with the Lepidoptera (butterflies and moths) arriving last on the scene, at the same time as the rise of the angiosperms. Reciprocal evolution and counterevolution between plants and herbivorous insects has almost certainly been, and still is, an important mechanism driving the increase in richness observed in both land plants and insects through their evolution.

extinctions of large animals: prehistoric overexploitation?

Toward the end of the last ice age, the continents were much richer in large animals than they are today. For example, Australia was home to many genera of giant marsupials; North America had its mammoths, giant ground sloths, and more than 70 other genera of large mammals; and New Zealand and Madagascar were home to giant flightless birds, the moas (Dinorthidae) and elephant bird (*Aepyornis*), respectively. Over the past 50,000 years or so, a major loss of this biotic diversity has occurred over much of the globe. The extinctions particularly affected large terrestrial animals (Figure 21.27a); they were more pronounced in some parts of the world than others; and they occurred at different times in different places (Figure 21.27b). The extinctions broadly mirror patterns of human migration. Thus, the arrival in Australia of ancestral aborigines occurred 40,000 or more years ago; stone spear points became abundant throughout the United States about 11,500 years ago; and humans have been in both Madagascar and New Zealand for about 1000 years. It seems likely, therefore, that the arrival of efficient human hunters led to the rapid overexploitation of vulnerable and profitable large prey. Africa, where humans originated, shows much less evidence of loss, perhaps because coevolution of large animals alongside early humans provided ample time for them to develop effective defenses (Owen-Smith, 1987).

The Pleistocene extinctions herald the modern age, in which the influence upon natural communities of human activities has been increasing dramatically (see Chapters 7, 15 and 22).

21.7 Species richness and ecosystem functioning

switching focus: how does species richness influence ecosystem functioning?

In this penultimate chapter section, rather than seeking to discern and explain patterns in species richness we switch focus to address the consequences of variations in species richness for ecosystem functioning. Specifically, we deal with productivity, decomposition and the flux of nutrients and water (discussed more fully in Chapters 11, 17 and 18). Understanding the role of biodiversity in ecosystem processes is important both for fundamental and practical reasons, because it has implications for how humans respond to biodiversity loss. We have already discussed the effects of richness on the stability of ecosystem functioning (see Section 20.3.6). Here we present examples of studies from various ecosystem types that reveal relationships between species richness and the ecosystem processes themselves, before proceeding to consider several hypotheses to account for such relationships.

21.7.1 Positive relationships between species richness and ecosystem functioning

increased species richness resulting in . . .

. . . higher productivity, . . .

As part of an international research effort, standard protocols were used at eight European field sites to investigate the effect of reduction in grassland species richness on primary productivity

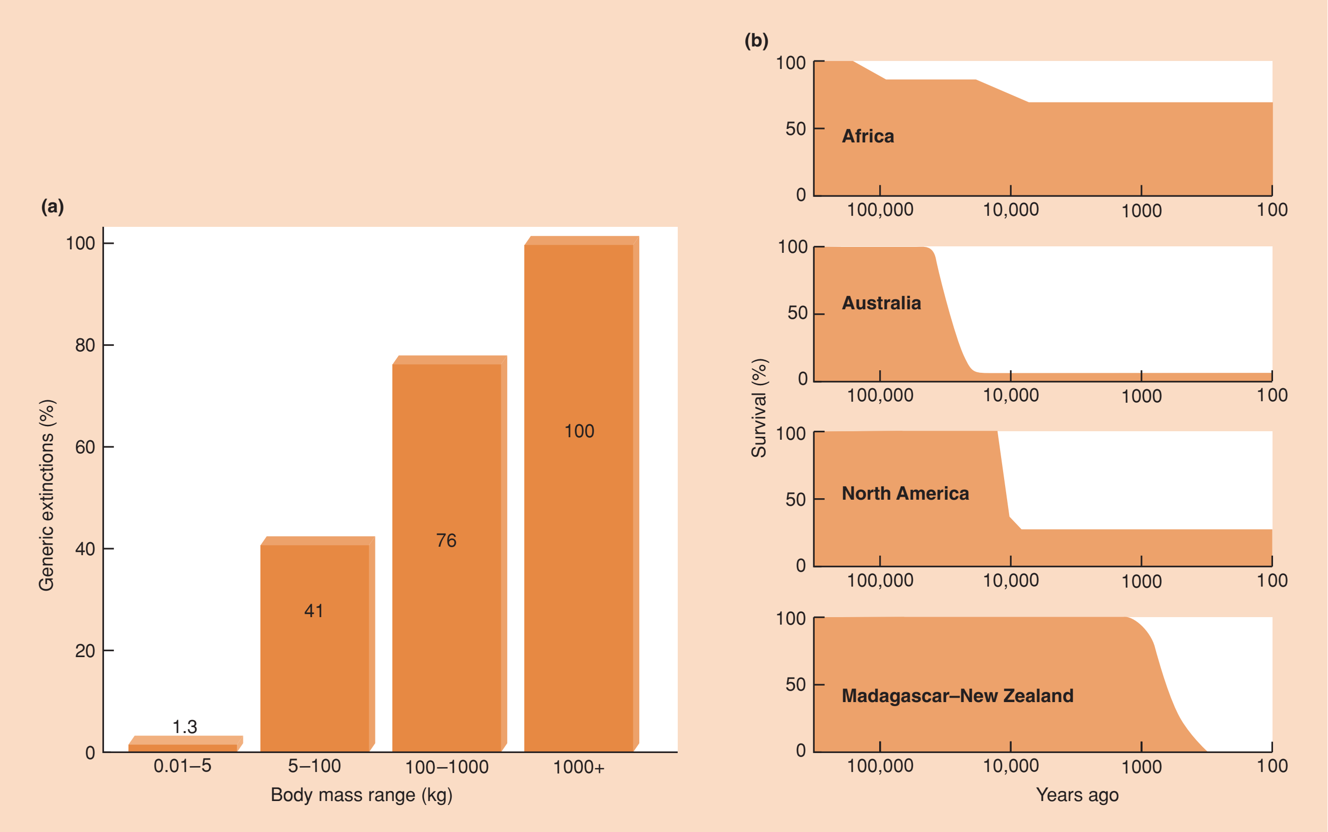


Figure 21.27 (a) The percentage of genera of large mammalian herbivores that have gone extinct in the last 130,000 years is strongly size dependent (data from North and South America, Europe and Australia combined). (After Owen-Smith, 1987.) (b) Percentage survival of large animals on three continents and two large islands (New Zealand and Madagascar). (After Martin, 1984.)

(measured as accumulation of above-ground biomass) by synthesizing grassland communities with different numbers of species of grasses, nitrogen-fixing legumes and other herbaceous species (herbs). While the detailed results differed among sites, there was an overall log-linear reduction of average productivity with loss of species (Figure 21.28a). For a given species richness, there was also a decline in productivity with a reduction in the number of functional groups (grasses, legumes, herbs) (Figure 21.28b).

. . . faster decomposition . . .

Jonsson and Malmqvist (2000) studied the effect on decomposition of species richness of the larvae of three stonefly species that feed on tree leaves falling into streams. Every replicate had 12 stonefly larvae present – 12 of one species, six of each of two species, or four of each of three species (with 10 replicates of all possible combinations). The rate of loss of leaf mass during a 46-day mesocosm experiment was positively related to species richness (Figure 21.28c).

. . . and reduced nutrient loss

The microbial decomposition of soil organic matter releases ammonium ions (nitrogen mineralization). Seven years after commencing a replicated manipulation of grassland species richness in Minnesota, USA, Zak *et al.* (2003) found that mineralization rates in soil samples were positively related to plant species richness (Figure 21.28d). Nutrient flux was also found to be related to species richness of submersed macrophytes in mesocosms simulating wetland communities – the uptake of phosphorus by algae growing on the surface of the macrophytes was greater (and total phosphorus loss from the mesocosms was reduced) when more macrophytes were present (Figure 21.28e).

21.7.2 Contrasting explanations for richness–ecosystem process relationships

contrasting hypotheses

In an intense and sometimes acrimonious debate (Kaiser, 2000; Loreau *et al.*, 2001), three principal hypotheses have been advanced to account for positive relationships between species richness and ecosystem functioning.

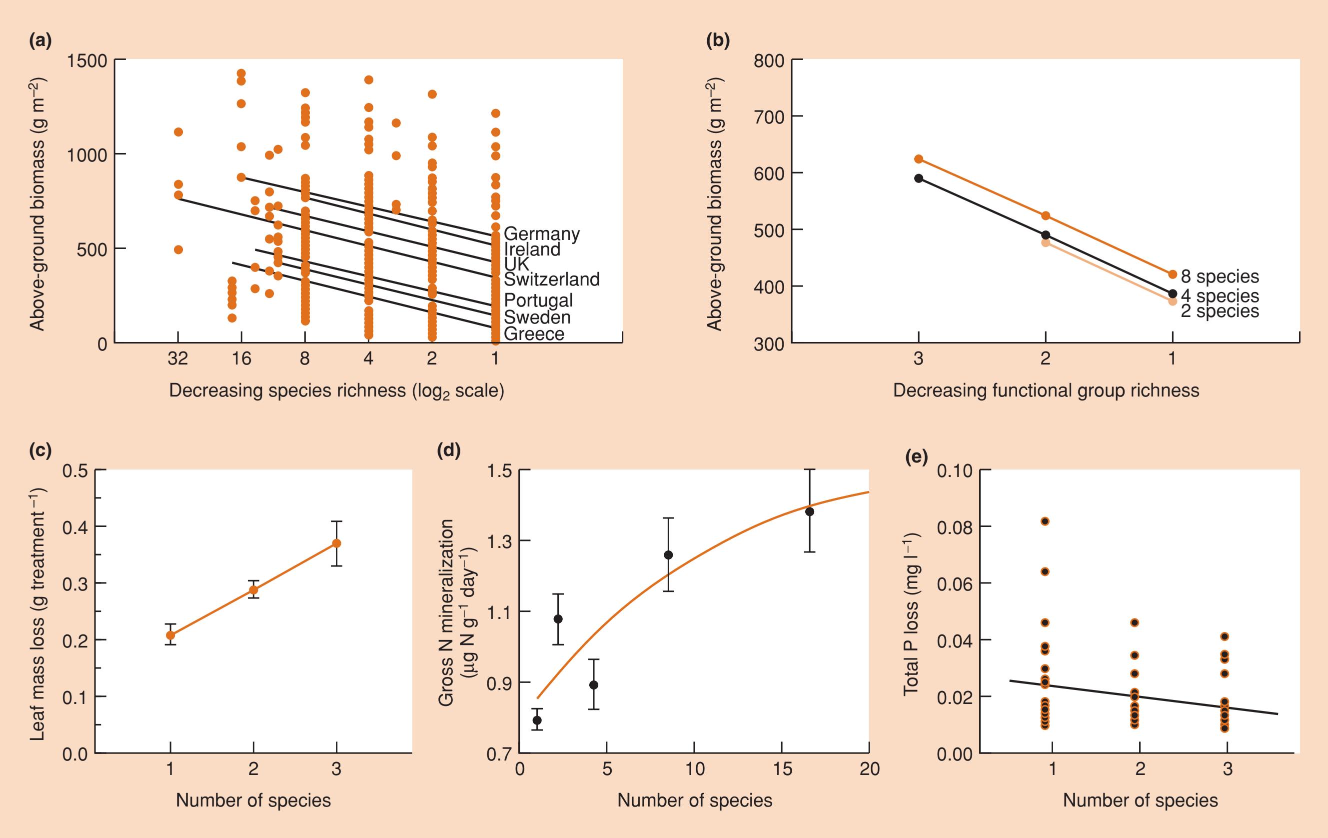


Figure 21.28 (a) Primary productivity (measured as above-ground biomass accumulation after 2 years) versus species richness in a large number of simulated grassland assemblages across Europe (regression lines are shown for each country). (After Hector *et al.*, 1999.) (b) Primary productivity versus functional group richness in the European grasslands combined. (After Hector *et al.*, 1999.) (c) Decomposition rate (loss of leaf mass) versus number of stream-dwelling shredding stonefly species present. (After Jonsson & Malmqvist, 2000.) (d) Gross nitrogen mineralization (per gram of soil) versus plant species richness in a 7-year grassland manipulation. (After Zak *et al.*, 2003.) (e) Rate of loss of phosphorus from mesocosms containing one, two or three submersed macrophyte species, simulating wetland communities. (After Engelhardt & Ritchie, 2002.)

complementarity . . .

On one hand, if species show niche differentiation (see Chapter 8) they may use resources in complementary ways, utilizing a greater proportion of available resources (see Figure 21.1d) and contributing to a higher level of ecosystem productivity (or decomposition or nutrient cycling). This is the *complementarity hypothesis*.

. . . and facilitation . . .

. . . predict 'overyielding' and point to the value of conserving biodiversity . . .

A second idea, the *facilitation hypothesis*, recognizes that some species may have positive effects on the ecosystem role played by other species. For example, some submersed wetland macrophytes facilitate colonization by algae more than others do (Figure 21.28d) (Engelhardt & Ritchie, 2002).

Both the complementarity and facilitation hypotheses predict 'overyielding', where productivity or decomposition rates in multispecies communities are faster than in communities with fewer species. As long as either of these hypotheses applies, a case can be made for the need for management to conserve biodiversity to maintain ecosystem functioning.

. . . but the sampling effect hypothesis does not

On the other hand, it may be that positive relationships between richness and functioning are artefacts of the species that happen to be assembled together in experiments. The so-called *sampling effect hypothesis* suggests that the more species are present in an assemblage, the more likely it is to contain, by chance, a highly competitive or productive species. Thus, species-rich communities may on average be more productive because they are more likely to contain an especially productive species. In this case, overyielding will not be seen (a monoculture of the productive species will be no less productive than a multispecies community containing it) and there will be no case for conserving biodiversity *per se* to maintain ecosystem functioning.

some studies have not revealed overyielding . . .

The multinational study of Hector *et al.* (1999) produced results consistent with the complementarity hypothesis because grassland productivity was greater when more functional plant types were present, something that is likely to be a reflection of niche differentiation. However, the work was criticized because of a failure to test properly for overyielding and because at least some of the observed patterns could be due to a sampling effect of whether the nitrogen-fixing legume *Trifolium pratense* happened to be in the mix (Kaiser, 2000). In a much smaller scale greenhouse experiment, Mikola *et al.* (2002) used two different experimental designs. In the first, like Hector *et al.* (2002), they selected plant species at random from a pool to produce a range of richnesses (richness design). In the second, richness levels included deliberately replicated monocultures, bicultures, tricultures and six-species mixes (richness and composition design). In both cases, there was a positive relationship between richness and productivity (total shoot mass); but whereas in the richness design 34% of total variation in productivity was explained by species richness, in the richness and composition design, this only explained 16% of variation. Mikola *et al.* (2002) found no evidence of overyielding and, moreover, noted from the second experimental design that productivity was greatly affected by the presence of one species, *Trifolium hybridum*, another nitrogen-fixing legume. Both observations are consistent with the sampling effect hypothesis.

. . . while other studies have

However, in another field-scale experiment, designed so that the most productive monocultures could be compared with multispecies plots that included the most productive species, Tilman *et al.* (2001) gathered evidence of overyielding, finding that many high-richness plots had greater productivity that the single best-performing monoculture. Moreover, there was clearly 'overyielding' of decomposition when more stonefly species were present in Jonsson and Malmqvist's (2000) stream experiment (see Figure 21.28c).

It is clear that the results of a range of experimental manipulations of species richness differ in the extent to which the three hypotheses apply, and it should be noted that these are by no means mutually exclusive. As further studies accumulate, generalizations can be expected to emerge. For example, it may be that complementarity will be most prominent in situations where niche differentiation is most marked.

a tri-trophic level experiment showing overyielding

In the studies discussed above, the emphasis has been on manipulating the richness of a single trophic level (plants or detritivores). In contrast, Downing and Leibold (2002) investigated the effect on ecosystem processes of changes in species richness across trophic levels (one, three or five species in each of three groups – macrophytes, benthic grazers and invertebrate predators – in field mesocosms mimicking ponds). They aimed to disentangle the effects of species richness from species composition (the sampling effect) by nesting and replicating seven particular combinations of species within each richness level. Ecosystem productivity (mainly by periphyton, phytoplankton and microorganisms) was significantly greater at the highest richness level than at the two lower ones; ecosystem respiration showed a similar but nonsignificant pattern; while decomposition (weight loss of tree leaves) was not related to richness. The effect of species composition on the ecosystem processes was at least as statistically significant as that of species richness (Figure 21.29) (Downing & Leibold, 2002).

practical importance of biodiversity loss (or gain?)

Taken overall, the consequences of the on-going loss of biodiversity can be expected to be complex and difficult to predict unless compositional changes are also accounted for, and this will be particularly so in the context of whole food webs. Paradoxically, however, while biodiversity is generally declining globally, local biodiversity is commonly increasing because of the arrival of invaders (Sax & Gaines, 2003). Thus, a more meaningful objective will in many cases be to determine the consequences for ecosystem processes of increased local biodiversity.

21.8 Appraisal of patterns in species richness

richness patterns: generalizations and exceptions

There are many generalizations that can be made about the species richness of communities. We have seen how richness may peak at intermediate levels of available environmental energy or of disturbance frequency, and how richness declines with a reduction in island area or an increase in island remoteness. We find also that species richness decreases with increasing latitude, and declines or shows a hump-backed relationship with altitude or depth in the ocean. It increases with a rise in spatial heterogeneity but may decrease with an increase in temporal heterogeneity (increased climatic variation). It increases, at least initially, during the course of succession and with the passage of evolutionary time. However, for many of these generalizations important exceptions can be found, and for most of them the current explanations are not entirely adequate.

bidirectional relationships between richness and ecosystem characteristics

The results of descriptive surveys of species richness may, at first glance, seem at odds with the outcomes of experimental manipulations. Many experiments, for example, have shown that increasing the number of species leads to more productivity (see Section 21.7). On the other hand, we saw in Section 21.3.1 that

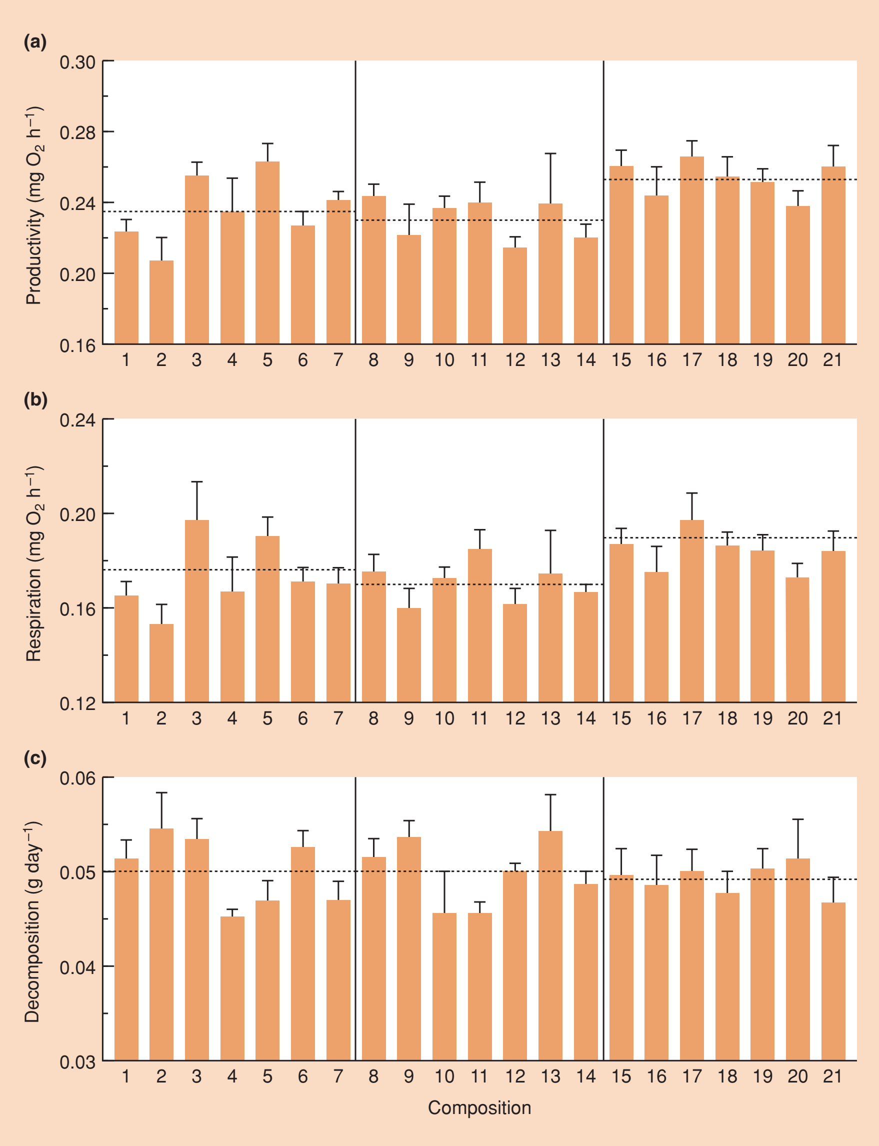


Figure 21.29 The response of (a) ecosystem productivity, (b) ecosystem respiration and (c) decomposition to species composition nested in species richness. Cases 1–7 are unique species combinations at low richness (one species each of macrophyte, benthic grazer and invertebrate predator), 8–14 at intermediate richness (three species of each group) and 15–21 at high richness (five species of each group). Average productivity was significantly higher in the high richness case (the dotted lines show the overall means for richness classes) but there were no significant richness effects on respiration or decomposition. The variability within richness classes reveals the strong effect of species composition on all the ecosystem processes. (After Downing & Leibold, 2002.)

more productive environments may contain more or fewer species than unproductive environments. It is important to understand that relationships such as these are bidirectional; changes in biodiversity can be both a cause and a consequence of changes in productivity (Worm & Duffy, 2003), further complicating the picture.

the pressing need to understand biodiversity and its significance

Unraveling richness patterns is one of the most difficult and challenging areas of modern ecology. No single mechanism is likely to adequately explain a particular pattern, and patterns at local scales are likely to be influenced by processes operating at both local and regional scales. Clear, unambiguous predictions and tests of ideas are often very difficult to devise and will require great ingenuity of future generations of ecologists. Because of the increasing importance of recognizing and conserving the world's biodiversity, though, it is crucial that we come to understand thoroughly these patterns in species richness. We assess the adverse effects of human activities, and how they may be remedied, in Chapter 22.

Summary

Why do some communities contain more species than others? Are there patterns or gradients of species richness? If so, what are the reasons for these patterns? There are plausible answers to the questions we ask, but these answers are by no means conclusive.

In simple terms, the number of species that can be packed into a community is determined by the size of the realized niches and the extent to which they overlap, in relation to the range of available resources. Competition and predation can modify the outcome in predictable ways. In addition, a community will contain more species the more fully saturated it is; a phenomenon that can be addressed by plotting the relationship between local diversity and regional diversity (the number of species that could theoretically colonize).

We describe the influence on species richness of a range of spatially varying factors (productivity, spatial heterogeneity, environmental harshness) and temporally varying factors (climatic variation, environmental age, habitat area) and describe patterns of richness that increase, decrease or show hump-backed relationships with these factors. Interactions among factors (e.g. productivity with grazing or disturbance) are frequently involved in determining patterns. We pay particular attention to island biogeography theory and the interaction between immigration and extinction rates in determining species richness – in relation to island area and remoteness.

Next we turn to gradients in species richness, drawing on examples relating to latitude, altitude, depth, succession and evolutionary history. Explanations for these patterns invoke all the factors discussed earlier.

In the final section, rather than seeking to discern and explain patterns in species richness we switch focus to address the consequences of variations in species richness for ecosystem functioning, discussing productivity, decomposition and the flux of nutrients in turn. Understanding the role of biodiversity in ecosystem processes is important for practical reasons, because it has implications for how humans should respond to biodiversity loss.

Chapter 22

Ecological Applications at the Level of Communities and Ecosystems: Management Based on the Theory of Succession, Food Webs, Ecosystem Functioning and Biodiversity

22.1 Introduction

This is the last of the trilogy of chapters dealing with the application of ecological theory. In the first, Chapter 7, we considered how our understanding at the level of individual organisms and of single populations – related to niche theory, life history theory, dispersal behavior and intraspecific competition – can provide solutions to a multitude of practical problems. The second, Chapter 15, used the theory of the dynamics of interacting populations to guide the control of pests and the sustainable harvesting of wild populations. This final synthesis recognizes that individuals and populations exist in a web of species interactions embedded in a network of energy and nutrient flows. Thus, we deal with the application of theory related to succession (Chapter 16), food webs and ecosystem functioning (Chapters 17–20) and biodiversity (Chapter 21).

application of community and ecosystem theory

Community composition is hardly ever static and, as we saw in Chapter 16, some temporal patterns are quite predictable. Management objectives, on the other hand, often seem to require stasis – the annual production of an agricultural crop, the restoration of a particular combination of species or the long-term survival of an endangered species. Management will sometimes be ineffective in these situations if managers fail to take into account underlying successional processes (see Section 22.2).

We turn to the application of theory about food webs and ecosystem functioning in Section 22.3. Every species of concern to managers has its complement of competitors, mutualists, predators and parasites, and an appreciation of such complex interactions is often needed to guide management action (see Section 22.3.1). Farmers seek to maximize economic returns by manipulating ecosystems with irrigation and by applying fertilizers. But nutrient runoff from farm land, together with treated or untreated human sewage, can upset the functioning of aquatic ecosystems through the process of cultural eutrophication (nutrient enrichment), increasing productivity, changing abiotic conditions and altering species composition. Our understanding of lake ecosystem functioning has provided guidelines for 'biomanipulation' of lake food webs to reverse some of the adverse effects of human activities (see Section 22.3.2). Moreover, knowledge of terrestrial ecosystem functioning can help determine optimal farm practices, where crop productivity involves minimal input of nutrients (see Section 22.3.3). The setting of ecosystem restoration objectives (and the ability to monitor whether these are achieved) requires the development of tools to measure 'ecosystem health', a topic we deal with in Section 22.3.4.

So much of the planet's surface is used for, or adversely affected by, human habitation, industry, mining, food production and harvesting, that one of our most pressing needs is to plan and set aside networks of reserved land. The augmentation of existing reserves by further areas needs to be done in a systematic way to ensure that biodiversity objectives are achieved at minimal cost (because resources are always limited). Section 22.4 describes how our knowledge of patterns of species richness (see

Chapter 21) can be used to design networks of reserves, whether specifically for conservation (see Section 22.4.1) or for multiple uses, such as harvesting, tourism and conservation combined (see Section 22.4.2).

ecological applications often involve economic and sociopolitical considerations

Finally, in Section 22.5 we deal with a reality that applied ecologists cannot ignore. The application of ecological theory never proceeds in isolation. First, there are inevitably economic considerations – how can farmers maximize production while minimizing costs and adverse ecological consequences; how can we set economic values for biodiversity and ecosystem functioning so that these can be evaluated alongside profits from forestry or mining; how can returns be maximized from the limited funds available for conservation? These issues are discussed in Section 22.5.1. Second, there are almost always sociopolitical considerations (see Section 22.5.2) – what methods can be used to reconcile the desires of all interested parties, from farmers and harvesters to tourism operators and conservationists; should the requirements for sustainable management be set in law or encouraged by education; how can the needs and perspectives of indigenous people be taken into account? These issues come together in the so-called triple bottom line of sustainability, with its ecological, economic and sociopolitical perspectives (see Section 22.5.3).

22.2 Succession and management

22.2.1 Managing succession in agroecosystems

farmers often have to resist successional processes

Gardeners and farmers alike devote considerable effort to fighting succession by planting desired species and weeding out unwanted competitors. In an attempt to maintain the characteristics of an early successional stage – growing a highly productive annual grass – arable farmers are forced to resist the natural succession to herbaceous perennials (and beyond, to shrubs and trees; see Section 16.4.5). Menalled *et al.* (2001) compared the impact of four agricultural management systems on the weed communities that developed in Michigan, USA, over a period of 6 years (consisting of two rotations from corn to soybean to wheat). Above-ground weed biomass and species richness were lowest in the conventional system (high external chemical input of synthetic fertilizer and herbicides, ploughed), intermediate in the no-till system (high external chemical input, no ploughing) and highest in the low-input (low external chemical input, ploughed) and organic systems (no external chemical input, ploughed) (Figure 22.1). A widely varying mixture of monocot (grass) and dicot species were represented in the conventional treatment and an equally unpredictable set of annual grasses dominated the no-till treatment.

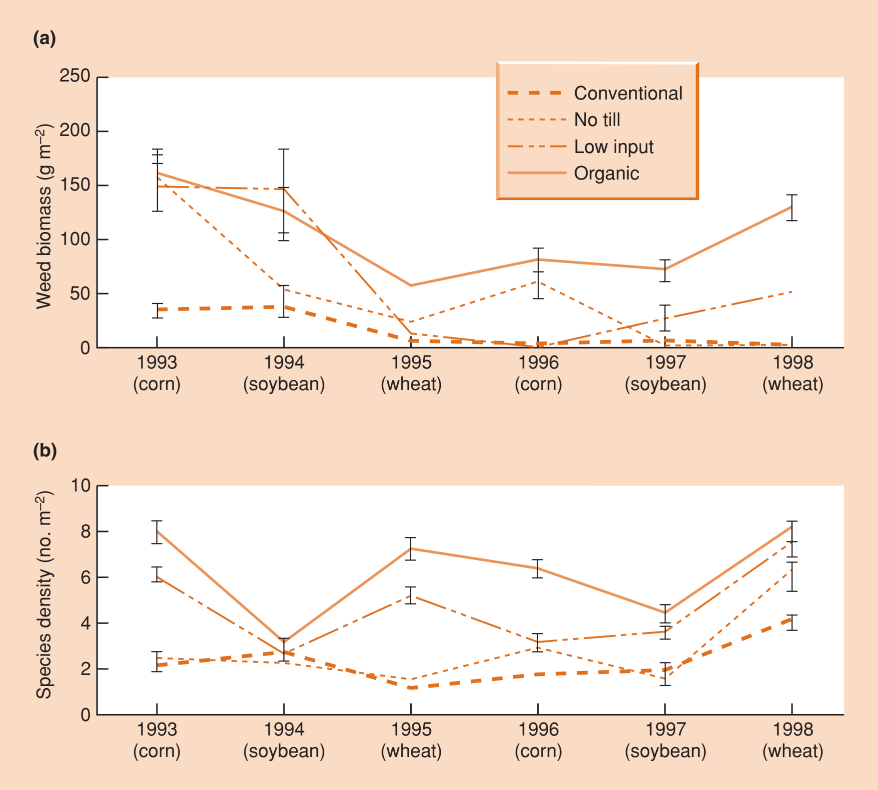


Figure 22.1 (a) Weed biomass and (b) weed species richness in four agricultural management treatments (see key; six replicate 1 ha plots in each treatment) over a period of 6 years consisting of two rotations of corn (*Zea mays*) to soybean (*Glycine max*) to wheat (*Triticum aestivum*). (After Menalled *et al.*, 2001.)

On the other hand, the weed communities of the low-input and organic treatments were more constant: an annual dicot (*Chenopodium album*) and two perennial weeds (*Trifolium pratense* and *Elytrigia repens*) were the dominant species under these conditions. Menalled *et al.* (2001) point out the potential advantages of a management system that fosters a more predictable weed community because control treatments can then be designed specifically against the species concerned.

benzoin 'gardening' in Sumatra – rapid reversion to forest

Other forms of agricultural 'gardening' pose fewer problems in the way they interrupt succession. Benzoin is an aromatic resin, used to make incense, flavoring and medicinal products, which for hundreds of years has been tapped from the bark of tropical trees in the genus *Styrax*. Benzoin still provides a significant income to many villagers in Sumatra who plant benzoin gardens (*S. paralleloneurum*) after clearing the understory in 0.5–3.0 ha areas of montane broadleaf forest. Two years later, farmers thin all the larger trees to allow light to reach the saplings (the thinnings are left in the garden) and annual tapping begins after 8 years. Yields typically decline after 30 years but resin may be harvested for up to 60 years before the garden is left to return to the forest. Garcia-Fernandez *et al.* (2003) identified three categories of garden: G1 was the most plantation-like, with intensive thinning and high densities of *S. paralleloneurum* trees, and G3 was the most forest-like. Total tree species richness was high in plots of primary (pristine) and 'secondary' forest (30–40 years after gardening had ceased) and also in the gardens, except for the most intensely managed situation where richness was significantly lower (but nevertheless with an average of 26 tree species) (Figure 22.2a). As predicted by succession theory (see Section 16.4), climax species typical of mature forest were most common in primary forest and there was a more even mix of pioneer and mid-successional tree species in secondary forest and in the least intensively managed gardens (G3) (Figure 22.2.b). However, gardens with an intermediate or high intensity of management were dominated by mid-successional trees (mainly because benzoin trees are in this class). It is not unusual for indigenous people to be aware of a wide range of uses for forest plants. Figure 22.2c shows the representation in the garden and forest plots of trees in each of four classes: no known use (12%), subsistence use (food, fiber or medicine; 42%), local market use (23%) and international market use (23%). The international category dominated in intensively managed gardens (i.e. benzoin and its products) whereas trees in the subsistence and local market categories were well represented in less intensively managed gardens and in primary and secondary forest. Although benzoin management requires competing vegetation to be trimmed, tree species richness remains quite high even in the most intensively managed gardens. This traditional form of forest gardening maintains a diverse community whose structure allows rapid recovery to a forest community when tapping ceases. It represents a good balance between development and conservation.

aboriginal burning regime provides resources and maintains biota

Fire is an important resource management tool for Australian aboriginal people such as the clan who own the Dukaladjarranj area of northeastern Arnhem Land (Figure 22.3a). Burning, to provide green forage for game animals, is planned by custodians (aboriginal people with special responsibilities for the land) and focuses initially on dry grasses on higher ground, moving progressively to moister sites as these dry out with the passage of the season. Each fire is typically of low intensity and small in extent, producing a patchy mosaic of burned and unburned areas and thus a diversity of habitats at different successional stages (see Section 16.7.1). Towards the end of the dry season, when it is very hot and dry, burning ceases except in controllable situations such as the reburning of previously burnt areas. In a collaboration between indigenous people and professional ecologists, Yibarbuk *et al.* (2001) lit experimental fires to assess their impact on the flora and fauna. They found that burned sites attracted large kangaroos and other favored game and that important plant foods, such as yams, remained abundant (results that would have hardly been a surprise to the indigenous collaborators) (Figure 22.3b). Fire-sensitive vegetation in decline elsewhere, such as *Callitris intratropica* woodlands and sandstone heath dominated by myrtaceaous and proteaceaous shrubs, remained well represented in the study area. In addition, the Dukaladjarranj area compares favorably with the Kakadu National Park, a conservation area with high vertebrate and plant diversity. Thus, Dukaladjarranj contains several rare species and a number of others that have declined in unmanaged areas and, moreover, the representation of exotic plant and animal invaders was remarkably low. The traditional regime, with its many small, low-intensity fires, contrasts dramatically with the more typical contemporary pattern of intensive, uncontrolled fires near the end of the dry season. These blaze across vast areas of western and central Arnhem Land (sometimes covering more than 1 million ha) that are unoccupied and unmanaged, and regularly find their way onto the western rim of the Arnhem Land plateau and into Kakadu and Nitmiluk National Parks (Figure 22.3a). It seems that continued aboriginal occupation of the study area and the maintenance of traditional fire management practices limits the accumulation of fuel (in fire-promoting grass species and in litter), reducing the likelihood of massive fires that can eliminate fire-sensitive vegetation types. A return to indigenous-style burning seems to hold promise for the restoration and conservation of threatened species and communities in these landscapes (Marsden-Smedley & Kirkpatrick, 2000) and provides important clues for the management of fire-prone areas in other parts of the world.

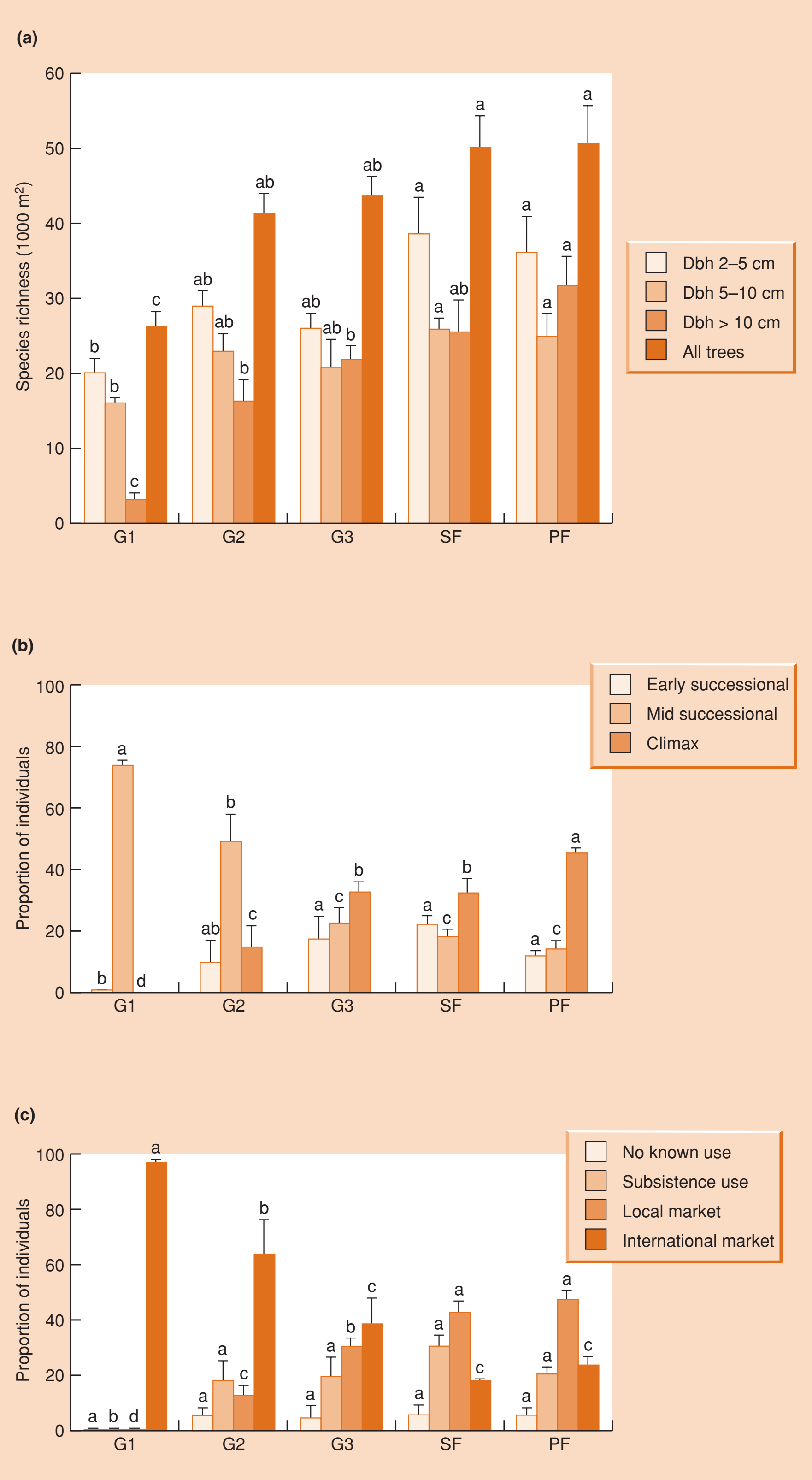


Figure 22.2 (a) Tree species richness in different tree size classes (Dbh is diameter at breast height) in three categories of benzoin garden (G1, most intensely managed; G2, intermediate; G3, least intensively managed) and in secondary forest (SF; 30–40 years after abandonment of benzoin gardens) and in primary forest (PF). (b) Percentage of individual trees in three successional categories. (c) Percentage of individual trees in various utility categories. Each data point is based on three replicate 1 ha plots. Different letters above each type of bar indicate statistically significant differences. (After Garcia-Fernandez *et al*., 2003.)

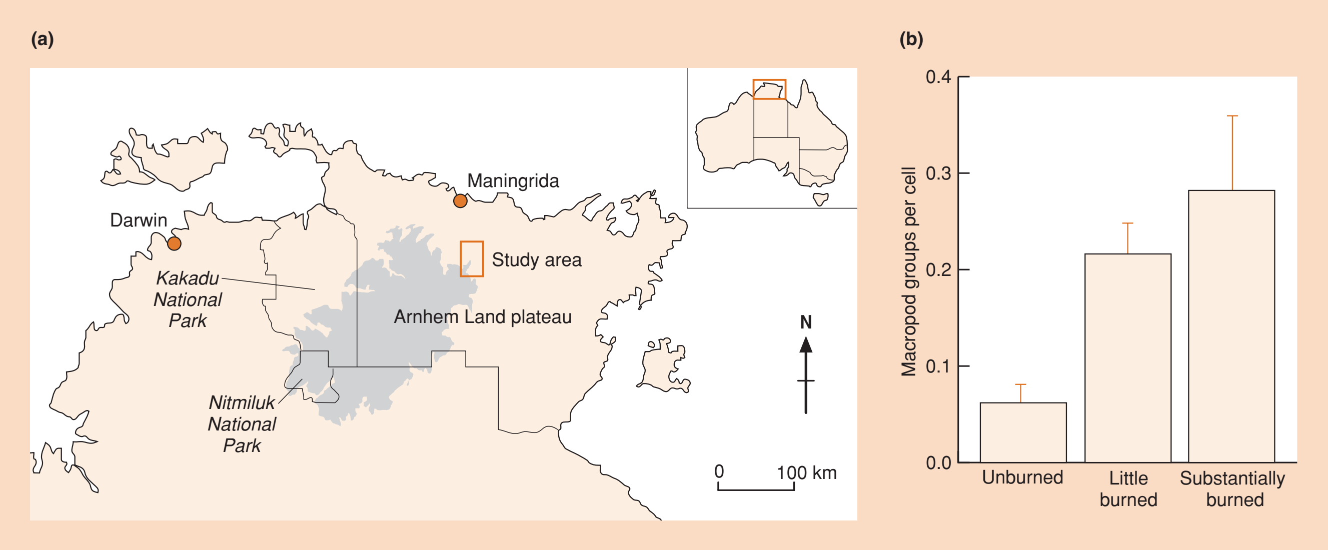


Figure 22.3 (a) Location of the fire management study area near the northeastern end of the Arnhem Plateau in the Northern Territory of Australia; the position of two National Parks is also shown. (b) Mean number (+2 SE) of kangaroo groups sighted during a helicopter survey of 0.25 km^2 plots with different recent burning histories. (After Yibarbuk *et al.*, 2001.)

22.2.2 Managing succession for restoration

restoration sometimes needs no intervention . . .

The goal of restoration ecology is often a relatively stable successional stage (Prach *et al.*, 2001) and ideally a climax. Once an undesirable land use ceases, managers need not intervene if they are prepared to wait for natural succession to run its course. Thus, abandoned rice fields in mountainous central Korea proceed from an annual grass stage (*Alopecurus aequalis*), through forbs (*Aneilema keisak*), rushes (*Juncus effusus*) and willows (*Salix koriyanagi*), to reach a species-rich and stable alder woodland community (*Alnus japonica*) within 10–50 years (Figure 22.4) (Lee *et al.*, 2002). Succession cannot always be counted on to promote habitat restoration, especially if natural sources of seeds are small and distant, but this was not the case here. In fact, the only active intervention worth considering is the dismantling of artificial rice paddy levees to accelerate, by a few years, the early stages of succession.

. . . but may be hastened by species introductions

Meadow grasslands subject to agricultural intensification, including the application of artificial fertilizers and herbicides and heavy grazing regimes, have dramatically fewer plant species than grasslands under historic 'traditional' management. The restoration of biodiversity in these situations involves a secondary succession that typically takes more than 10 years; it can be achieved by returning to a traditional regime without mineral fertilizer in which hay is cut in mid-July and cattle are grazed in the fall (Smith *et al.*, 2003). However, in contrast to the mountain rice field case discussed above, meadow community recovery in lowland England by natural colonization from seed rain or the seed bank is a slow and unreliable process (Pywell *et al.*, 2002). Fortunately, recovery can be speeded up by sowing a species-rich mixture of seeds of desirable plants adapted to the prevailing conditions. Thus, in a 4-year study comparing species richness of grasses and forbs in plots that were unsown (natural regeneration from cereal stubble) or sown with a species-rich seed mixture (containing more than 25 species), the sown plots had twice as many established species in years 1 and 2 than naturally regenerating plots (means of 26.4 and 22.0 compared with 10.4 and 11.3, respectively). By year 4 there was little difference in species richness (22.0 versus 18.7) but the sown treatment had a species composition that included late successional grassland species and was much closer to that found in local nonintensively farmed grasslands (Pywell *et al.*, 2002).

restoration timetable for salt marsh animal communities

Restoration objectives often include recovery not just of plants but of the animal components of communities too. Tidal salt marshes are much rarer than they once were because of drainage and tidal interference through the installation of tide gates, culverts and dykes. The restoration of tidal action (by removing tide gates, etc.) and thus of links between the marshes, estuaries and the larger coastal system along the Long Island Sound shoreline of Connecticut, USA, led to the recovery of salt marsh vegetation, including *Spartina*

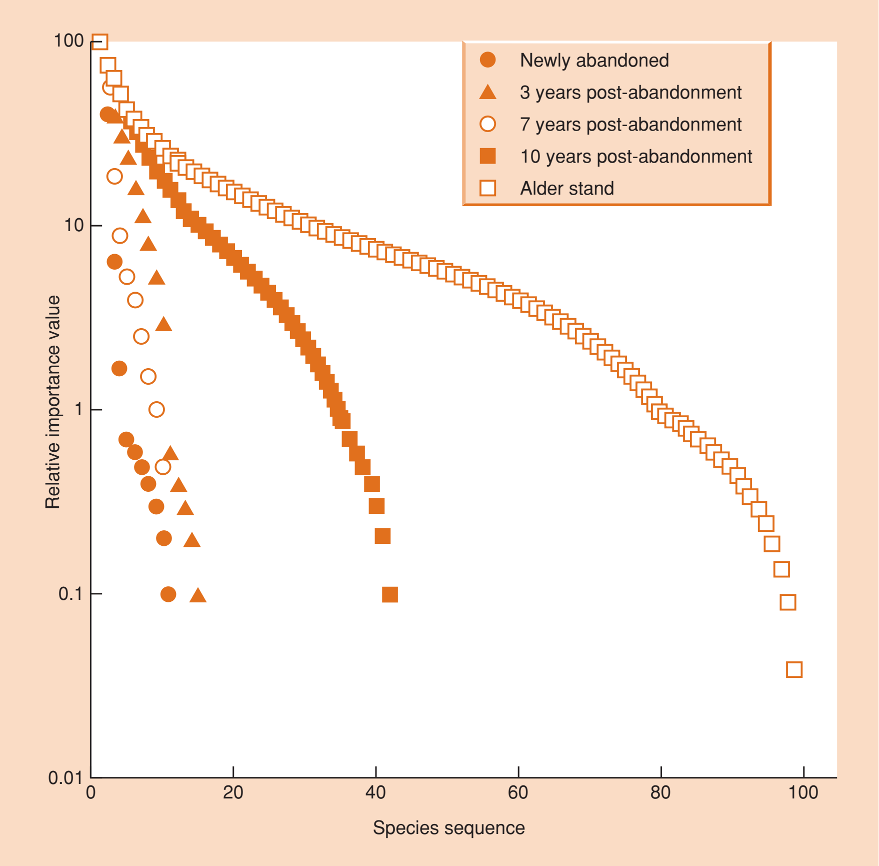


Figure 22.4 Rank–abundance diagram of plant species grouped by site age (time since abandonment of rice paddy field). Importance values are the relative ground cover of the plant species present. The alder stand was 50 years old. (After Lee *et al*., 2002.)

alterniflora, *S. patens* and *Distichlis spicata*. Recovery was relatively fast (increasing at a rate of 5% of total area per year) where tidal flooding was frequent (i.e. at lower elevations and with higher soil watertables) but was otherwise slow (about 0.5% of total area per year). In the fast recovery sites, it took 10–20 years to achieve 50% coverage of specialist salt marsh plants. Characteristic salt marsh animals followed a similar timetable. Thus, in five sites in marshes at Barn Island that have been recovering for known periods (and for which nearby reference marshes are available for comparison), the high marsh snail *Melampus bidentatus* only achieved densities comparable to reference conditions after 20 years (Figure 22.5a). The bird community also took 10–20 years to reach a community composition similar to reference circumstances. Marsh generalists that forage and breed both in uplands and tidal wetlands (such as song sparrows *Melospiza melodia* and red-winged blackbirds *Agelaius phoeniceus*) dominated early in the restoration sequence, to be replaced later by marsh specialists such as marsh wrens *Cistothorus palustris*, snowy egrets *Egretta thula* and spotted sandpipers *Actitis macularia*) (Figure 22.5b). Typical fish communities in restoration salt marsh creeks recovered more quickly, within 5 years. It seems that the restoration of a natural tidal regime sets marshes on trajectories towards restoration of full ecological functioning, although this generally takes one or more decades. The process can probably be speeded up if managers plant salt marsh species.

22.2.3 Managing succession for conservation

understanding succession is crucial for the conservation of a rare insect

Some endangered animal species are associated with a particular stage of succession and their conservation then depends on an understanding of the successional sequence; intervention may be required to maintain their habitat at an appropriate successional stage. An intriguing example is provided by a giant New Zealand insect, the weta *Deinacrida mahoenuiensis* (Orthoptera; Anostostomatidae). This species, which was believed extinct after being formerly widespread in forest habitats, was discovered in the 1970s in an isolated patch of gorse (*Ulex europaeus*). Ironically, in New Zealand gorse is an introduced weed that farmers spend much time and effort attempting to control. Its dense, prickly sward provides a refuge for the giant weta against other introduced

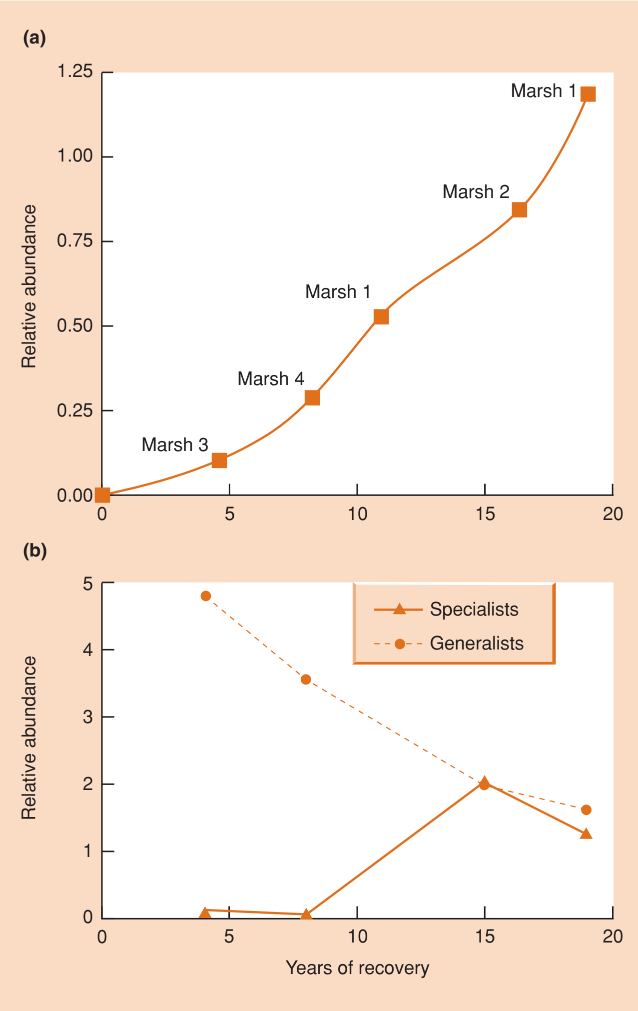


Figure 22.5 (a) Relative abundance of the snail *Melampus bidentatus* (expressed as mean density in the restoration area divided by density in a nearby reference marsh) in five sites in four marshes at Barn Island, Connecticut, that differ in the period since a natural tidal regime was restored. A relative abundance of 1.0 indicates a full recovery of this species. (b) Relative abundance (recovering/reference) of birds considered as salt marsh specialists (▲) and salt marsh generalists (●) on Barn Island marshes plotted against years of restoration at the time the counts were conducted. Again a relative abundance of 1.0 indicates full restoration of the specialist or generalist guild. (After Warren *et al.*, 2002.)

pests, particularly rats but also hedgehogs, stoats and possums, which readily captured wetas in their original forest home. New Zealand's Department of Conservation purchased this important patch of gorse from the landowner who insisted that cattle should be permitted to overwinter in the reserve. Conservationists were unhappy about this but the cattle subsequently proved to be part of the weta's salvation. By opening up paths through the gorse, the cattle provided entry for feral goats that browse the gorse, producing a dense hedge-like sward and preventing the gorse habitat from succeeding to a stage inappropriate to the wetas. This story involves a single endangered endemic insect together with a whole suite of introduced pests (gorse, rats, goats, etc.) and introduced domestic animals (cattle). Before the arrival of people in New Zealand, the island's only land mammals were bats, and New Zealand's endemic fauna has proved to be extraordinarily vulnerable to the mammals that arrived with people. However, by maintaining gorse succession at an early stage, the grazing goats provide a habitat in which the weta can escape the attentions of the rats and other predators.

22.3 Food webs, ecosystem functioning and management

22.3.1 Management guided by food web theory

understanding food webs for management . . .

Studies that unravel the complex interactions in food webs (dealt with in Chapter 20) can provide key information for managers on issues as diverse as minimizing human disease risk, setting objectives for marine protected areas or predicting invaders with the most potential to disrupt ecosystem functioning.

22.3.1.1 Lyme disease

. . . of disease . . .

Lyme disease, which if untreated can damage the heart and nervous system and lead to a type of arthritis, each year affects tens of thousands of people around the world. It is caused by a spirochete bacterium (*Borrelia burgdorferi*) carried by ticks in the genus *Ixodes*. The ticks take 2 years to pass through four developmental stages, involving a succession of vertebrate hosts. Eggs are laid in the spring and uninfected larvae take a single blood meal from a host (usually a small mammal or bird) before dropping off and molting into the overwintering nymphal stage. Infected hosts transmit the spirochete to the larval ticks, which remain infective throughout their lives (i.e. after they have molted into nymphs and subsequently into adults). Next year the nymph seeks a host in the spring/early summer for another single blood meal; this is the most risky stage for human infection because the nymphs are small and difficult to detect and attach to hosts at a time of peak human recreation in forests and parks. Between 1 and 40% of nymphs carry the spirochete in Europe and the USA (Ostfeld & Keesing, 2000). The nymph drops off and molts into an adult that takes a final blood meal and reproduces on a third host, often a larger mammal such as a deer.

The most abundant small mammal host in the eastern USA, and by far the most competent transmitter of the spirochete, is the white-footed mouse (*Peromyscus leucopus*). Jones *et al.* (1998) added acorns, a preferred food of the mice, to the floor of an oak forest to simulate one of the occasional crop masting years that occur, and found mice numbers increased the following year and that the prevalence of spirochete infection in nymphal black-legged ticks (*Ixodes scapularis*) increased 2 years after acorn addition. It seems that despite the complexity of the food web of which the spirochetes are part, it may be possible to predict high-risk years for transmission to humans well in advance by monitoring the acorn crop. Of further interest to managers is evidence that outbreaks of pest moths, whose caterpillars can cause massive defoliation of forest, may be more likely to occur 1 year after very poor acorn crops, when mice, which also feed on moth pupae, are rare (Jones *et al.*, 1998).

A final point about disease transmission is worth emphasizing. The potential mammal, bird and reptile hosts of ticks show a great variation in the efficiency with which they are competent to transmit the spirochete to the tick. Ostfeld and Keesing (2000) hypothesized that a high species richness of potential hosts would result in lower disease prevalence in humans if the high transmission efficiency of the key species (such as white-footed mice) is diluted by the presence of a multitude of less competent species. (Note that what really matters is whether the total number of individuals of the more competent species is 'swamped' by a large number of individuals of the less competent ones; relative abundance is important as well as species richness.) Ostfeld and Keesing produced evidence in favor of their hypothesis in the form of a negative relationship between disease cases and small mammal host richness in 10 regions of the USA. Unfortunately, cases of Lyme disease were concentrated in more northerly states, where species richness was lower, suggesting that both disease and mammal richness follow a latitudinal pattern. Thus, whether the link between the two is causal or incidental remains to be determined. This is an important question, however, because a negative relationship between host diversity and disease transmission for vector-borne diseases (including Chagas' disease, plague and Congo hemorrhagic fever) would provide one more reason for managers to act to maintain biodiversity.

22.3.1.2 *Management for an abalone fishery*

. . . and of both harvested shellfish and a charismatic top predator

Sometimes biodiversity can be too high to achieve particular management objectives! Commercial and recreational fisheries for abalones (gastropods in the family Haliotidae) are prone to collapse through overfishing. Adult abalones do not move far and the protection of broodstock in reserved portions of their coastal marine habitat has potential for promoting the export of planktonic larvae to enhance the harvested populations outside the reserves (see Section 15.4.2). However, the most common function of marine-protected areas is the conservation of biodiversity, and the question arises whether protected areas can serve both fisheries management and biodiversity objectives. A keystone species in coastal habitats along the Pacific coast of North America, including those in California, is the sea otter (*Enhydra lutris*), hunted almost to extinction in the 18th and 19th centuries but increasingly widespread as a result of protected status. Sea otters eat abalones, and valuable fisheries for red abalone (*Haliotus rufescens*) developed while sea otters were rare; now there is concern that the fisheries will be unsustainable in the presence of sea otters. Fanshawe *et al.* (2003) compared the population characteristics of abalone in sites along the Californian coast that varied in harvest intensity and sea otter presence: two sites lacked sea otters and had been 'no-take' abalone zones for 20 years or more, three sites lacked sea otters but permitted recreational fishing, and four sites were 'no-take' zones that contained sea otters. The aim was to determine whether marine-protected areas can help make the abalone fishery sustainable when all links in the food web are fully restored. Sea otters and recreational harvest influenced red abalone populations in similar ways but the effects were very much stronger where sea otters were present. Red abalone populations in protected areas had substantially higher densities (15–20 abalone per 20 m^2) than in areas with sea otters (< 4 per 20 m^2), while harvested areas generally had intermediate densities. In addition, 63–83% of individual abalones in protected areas were larger than the legal harvesting limit of 178 mm, compared with 18–26% in harvested areas and less than 1% in sea otter areas. Finally, in the presence of sea otters the abalones were mainly restricted to crevices where they are least vulnerable to predation. Multiple-use protected areas are not likely to be feasible where a desirable top predator feeds intensively on prey targeted by a fishery. Fanshawe *et al.* (2003) recommend separate single-purpose categories of protected area, but this may not work in the long term either; the maintenance of the *status quo* when sea otters are expanding their range is likely eventually to require culling of the otters, something that may prove politically unacceptable.

22.3.1.3 *Invasions by salmonid fish in streams and lakes*

food web and ecosystem consequences of invading fish

Just as sea otters alter the behavior of their abalone prey, so the introduced brown trout (*Salmo trutta*) in New Zealand changes the behavior of herbivorous invertebrates (including nymphs of the mayfly *Deleatidium* spp.) that graze algae on the beds of invaded streams – daytime activity is significantly reduced in the presence of trout (Townsend, 2003). Brown trout rely principally on vision to capture prey, whereas the native fish they have replaced (*Galaxias* spp.) rely on mechanical cues. The hours of

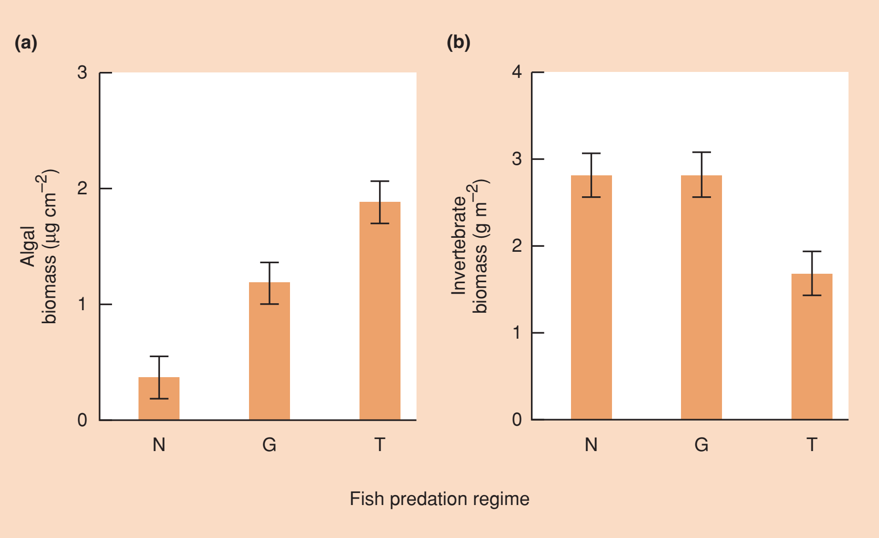


Figure 22.6 (a) Total algal biomass (chlorophyll *a*) and (b) invertebrate biomass (± SE) for an experiment performed in the summer in a small New Zealand stream. G, *Galaxias* present; N, no fish; T, trout present. (After Flecker & Townsend, 1994.)

darkness thus provide a refuge against trout predation analogous to the crevices occupied by the abalone. That an exotic predator such as trout has direct effects on *Galaxias* distribution or mayfly behavior is not surprising, but the influence also cascades to the plant trophic level. Three treatments were established in artificial flow-through channels placed in a real stream – no fish, *Galaxias* present or trout present, at naturally occurring densities. After 12 days, algal biomass was highest where trout were present (Figure 22.6a), partly because of a reduction in grazer biomass (Figure 22.6b) but also because of a reduction of grazing (only feeding at night) by the grazers that remain. This trophic cascade also changed the rate at which radiant energy was captured by the algae (annual net primary production was six times greater in a trout stream than in a neighboring *Galaxias* stream; Huryn, 1998) and, this in turn, resulted in more efficient cycling of nitrogen, the limiting nutrient in these streams (Simon *et al.*, 2004). Thus, important elements of ecosystem functioning, namely energy flux (see Chapter 17) and nutrient flux (see Chapter 18), were altered by the invading trout.

managers should beware invaders that link ecosystem compartments in new ways

Other salmonids, including rainbow trout (*Oncorhyncus mykiss*), have invaded many fishless lakes in North America where a similar increase in plant (phytoplankton) biomass has been recorded. A fish-induced reduction in benthic and planktonic grazers is partly responsible, but Schindler *et al.* (2001) argue that the main reason for increased primary production is that trout feed on benthic and littoral invertebrates and then, via their excretion, transfer phosphorus (the limiting nutrient) into the open water habitat of the phytoplankton. In their review of the impacts of these and other freshwater invaders on community and ecosystem functioning, Simon and Townsend (2003) conclude that biosecurity managers should pay particular attention to invaders that have a novel method of resource acquisition or a broad niche that links previously unlinked ecosystem compartments.

22.3.1.4 Conflicting hypotheses about invasions

where do invaders fit into food webs?

A widely cited hypothesis in invasion biology related to population and food web interactions (see Chapters 19 and 20) and species richness (see Chapter 21) is that species-rich communities are more resistant to invasion than species-poor communities. This is because resources are more fully utilized in the former and competitors and predators are more likely to be present that can exclude potential invaders (Elton, 1958). On this basis, as invaders accumulate in an ecosystem, the rate of further invasions should be reduced (Figure 22.7a). But the opposite has also been postulated – the 'invasional meltdown' hypothesis (Figure 22.7b) (Simberloff & Von Holle, 1999). This argues that the rate of invasions will actually increase with time, partly because the disruption of native species promotes further invasions and partly because some invaders have facilitative rather than negative effects on later arrivals. Ricciardi's (2001) review of invasions of the Great Lakes of North America reveals a pattern that conforms closely to the meltdown hypothesis (Figure 22.7c). Among interactions between pairs of invaders, it is usually competition (−/−) and predation (+/−) that are given prominence. Ricciardi's review is unusual because it also accounted for mutualisms (+/+), commensalisms (+/0) and

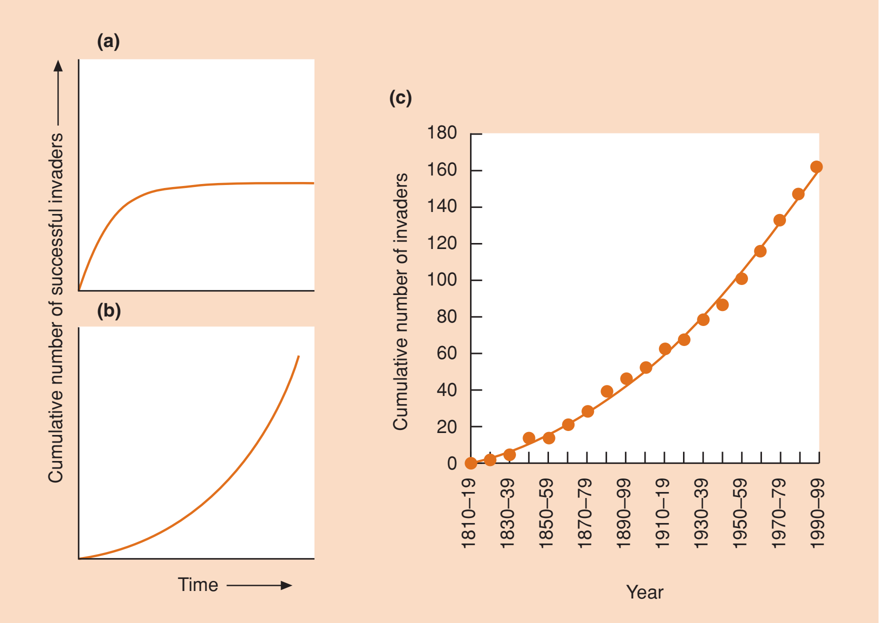


Figure 22.7 Predicted temporal trends in the cumulative number of successful invasions according to (a) the biotic resistance hypothesis and (b) the invasional meltdown hypothesis. (c) Cumulative number of invaders of the Great Lakes of North America – the pattern conforms to the invasional meltdown hypothesis. (After Ricciardi, 2001.)

amensalisms (−/0). There were 101 pairwise interactions in all, three cases of mutualism, 14 of commensalism, four of amensalism, 73 of predation (herbivory, carnivory and parasitism) and seven of competition. Thus, about 17% of reported cases involved one invader facilitating the success of another, whether directly or indirectly. An example of direct facilitation is the provision by invading dreissenid mussels of food in the form of fecal deposits and of increased habitat heterogeneity that favor further invaders such as the amphipod *Echinogammarus ischnus* (Stewart *et al.*, 1998). Indirect facilitation occurred in the 1950s and 1960s when the parasitic sea lamprey *Petromyzon marinus* suppressed native predatory salmonid fish to the benefit of invading fish such as *Alosa pseudoharengus* (Ricciardi, 2001). In addition, one-third of the cases of predation in Ricciardi's analysis could be said to involve 'facilitation' because a newcomer benefitted from a previously established invader. We do not know how widely the invasional meltdown hypothesis applies in different ecosystems, but the history of the Great Lakes suggests that it would generally be unwarranted for managers to take no further action just because several invaders were already established.

22.3.2 Managing eutrophication by manipulating lake food webs

which lakes can be managed to reverse nutrient enrichment?

The excess input of nutrients (particularly phosphorus; Schindler, 1977) from sources such as sewage and agricultural runoff has caused many 'healthy' oligotrophic lakes (low nutrients, low plant productivity with abundant macrophytes, and clear water) to switch to a eutrophic condition. Here, high nutrient inputs lead to high phytoplankton productivity (sometimes dominated by bloom-forming toxic species), making the water turbid and, in the worst situations, leading to anoxia and fish kills (see Section 18.4.3). In some cases the obvious management response of reducing phosphorus input (by sewage diversion, for example) may cause rapid and complete reversal. Lake Washington provides a success story in this *reversible* category (Edmondson, 1991), which includes lakes that are deep, cold and rapidly flushing and lakes that have only been briefly subject to cultural eutrophication (Carpenter *et al.*, 1999). At the other end of the scale are lakes that seem to be *irreversible* because the minimum attainable rate of phosphorus input, or phosphorus recycling from accumulated reserves in lake sediment, is too high to allow the switch back to oligotrophy. This applies particularly to lakes in phosphorus-rich regions (e.g. related to soil chemistry) and lakes that have received very high phosphorus inputs over an extended period. In an intermediate category, which Carpenter *et al.* (1999) refer to as *hysteretic* lakes, eutrophication can be reversed by combining the control of phosphorus inputs with interventions such as chemical treatment to immobilize phosphorus in the sediment or a biological intervention known as biomanipulation. Our discussion focuses on this final category because it depends on a knowledge of interactions in food webs (see Chapter 20) between piscivorous fish, planktivorous fish, herbivorous zooplankton and phytoplankton to guide the management of lakes towards a particular ecosystem endpoint (Mehner *et al.*, 2002).

biomanipulation of food webs

The primary aim of biomanipulation is to improve water quality by lowering phytoplankton density and thus increasing water clarity. The approach involves increasing the grazing of zooplankton on phytoplankton via a reduction in the biomass of zooplanktivorous fish (by fishing them out or by increasing piscivorous fish biomass). Major successes have occurred in shallow lakes where nutrient levels are not too excessive (Meijer *et al.*, 1999). Lathrop *et al.* (2002) were more ambitious than most in attempting to biomanipulate the relatively large and deep eutrophic Lake Mendota in Wisconsin, USA. They combined the management objective of improving water quality with one of augmenting the recreational fishery for piscivorous walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*). In total, more than 2 million fingerlings of the two species were stocked beginning in 1987, and piscivore biomass rapidly responded and stabilized at 4–6 kg ha^{-1} (Figure 22.8a). The combined biomass of zooplanktivorous fish declined, as expected, from 300–600 kg ha^{-1} prior to biomanipulation to 20–40 kg ha^{-1} in subsequent years. The reduction in predation pressure on zooplankton (Figure 22.8b) led, in turn, to a switch from small zooplanktivorous grazers (*Daphnia galeata mendotae*) to the larger and more efficient grazer *D. pulicaria*. In many years when *D. pulicaria* were dominant, their high grazing pressure reduced phytoplankton density and increased water clarity (Figure 22.8c). The desired response would probably have been more emphatic had there not been an increase in phosphorus concentrations during the biomanipulation period, mainly as a result of increased agricultural and urban runoff. Lathrop *et al.* (2002) conclude that the favorable biomanipulation state of high grazing pressure should see further improvements as new management actions to reduce phosphorus inputs take effect.

Cultural eutrophication has equally dramatic effects in rivers, estuaries and marine ecosystems. Coastal eutrophication has become a major cause for concern. The United Nations Environment Program (UNEP) has reported that 150 sea areas worldwide are now regularly starved of oxygen as a result of the decomposition of algal blooms fueled particularly by nitrogen from agricultural runoff of fertilizers and sewage from large cities (UNEP, 2003).

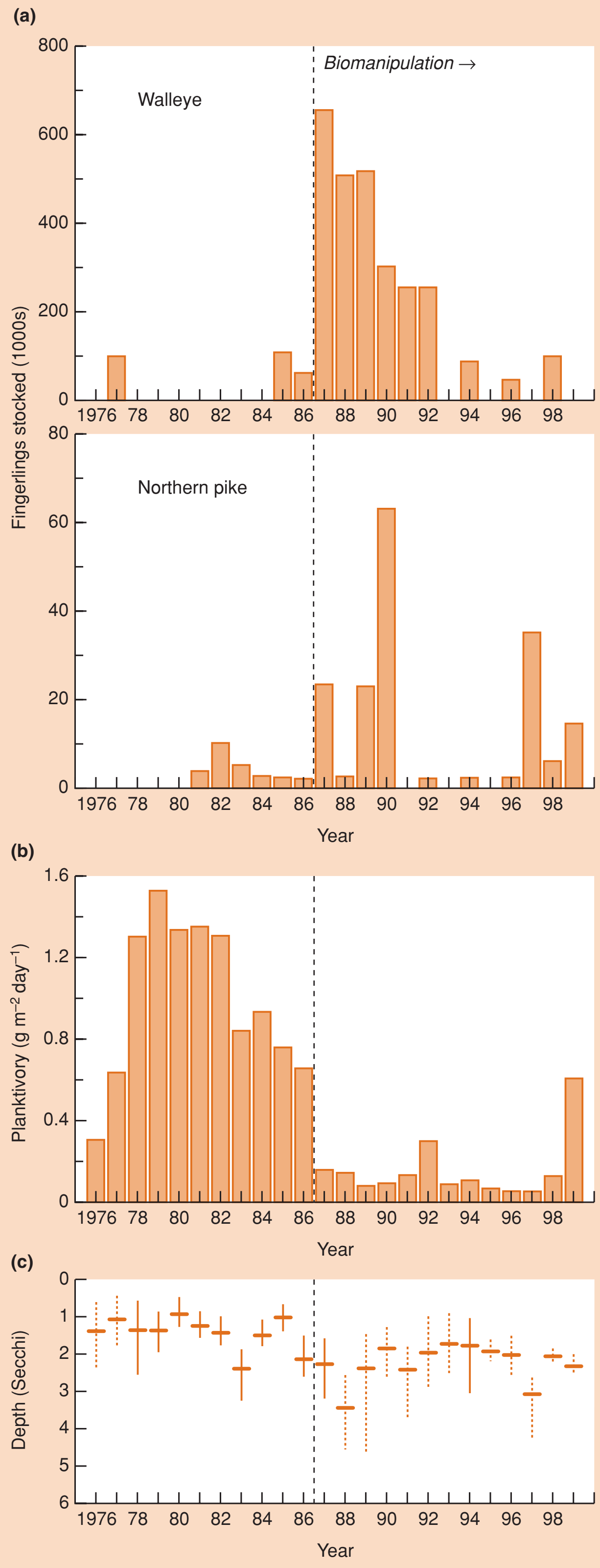


Figure 22.8 (*right*) (a) Fingerlings of two piscivorous fish stocked in Lake Mendota; the major biomanipulation effort started in 1987. (b) Estimates of zooplankton biomass consumed by zooplanktivorous fish per unit area per day. The principal zooplanktivore species were *Coregonus artedi*, *Perca flavescens* and *Morone chrysops*. (c) Mean and range during summer of the maximum depth at which a Secchi disc is visible (a measure of water clarity); dotted vertical lines are for periods when the large and efficient grazer *Daphnia pulicaria* was dominant. (After Lathrop *et al.*, 2002.)

22.3.3 Managing ecosystem processes in agriculture

Intensive land use is not only associated with phosphorus pollution but also with an increase in the amount of the nitrate that leaches into the groundwater and thence into rivers and lakes, affecting food webs and ecosystem functioning (see Section 18.4.4). The excess nitrate also finds its way into drinking water where it is a health hazard, potentially contributing to the formation of carcinogenic nitrosamines and in young children to a reduction in the oxygen-carrying capacity of the blood. The Environmental Protection Agency in the United States recommends a maximum concentration of nitrate of 10 mg l^{-1}.

problems with nutrient enrichment of land

Pigs, cattle and poultry are the three major nitrogen contributors in industrialized agriculture feedlots. The nitrogen-rich waste from factory-farmed poultry is easily dried and forms a transportable, inoffensive and valuable fertilizer for crops and gardens. In contrast, the excreta from cattle and pigs are 90% water and have an unpleasant smell. A commercial unit for fattening 10,000 pigs produces as much pollution as a town of 18,000 inhabitants. The law in many parts of the world increasingly restricts the discharge of agricultural slurry into watercourses. The simplest practice returns the material to the land as semisolid manure or as sprayed slurry. This dilutes its concentration in the environment to what might have occurred in a more primitive and sustainable type of agriculture and converts pollutant into fertilizer. However, if nitrate ions are not taken up again by plants, rainfall leaches them into the groundwater. In fact, the disassociation of livestock and crops in farms specializing in one or the other, rather than mixed farms, has made a major contribution to nitrate pollution of waterways. For example, the centralization of livestock production in the USA has tended to occur in regions that produce little crop feed (Mosier *et al.*, 2002). Thus, for example, of the 11 Tg of nitrogen excreted in animal waste in the USA in 1990 only 34% was returned to cropped fields. Much of the remainder will eventually have found its way into waterways.

Most of the fixed nitrogen in natural communities is present in the vegetation and in the organic fraction of the soil. As organisms die they contribute organic matter to the soil, and this decomposes to release carbon dioxide so that the ratio of carbon to nitrogen falls; when the ratio approaches 10 : 1, nitrogen begins to be released from the soil organic matter as ammonium ions. In aerated regions of the soil, the ammonium ions become oxidized to nitrite and then to nitrate ions, which are leached by rainfall down the soil profile. Both the processes of organic matter decomposition and the formation of nitrates are usually fastest in the summer, when natural vegetation is growing most quickly. Nitrates may then be absorbed by the growing vegetation as fast as they are formed – they are not present in the soil long enough for significant quantities to be leached out of the plants' rooting zone and lost to the community. Natural vegetation most often is a 'nitrogen-tight' ecosystem.

In contrast, there are several reasons why nitrates leach more easily from agricultural land and managed forests than from natural vegetation.

1 For part of the year agricultural land carries little or no living vegetation to absorb nitrates (and for many years forest biomass is below its maximum).
2 Crops and managed forests are usually monocultures that can capture nitrates only from their own rooting zones, whereas natural vegetation often has a diversity of rooting systems and depths.
3 When straw and forestry waste are burned, the organic nitrogen within them is returned to the soil as nitrates.
4 When agricultural land is used for grazing animals their metabolism speeds up the rate at which carbon is respired, reduces the C : N ratio, and increases nitrate formation and leaching.
5 Nitrogen in agriculture fertilizer is usually applied only once or twice a year rather than being steadily released as it is during the growth of natural vegetation; it is therefore more readily leached and finds its way into drainage waters.

the problem is getting worse

Because nitrogen is not efficiently recycled on agricultural land or in managed forests, repeated cropping leads to losses of nitrogen from the ecosystem and thus to decreasing crop productivity. To maintain crop yields the available nitrogen has to be supplemented with fertilizer nitrogen, some of which is obtained by mining potassium nitrate in Chile and Peru, but the majority comes from the energy-expensive industrial process of nitrogen-fixation, in which nitrogen is catalytically combined with hydrogen under high pressure to form ammonia and, in turn, nitrate. Nitrogen fertilizers are applied in agriculture either as nitrates or as urea or ammonium compounds (which are oxidized to nitrates). However, it is wrong to regard artificial fertilization as the only practice that leads to nitrate pollution; nitrogen fixed by crops of legumes such as alfalfa, clover, peas and beans also finds its way into nitrates that leach into drainage water. Figure 22.9 shows how the amounts of synthetic fertilizer and nitrogen-fixing crops have increased in the last 50 years, and the dramatic increases are set to continue over the next half century (Tilman *et al.*, 2001), particularly in developing countries.

management of the nutrient enrichment of land

A variety of approaches are available to tackle the problems of nitrate in drinking water and eutrophication, for example by maintaining ground cover of vegetation year-round, by practising mixed cropping rather than monoculture, by integrating animal and crop production and more generally returning organic matter to the soil, by maintaining low

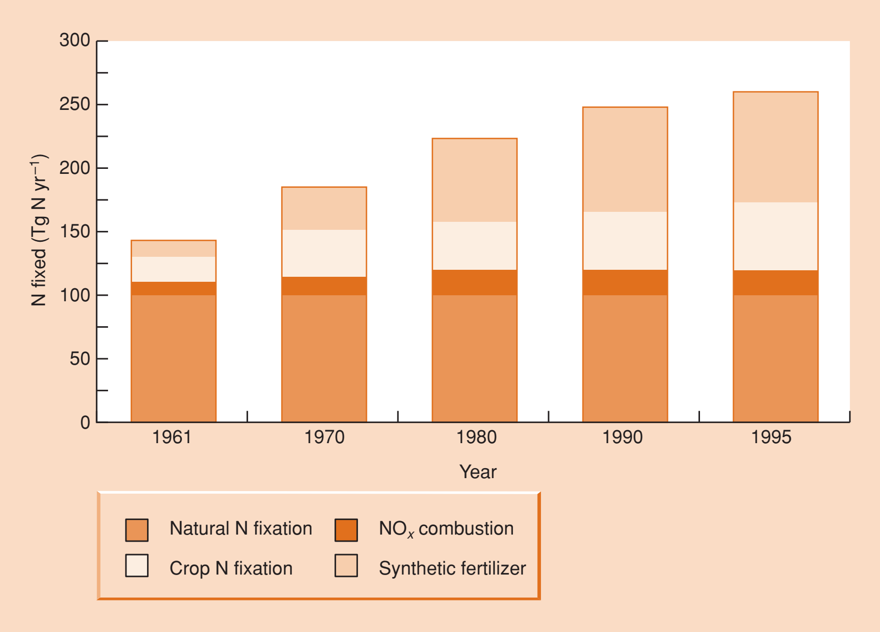


Figure 22.9 Estimates of global nitrogen fixation for representative years since 1961 in four categories. Natural nitrogen fixation remained constant but fixation by crops and in the production of synthetic fertilizer both increased dramatically. NO$_x$ combustion refers to the oxidation of atmospheric nitrogen when fossil fuels are burnt; NO$_x$ is deposited in downwind ecosystems. (After Galloway *et al.*, 1995.)

stocking levels, by matching nitrogen supply to crop demand and by using advanced 'controlled release' fertilizers (Mosier *et al.*, 2002). The role played by nitrogen-fixing symbionts (both fungal arbuscular mycorrhizae and bacterial rhizobia) is of particular interest. Root symbionts do not augment crop productivity consistently. Rather, different species, or the same species under different soil conditions, can range from acting parasitically (when they act as a sink for plant resources in the relationship) to mutualistic (when they significantly enhance plant performance). Kiers *et al.* (2002) argue that research is needed to determine how farm management practices, including fertilization, ploughing and crop rotation, influence the short-term responses and, over a slightly longer timeframe, the evolution of nitrogen-fixing symbionts. Such knowledge would help identify management regimes to enhance mutualistic rather than parasitic interactions.

22.3.4 Ecosystem health and its assessment

characterizing the state of degraded ecosystems – an analogy with human health

Many ecosystems around the world have been degraded by human activities. Using an analogy with human health, managers frequently describe ecosystems as 'unhealthy' if their community structure (species richness, species composition, food web architecture – see Chapters 16, 20 and 21) or ecosystem functioning (productivity, nutrient dynamics, decomposition – see Chapters 17 and 18) has been fundamentally upset by human pressures. Aspects of ecosystem health are sometimes reflected directly in human health (nitrogen content in groundwater and thus drinking water, toxic algae in lakes and oceans, species richness of animal hosts that transmit human diseases in oak forests) but also in natural processes (ecosystem services) that people value, such as flood control, the availability of wild food (including hunted animals and gathered fungi and plants) and recreational opportunities. Management strategies are often framed in the context of *pressure* (human actions), *state* (resulting community structure and ecosystem functioning) and management *response* (Figure 22.10) (Fairweather, 1999). Just as physicians use indicators in their assessment of human health (body temperature, blood pressure, etc.), ecosystem managers need ecosystem health indicators to help set priorities for action and to determine the extent to which their interventions have been successful.

ecosystem health of a forest

The ponderosa pine forests (*Pinus ponderosa*) of the western USA can be used to illustrate the relationship between pressure, state and response (Rapport *et al.*, 1998). A variety of human influences are at play but Yazvenko and Rapport (1997) consider the most important pressure has been fire suppression (just as we saw in the Australian ecosystem described in Section 22.2.1, ponderosa pine forests evolved in a situation where periodic natural fires occurred). With fire suppression, the state of the forest has shifted towards decreased productivity and increased tree mortality, changed patterns of nutrient cycling, and an increased rate and magnitude of outbreaks of tree pests and diseases. These changed properties

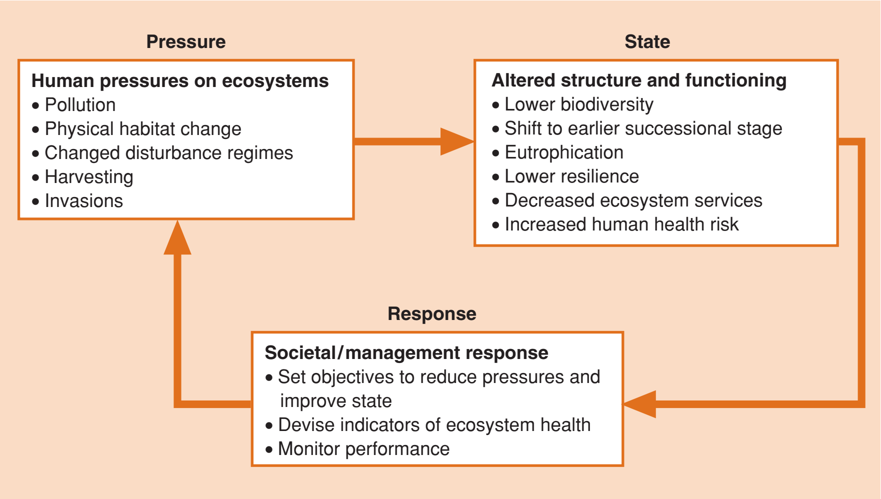


Figure 22.10 The linkage between *pressures* caused by human activities, *state* in terms of community composition and ecosystem processes, and management *response*. Adverse effects on ecosystems sometimes involve processes with clear value in human terms; such impacted ecosystem services include reduced recreational opportunities, poor water quality, diminished natural flood control, negative impacts on harvestable wildlife and on biodiversity generally.

can be taken as indicators of ecosystem health and successful restoration (response) will be evident when the indicators reverse the trends.

ecosystem health of a river

River health has been measured in a number of ways, from assessment of abiotic evidence of pressures (e.g. nutrient concentrations and sediment loads), through community composition to ecosystem functioning (such as the rate of decomposition of leaves of overhanging vegetation that fall naturally into rivers; Gessner & Chauvet, 2002). Some health indexes include more than one of these indicators; in other cases managers rely on a single measure. In New Zealand, for example, river managers use the macroinvertebrate community index (MCI) (Stark, 1993). This is based on the presence or absence of certain types of river invertebrates that differ in their ability to tolerate pollution; healthy streams with abundant species that are intolerant of pollution have high values of MCI (120 or above) whereas unhealthy streams have values as low as 80 or less. Figure 22.11a shows the relationship, for sites on the Kakaunui River on the east coast of New Zealand's South Island, between MCI and the percentage of the catchment area that has been developed (for pasture or urban development; here land development is the pressure).

ecosystem health as a social construct

We should not lose sight of the fact that the concept of ecosystem health is generally a social construct. A healthy ecosystem is one that the community believes to be healthy and different social groups hold different ideas about this (e.g. anglers consider that a river is healthy if it contains many big representatives of preferred fish species; parents if their children do not get sick swimming in the river; conservationists if native species are abundant). The Kakaunui River is within the territory of a Maori group who wished to develop a tool so their perceptions of river health could be taken into account by managers. Their Cultural Stream Health Measure (CSHM) includes components related to the extent to which the surrounding catchment area, the riparian zone, the banks and the stream bed appear impacted by human activities. The CSHM (Figure 22.11b) turned out to be strongly correlated with the MCI despite the fact that it included no invertebrate component.

22.4 Biodiversity and management

22.4.1 Selecting conservation areas

multispecies or single-species management plans?

Producing individual species survival plans may be the best way to deal with species recognized to be in deep trouble and identified to be of special importance (e.g. keystone species, evolutionarily unique species, charismatic large animals that are easy to 'sell' to the public). However, there is no possibility that all endangered species could be dealt with one at a time. For instance, the US Fish and Wildlife Service calculated it would need to spend about $4.6 billion over 10 years to fully recover all gazetted species in the USA (US Department of the Interior, 1990), whereas the annual budget for 1993 was $60 million (Losos, 1993). In the face of such funding shortfalls, there has been a growing trend towards multispecies rather than single-species protection plans, but this carries a risk that the specific requirements of endangered species will receive insufficient attention. Thus, an analysis of USA cases showed that species in multispecies plans were significantly more likely to exhibit declining population trends (Boersma *et al.*, 2001). For this reason, Clark and Harvey (2002) advocate the grouping together of species according to the threats they face. Despite

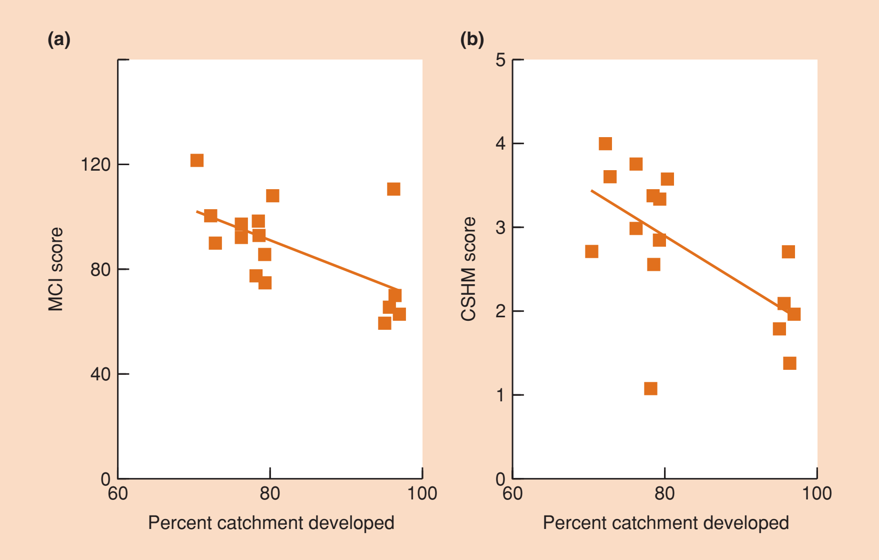


Figure 22.11 Relationships between percentage development of the catchment area of sites in the Kakaunui River (for pasture and urban use) and (a) the macroinvertebrate community index (MCI), commonly used by river managers in New Zealand, and (b) the Maori Cultural Stream Health Measure (CSHM). (After Townsend *et al.*, 2004.)

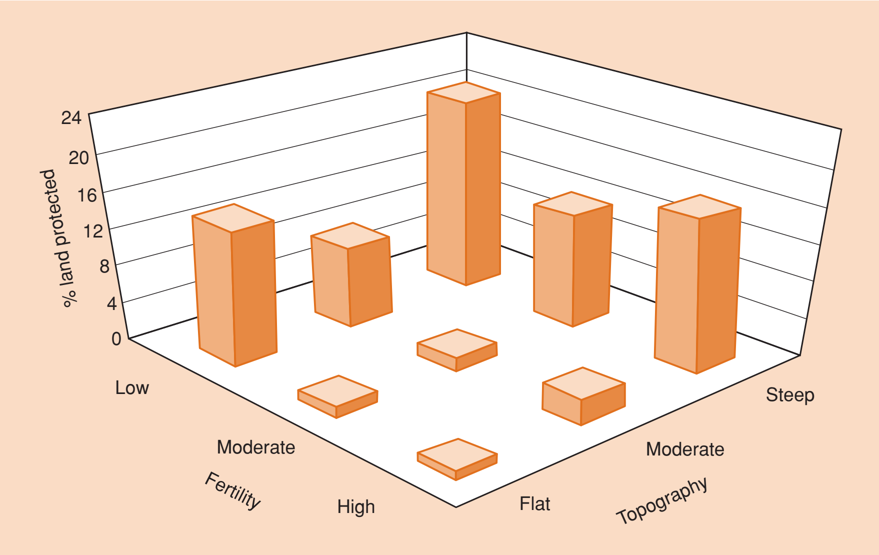


Figure 22.12 Protected areas in southwest Australia are most often situated in steeply sloping and poorly productive areas that are not in demand for agriculture or urban development. (After Pressey, 1995; Bibby, 1998.)

some shortcomings, however, we can generally expect to conserve the greatest biodiversity if we protect whole communities by setting aside protected areas.

protected areas: limits to growth

Protected areas of various kinds (national parks, nature reserves, multiple-use management areas, etc.) grew in number and area through the 20th century, with the greatest expansion occurring since 1970. However, the 4500 protected areas in existence in 1989 still only represented 3.2% of the world's land area. At best, and given the political will, perhaps 6% of land area may eventually be provided protection – the rest would be considered necessary to provide the natural resources needed by the human population (Primack, 1993). Understandably, but nevertheless disturbingly, reserves have often been established on land that no one else wants (Figure 22.12). Areas of high species richness and distributions of endangered plant and animal species often overlap with human population centers (Figure 22.13). Thus, although protection of wilderness is of value and relatively easy, conserving maximum diversity will require greater focus on areas of high human value.

priorities for marine protected areas

Priorities for marine conservation, which have lagged behind terrestrial efforts, are now being urgently addressed. In taxonomic terms, most of the world's biota is found in the sea (32 of the 33 known animal phyla are marine, 15 exclusively so) and marine communities are

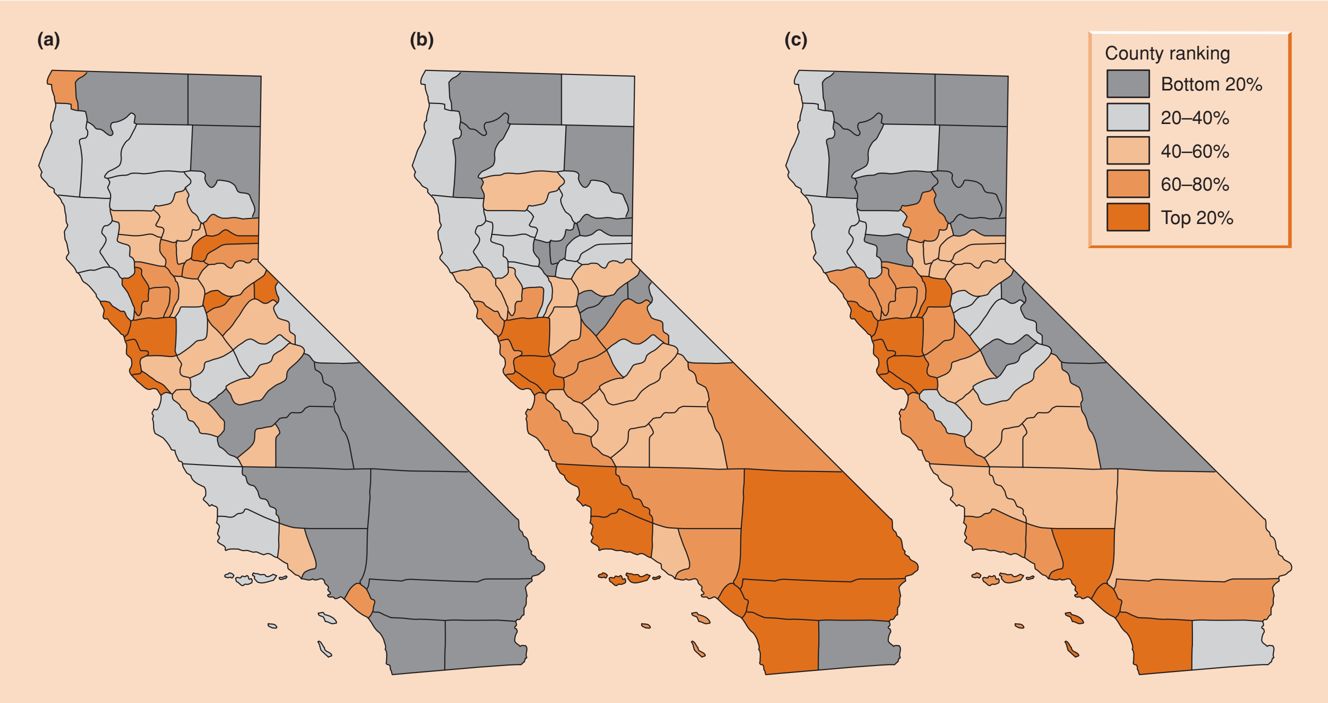


Figure 22.13 Counties of California ranked according to: (a) plant species richness (number per 2.59 km^2 sample area); (b) the proportion of plant species listed as threatened or endangered; and (c) human population density. (After Dobson *et al.*, 2001.)

subject to a number of potentially adverse influences, including overfishing, habitat disruption and pollution from land-based activities. There are some fundamental distinctions between marine and terrestrial ecosystems that need to be borne in mind when designing marine reserves. Most prominent among these is the greater 'openness' of marine areas, with long-distance dispersal of nutrients, organic and inorganic matter, planktonic organisms and the reproductive propagules of benthic organisms and fish (Carr *et al.*, 2003; see also Section 15.4.2).

systematic approach to conservation planning

The overall aim of conservation areas, whether terrestrial or marine, is to represent the biota of each region in a way that separates the biodiversity from the processes that threaten it. Margules and Pressey (2000) recommend the following steps for systematic conservation planning.

1. Compile data on biodiversity and on the distribution of rare and endangered species in the planning region.
2. Identify conservation goals and set explicit conservation targets for species and community types as well as quantitative targets for minimum reserve size and connectivity.
3. Review existing conservation areas to measure the extent to which quantitative goals have already been achieved and identify imminent threats to underrepresented species and community types.
4. Select additional conservation areas to augment existing reserves in a way that best achieves the conservation goals (discussed further below).
5. Implement conservation actions having decided the most appropriate form of management for each area and having established an implementation timetable if resources are not available for all actions to be carried out at once.
6. Maintain the required values of conservation areas and monitor key indicators that will reflect management success, modifying management as required.

centers of diversity, endemism, extinction and utility

We know that the biotas of different locations vary in species richness (centers of diversity – see Section 21.1), the extent to which the biota is unique (centers of endemism) and the extent to which the biota is endangered (hot spots of extinction, for example because of imminent habitat destruction). One or more of these criteria could be used to prioritize potential areas for protection (Figure 22.14). Moreover, if we were to give less weight to the 'existence' value of species (every species equal) and more weight to the potential value of species that may provide future

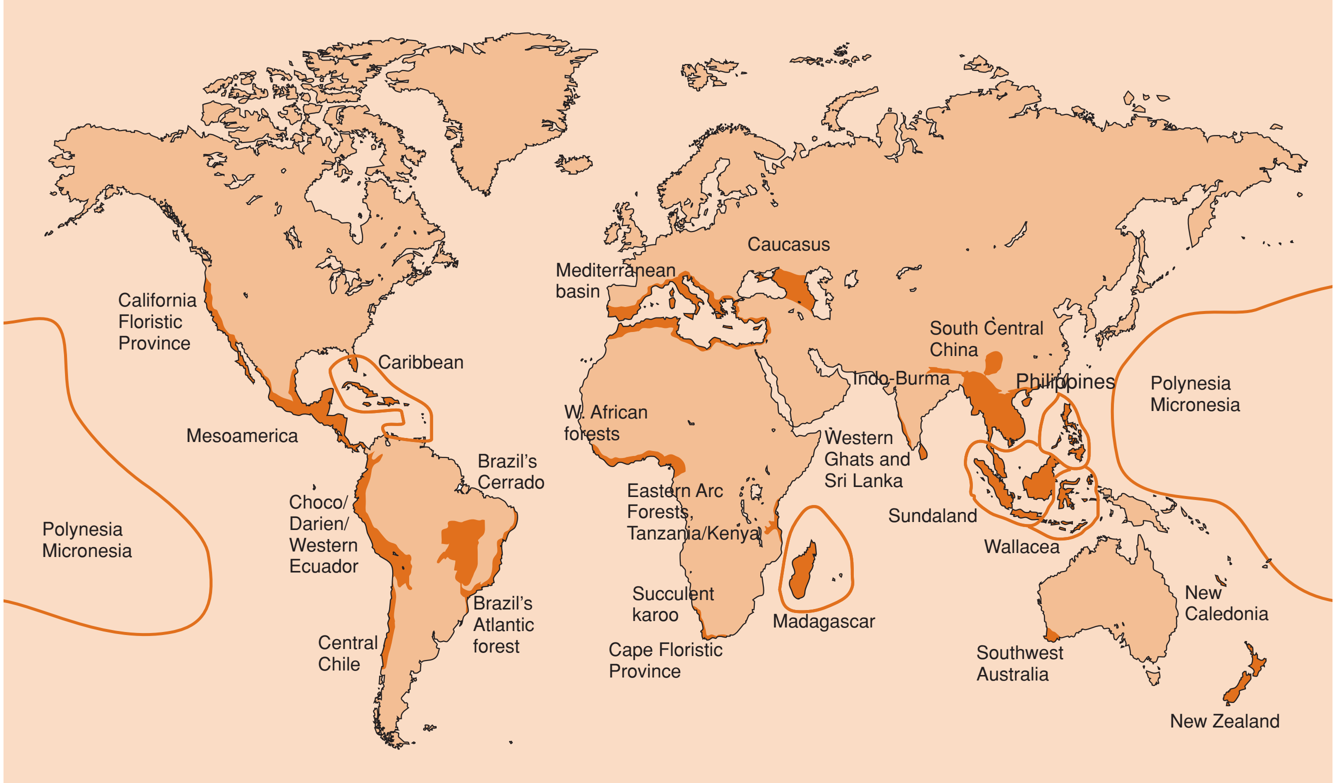


Figure 22.14 The global distribution of biodiversity hot spots where exceptional concentrations of endemic species are undergoing exceptional loss of habitat. As many as 44% of all species of the earth's vascular plants and 35% of its vertebrates are confined to 25 hot spots that make up only 1.4% of its land surface. (After Myers *et al.*, 2000.)

benefit (for food, domestication, medical products, etc.) we could prioritize locations that contained more species likely to be useful (centers of utility).

the key concepts of complementarity and irreplaceability

But, biodiversity encompasses more than just species richness. The selection of new areas should also try to ensure protection of representatives of as many types of community and ecosystem as possible. Two key principles here are *complementarity* and *irreplaceability* (Pressey *et al.*, 1993).

With limited resources, the ideal strategy is to assess the content of candidate areas and to proceed in a stepwise fashion, selecting at each step the site that is most complementary to the others in the features it contains. A number of algorithms are now available to carry out this procedure efficiently. For example, one algorithm lays more stress on the degree of uniqueness of the community or land system, while another lays more stress on the average rareness of the land systems present in the different locations (Figure 22.15a).

A related but subtly different approach identifies irreplaceability as a fundamental measure of the conservation value of a site. Irreplaceability is an index of the potential contribution that a site will make to a defined conservation goal and the extent to which the options for conservation are lost if the site is lost (Figure 22.15b). The notions of complementarity and irreplaceability can equally well be applied to strategies designed to maximize species richness. However, complementarity algorithms for species richness should be implemented with care because they have a tendency to select areas that are at the margins of species ranges more often than would be expected by chance (Araujo & Williams, 2001), and rare species could do less well at the margins than in the centers of their ranges.

design of nature reserves: clues from island biogeography theory

A perhaps rather surprising application of island biogeography theory (see Section 21.5) is in nature conservation. This is because many conserved areas and nature reserves are surrounded by an 'ocean' of habitat made unsuitable, and therefore hostile, by people. Can the study of islands in general provide us with 'design principles' that can be used in the planning of nature reserves? The answer is a cautious 'yes' (Soulé, 1986); some general points can be made.

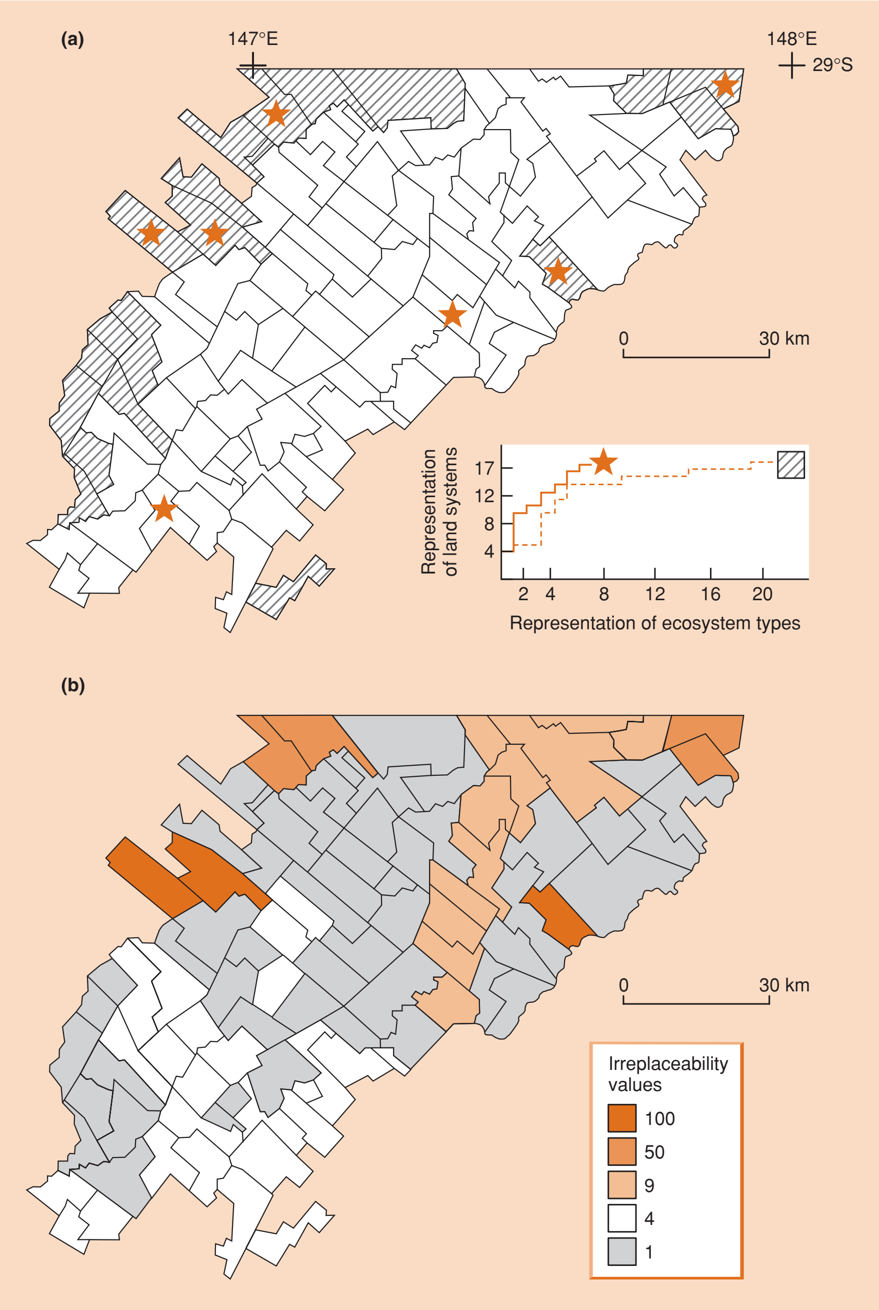


Figure 22.15 (a) A map of 95 pastoral holdings in New South Wales, Australia, showing two sets of holdings needed to represent all 17 ecosystem types at least once. Stars indicate a minimum set identified by a complementarity algorithm that selects sites with unique ecosystems, and then proceeds stepwise to select the site with the rarest unrepresented ecosystem type. Shading indicates the set required if all holdings are scored according to the average rareness of the ecosystem types they contain. (b) A landscape of conservation value for each holding derived by predicting irreplaceability levels. (After Pressey *et al.*, 1993.)

1 One problem that conservation managers sometimes face is whether to construct one large reserve or several small ones adding up to the same total area (sometimes referred to as the SLOSS (single large or several small) debate). If each of the small reserves supported the same species, then it would be preferable to construct the larger reserve in the expectation of conserving more species (this recommendation derives from the species–area relationships discussed in Section 21.5.1).

2 On the other hand, if the region as a whole is heterogeneous, then each of the small reserves may support a different group of species and the total conserved might exceed that in a large reserve. In fact, collections of small islands tend to contain more species than a comparable area composed of one or a few large islands. The pattern is similar for habitat islands and, most significantly, for national parks. Thus, several small parks contained more species than larger ones of the same area in studies of mammals and birds in East African parks, of mammals

Table 22.1 Activities permitted or prohibited for each of four planned levels of protection (from left to right in order of decreasing protection) for the Asinara Island National Marine Reserve of Italy. (After Villa *et al.*, 2002.)

Category	*Activity*	*No-take, no-entry*	*Entry, no-take*	*General reserve*	*Partial reserve*
Research	Nondestructive research	Aa	Aa	A	A
Sea access	Sailing	P	L	A	A
	Motor boating	P	P	L	L
	Swimming	P	P	A	A
Staying	Anchorage	P	P	L	L
	Mooring	P	L	Aa	A
Recreation	Diving	P	L	Aa	A
	Guided tours	P	L	Aa	A
	Recreational fishing	P	P	L	A
Exploitation	Artisanal	P	P	L	L
	Sport	P	P	P	L
	Scuba	P	P	P	P
	Commercial fishing	P	P	P	P

A, allowed without authorization; Aa, allowed upon authorization; L, subject to specific limitations; P, prohibited.

and lizards in Australian reserves, and of large mammals in national parks in the USA (Quinn & Harrison, 1988). It seems likely that habitat heterogeneity is a general feature of considerable importance in determining species richness.

3 A point of particular significance is that local extinctions are common events (see Section 7.5), and so recolonization of habitat fragments is critical for the survival of fragmented populations. Thus, we need to pay particular attention to the spatial relationships amongst fragments, including the provision of dispersal corridors. There are potential disadvantages – for example, corridors could increase the correlation among fragments of catastrophic effects such as the spread of fire or disease – but the arguments in favor are persuasive. Indeed, high recolonization rates (even if this means conservation managers themselves moving organisms around) may be indispensable to the success of conservation of endangered metapopulations (see Section 15.5.3). Note especially that human fragmentation of the landscape, producing subpopulations that are more and more isolated, is likely to have had the strongest effect on populations with naturally low rates of dispersal. Thus, the widespread declines of the world's amphibians may be due, at least in part, to their poor potential for dispersal (Blaustein *et al.*, 1994).

22.4.2 Multipurpose reserve design

managing for multiple objectives – beyond conservation

Many of the new generation of marine protected areas are designed as multiple-use reserves, accommodating many different users (environmentalists, cultural harvesters, commercial fishers, tourism operators, etc.) (Airame *et al.*, 2003). It is clear, too, that conservation and sustainable use on land (forestry, agriculture) can often proceed hand in hand as long as the planning has a scientific basis and the negotiated objectives are clear (Margules & Pressey, 2000).

A good example of multipurpose design is provided by Villa *et al.* (2002), who used a systematic approach to design one of the first marine reserve zoning plans in Italy. They involved all the different interest groups (fishing, recreation, conservation) in defining priorities, and used a GIS (geographic information system) to map marine areas for different uses and degrees of protection. Italian law recognizes reserves with three levels of protection: 'integral' reserves (only available for research), 'general' reserves and the less restrictive 'partial' reserves. Villa *et al.*'s starting point was to accept 'partial' and 'general' reserves but to split 'integral' reserves into two categories: no-entry, no-take zones (where only nondestructive research is permitted) and public entry, no-take zones, which allow visitors a full experience of the reserve, apart from exploitation. Permitted activities for the four categories are shown in Table 22.1.

The next step was to produce maps of 27 variables important to one or more interest groups. These included fish diversity, fish nursery areas, sites used by life history stages of key species (e.g. limpets, sea mammals, marine birds), archeological interest, suitability for various forms of fishing (e.g. traditional artisanal, commercial), suitability for various recreational activities (e.g. snorkeling, whale watching), tourist infrastructure and pollution status. Planning sessions with each interest group yielded weightings or relative importance values for the variables. Taking these into account, five higher level maps were produced (using an approach developed for economic analysis and urban planning known as multiple-criteria analysis): (i) the natural value of the marine environment (NVM – aggregating values related to biodiversity, rarity and crucial habitats such as nursery areas); (ii) the natural value of the coastal environment (NVC – aggregating values related to endemic coastal species including seabirds, and habitat suitable for the reintroduction of turtles and seals); (iii) the recreational activity value (RAV – aggregating values for all recreational activities); (iv) the commercial resource value (CRV – aggregating traditional fishing sites plus other suitable areas); and (v) the ease of access value (EAV – aggregating marine access routes and harbors). Aggregated maps for NVM, NVC and RAV are shown in Figure 22.16a–c.

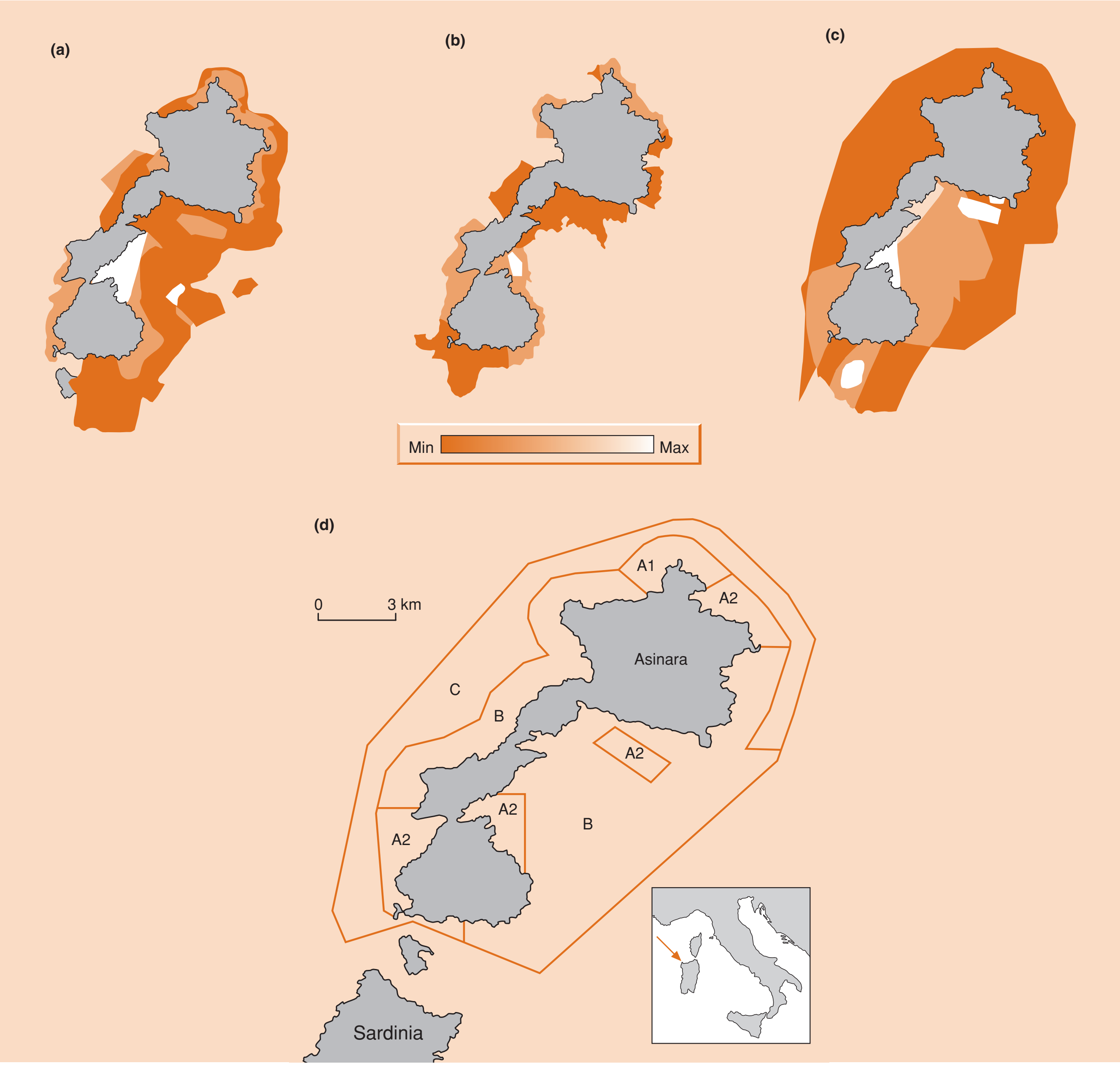


Figure 22.16 Maps of the natural value of (a) the marine environment (NVM), (b) the coastal environment (NVC) and (c) recreational activity value (RAV) for areas around Asinara Island (the island land area is shown in the center in gray). Lighter shades of color represent higher values. (d) Final zoning plan for the Asinara Island National Marine Reserve. A1, no-entry, no-take; A2, entry, no-take; B, general reserve; C, partial reserve. The inset map shows the location of the reserve in relation to the mainland of Italy. (After Villa *et al*., 2002.)

The final stage was the production of a zoning plan. The researchers sought to avoid complex zoning that would make management and enforcement difficult and paid particular attention to the views of the various interest groups to reduce remaining conflicts to a minimum. The final plan (Figure 22.16d) had one no-entry, no-take zone (reflecting biological importance and relative remoteness), four entry, no-take zones to protect specific values such as endangered species (reflecting biological value but with easy access), two general reserve zones (to protect sensitive benthic assemblages, such as seagrass meadows that suffer little from the permitted activities; see Table 22.1) and one partial reserve zone as a buffer for adjacent reserve zones (in an area where traditional fishing practices are compatible with conservation). The zoning proposal also identified three channels providing maximum boat access with minimal environmental disturbance.

22.5 Triple bottom line of sustainability

The main emphasis up to this point has been on the use of ecological theory to help solve environmental problems and establish strategies that are likely to be sustainable in the long term. However, we have already come across a variety of examples where ecological aspects of sustainability cannot be divorced from economic (e.g. limited funds for conservation action) or social aspects (e.g. related to disease risk or the importance of involving diverse interest groups, including indigenous peoples, in resource management). Similar examples were also encountered in the two earlier chapters dealing with ecological applications (e.g. Sections 7.2.3, 7.5.5.2, 7.5.6, 15.2.1, 15.2.3 and 15.3.9). Here we deal more explicitly with the economic and sociopolitical threads of environmental sustainability.

22.5.1 Economic perspective

importance of the economic perspective

The importance of economics in resource management is obvious for activities such as harvest management (see Section 15.3), agricultural management (including pest control; see Sections 15.2 and 22.2.1) and the use of scarce funds when planning conservation management and protected areas (see Sections 7.5 and 22.4). When it comes to conservation of species, biodiversity or ecosystems, however, it is more difficult to assign economic value to the entities to be conserved. It is necessary to do this because of the economic arguments in favor of human activities that make conservation a necessity: agriculture, the felling of trees, the harvesting of wild animal populations, the exploitation of minerals, the burning of fossil fuels, irrigation, the discharge of wastes and so on. While there are not really arguments against conservation, the case for conservation will be most likely to be effective if framed in cost–benefit terms because governments determine their policies against a background of the money they have to spend and the priorities accepted by their electorates.

how can species be assigned economic value?

We first consider how individual species can be valued. There are three main components: (i) the direct value of the products that are harvested; (ii) the indirect value where aspects of biodiversity bring economic benefit without the need to consume the resource; and (iii) the ethical value.

Many species are recognized as having actual direct value as living resources; many more species are likely to have a potential value which as yet remains untapped (Miller, 1988). Wild meat and plants remain a vital resource in many parts of the world, whilst most of the world's food is derived from plants that were originally domesticated from wild plants in tropical and semiarid regions. In the future, wild strains of these species may be needed for their genetic diversity in attempts to breed for improved yield, pest resistance, drought resistance and so on, and quite different species of plants and animals may be found that are appropriate for domestication. In another context, we have seen in Section 15.2 the potential benefits that could come from natural enemies if they can be used as biological control agents for pest species. Most natural enemies of most pests remain unstudied and often unrecognized. Finally, about 40% of the prescription and nonprescription drugs used throughout the world have active ingredients extracted from plants and animals. Aspirin, probably the world's most widely used drug, was derived originally from the leaves of the tropical willow, *Salix alba*. The nine-banded armadillo (*Dasypus novemcinctus*) has been used to study leprosy and prepare a vaccine for the disease; the Florida manatee (*Trichechus manatus*), an endangered mammal, is being used to help understand hemophilia. These are by no means isolated cases and a large-scale worldwide search is underway to discover organisms with new medicinal applications. The vast majority of the world's animals and plants have yet to be screened – the potential value of any that go extinct can never be realized. By conserving species, we maintain their option value – the potential to provide benefit in the future.

Nonconsumptive, indirect economic value is sometimes relatively easy to calculate. For example, a multitude of wild insect species are responsible for pollinating crop plants. The value of these pollinators could be assigned either by calculating the extent to which the insects increase the value of the crop or by the expenditure necessary to hire hives of honeybees to do the pollinating (Primack, 1993). In a related context, the monetary value of recreation and ecotourism, often called amenity value, is becoming ever more considerable. On a smaller scale, a multitude of natural history films, books and educational programs are 'consumed' annually without harming the wildlife upon which they are based.

The final category is ethical value. Many people believe that there are ethical grounds for conservation, arguing that every species is of value in its own right, and would be of equal value even if people were not here to appreciate or exploit it. From this perspective even species with no conceivable economic value require protection.

Of these three main reasons for conserving biodiversity, the first two, direct and indirect economic value, have a truly objective basis. The third, ethics, on the other hand, is subjective and is faced with the problem that a subjective reason will inevitably carry less weight with those not committed to the conservationist cause.

valuing the functioning of ecosystems: 'ecosystem services'

It is clear that assigning a value to species is not always straightforward. However, even more ingenuity is required to assign value to benefits that accrue to people from natural ecosystems as a whole – ecosystem services such as the production of wild species for food, fiber and pharmaceuticals, maintenance of the chemical quality of natural waters, buffering of communities against floods and droughts, ecosystem resistance to pest invasion, protection and maintenance of soils, regulation of local and global climate, the breakdown of organic and inorganic wastes, recreational opportunities, etc. The value of all ecosystem services was estimated globally at US$33 trillion per year (Costanza *et al.*, 1997), updated for the year 2000 to US$38 trillion per year, an amount that is similar to the gross national product of all the world's economies (Balmford *et al.*, 2002).

Such gross estimates are fraught with difficulty and have been criticized, partly because of the assumption that limited local knowledge can be safely extrapolated to a global sum as though demand and value are the same in different parts of the world. Balmford *et al.* (2002) argue that the value of retaining habitat in a relatively undisturbed condition would be best determined by estimating the differences in benefit from relatively intact and exploited versions of a particular ecosystem. They go beyond the mere calculation of private benefit to the exploiters to incorporate the dollar values of diverse public benefits of ecosystem services. The results of three case studies are presented in Figure 22.17. In each case, the estimates of private benefit and ecosystem services are for 30–50-year periods.

including ecosystem services in the valuation of natural resources

The first case study deals with tropical forest in Cameroon and compares low-impact forestry, conversion to small-scale agriculture and conversion to oil palm and rubber plantations. The value of all ecosystem services combined was highest under sustainable forestry; here ecosystem services included the control of sedimentation, flood prevention, carbon sequestration by the vegetation (i.e. contributing to a reduction of carbon dioxide in the atmosphere and thus counteracting global warming) and a range of species values (see Section 7.5). Overall the total economic value (combining private benefit with the value of ecosystem services, expressed as net present value – NPV) over 32 years for low-impact forestry was 18% greater than for small-scale farming, while plantations actually made a net loss when both private benefit and ecosystem services were taken into account.

Analysis of a mangrove ecosystem in Thailand showed that the private benefit from shrimp farming shrank almost to nothing when the economics took into account the loss of ecosystem services from timber and nontimber products, charcoal, offshore fisheries and storm protection associated with the natural ecosystem (Figure 22.17b). The total value of intact mangroves exceeded that of shrimp farming by 70%.

Finally, the draining of freshwater marshes often produces private benefit (sometimes, as in this Canadian example, in large part because of drainage subsidies provided by the government). However, ecosystem services from intact wetland include hunting, trapping and angling and when the dollar values of these are taken into account the overall economic value of intact wetland exceeded converted land by about 60% (Figure 22.17c).

These analyses prompted Balmford *et al.* (2002) to suggest that a large-scale expansion of the world's network of protected areas (costing as much as US$45 billion per year) would actually represent a 'strikingly good bargain' in comparison to the US$38 trillion per year that ecosystem services may be worth.

22.5.2 Social perspectives

In his analysis of the history of fisheries, Pitcher (2001) points out how successive technological advances have driven the inexorable decline in abundance, diversity and representation of high-value species in catches (Figure 22.18). He identified three stages that can be recognized during depletion episodes: the first stage is ecological, comprising depletion and local extinction; the second is economic, comprising a positive feedback loop between increased catching power and depletion, driven by the need to repay money; and the third is social, comprising a shifting baseline in what each generation considers acceptable (or primal) abundance and diversity. It is possible to devise sustainable regimes at any stage but this has not often happened. At the current stage, the question arises should managers simply devise a sustainable management policy or actually attempt to rebuild the fishery? Pitcher challenges communities to attempt a 'back to the future' strategy, in which models of past ecosystems (constructed on the basis of local and traditional environmental knowledge) are subjected to economic comparison with current and alternative ecosystems. He suggests that large no-take reserves and the reintroduction of high-value species will figure prominently in the restoration of such historic ecosystems.

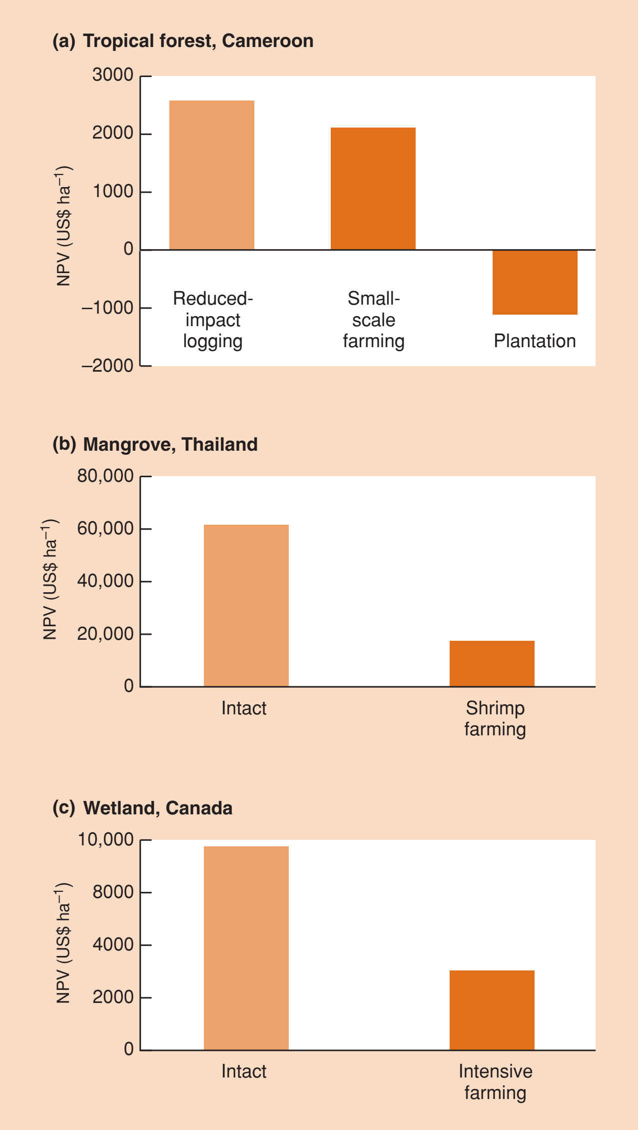


Figure 22.17 The marginal values of retaining or converting natural habitats expressed as net present value (NPV; in terms of US$ in the year 2000). (a) Tropical forest in Cameroon – estimates for three land uses over a 32-year time period, using a discount rate of 10%. Discounting allows for the fact that in economic terms each tree (or fish or bird) in the hand now is worth more than an equivalent bird some time in the future (see Section 15.3.8). The discount rate used was that adopted by the original researchers. (b) Mangrove in Thailand – estimates for intact mangrove forest and for conversion to shrimp farming over a 30-year period with a 6% discount rate. (c) Wetland in Canada – estimates for intact wetland and for conversion to intensive farming over a 50-year period with a discount rate of 4%. (After Balmford *et al.*, 2002; from original studies by G. Yaron, S. Sathirathai and W. van Vuuren & P. Roy, respectively.)

community action . . . and the role of aboriginal people

Managers can benefit from a coalescence of the economic approach of Balmford *et al.* (2002) and the social approach of Villa *et al.* (2002), where diverse local interest groups were involved in developing a management strategy. Aboriginal people can be expected to play a central role in sustainability developments in their territories not least because of their extensive knowledge of both the contemporary and historical situation. We have referred frequently in this chapter to lessons to be learnt from indigenous people and the importance of their involvement in resource management (benzoin gardening in Sumatra, fire management by Australian aborigines, Maori development of river health indicators). Maori have also been one of the groups, along with commercial and recreational fishers, tourism operators and environmentalists, comprising the Guardians of Fiordland's Fisheries and Marine Environment (GOFF). Over 3 years, they developed a zoning plan for New Zealand's Fiordland area on the west coast of New Zealand's South Island (Teirney, 2003). This was an entirely bottom-up effort by the local community (not directed top-down by governmental or nongovernmental agencies) and the diverse groups have worked face-to-face from the beginning. While challenging to manage (a skilled facilitator was involved), this approach provides a model for minimizing conflict, stimulating reciprocal learning and formulating objectives for sustainable ecosystem use that have proved difficult to achieve by top-down means. The New Zealand government has committed itself to implement the GOFF plan.

22.5.3 Putting it all together

applying a triple bottom line approach . . .

In the past, the importance of ecosystem services was only appreciated after they had been lost. However, as ecological understanding has increased and now the economic significance is appreciated, sociopolitical change has become evident in a number of ways. In Costa Rica, for example, the government has been paying landowners since 1997 for ecosystem services such as carbon sequestration, protection of catchment areas, biodiversity and scenic beauty (payments of about US$50 ha^{-1}, which come mainly from taxes on fossil fuels) (Daily *et al.*, 2000). Private enterprise has also begun to respond. Thus, a company called Earth Sanctuaries Ltd became the world's first conservation company to go public when it was listed on the Australian Stock Market. It bought and restored land, earning income from tourism and wildlife sales. The company lobbied and won a change in Australian accounting law so that it could include its rare native animals as assets (Daily *et al.*, 2000). Such approaches, involving far-reaching political change, require price tags to be placed on natural ecosystems.

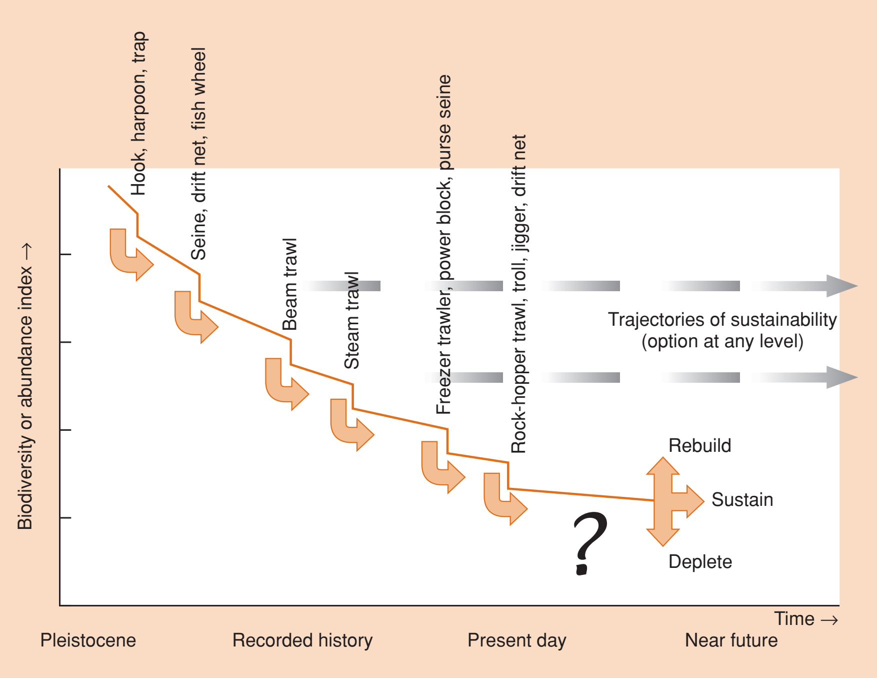


Figure 22.18 Representation of the reduction in abundance and diversity of fish catches since prehistory. The downward steps depict serial depletion as new fishing technologies are invented. Horizontal gray arrows represent sustainable management regimes, which in theory could be devised at any stage. Future options are indicated by the three-way arrow. (After Pitcher, 2001.)

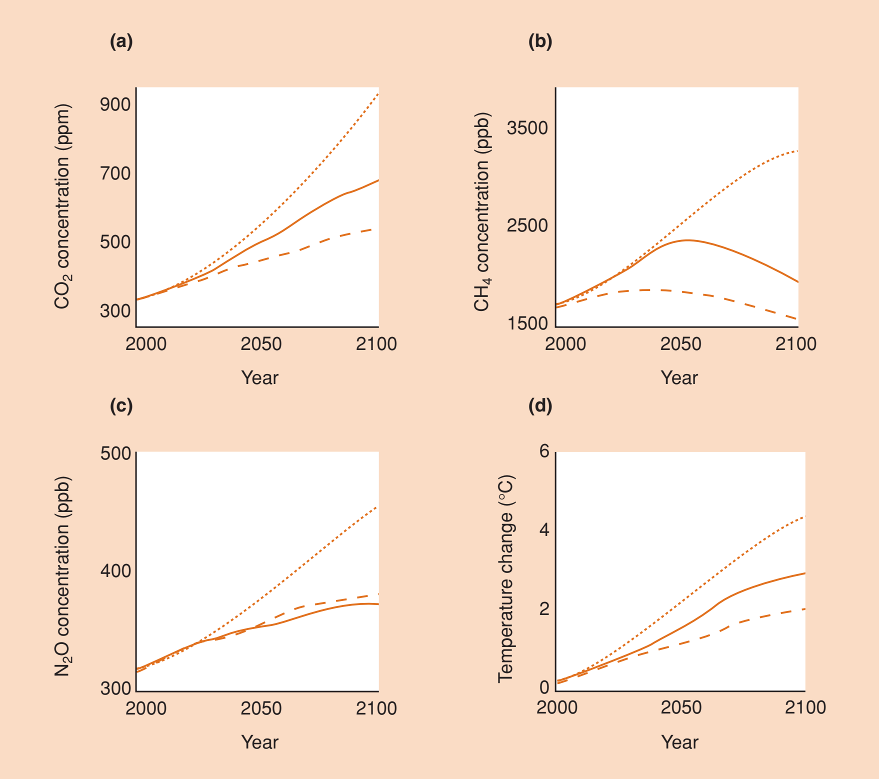


Figure 22.19 Predicted changes in concentration in the atmosphere of (a) carbon dioxide, (b) methane, (c) nitrous oxide and (d) predicted temperature changes to 2100 based on three scenarios. The solid lines show the predicted patterns for a future world of very rapid economic growth, a global population that peaks midcentury, the rapid increase of more efficient technologies, and a population that does not rely heavily on any one particular energy source. The dotted lines show patterns for a similar scenario but one where energy use is fossil-fuel intensive (as it has been until now). The dashed lines are for a more optimistic and sustainable scenario with a similar pattern of population growth but with a rapid change toward a service and information economy, with reductions in the use of materials and the introduction of clean and resource-efficient technologies. (After IPCC, 2001.)

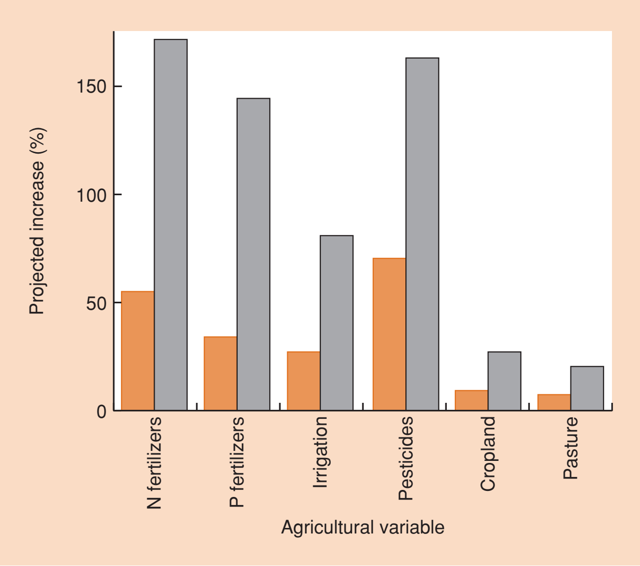


Figure 22.20 Projected increases in nitrogen (N) and phosphorus (P) fertilizers, irrigated land, pesticide use and total areas under crops and pasture by the years 2020 (orange bars) and 2050 (gray bars). (From Laurance, 2001; data from Tilman *et al.*, 2001.)

. . . to global climate change . . .

As with other pressing problems where the application of ecological knowledge is important, dealing with future climate change also requires a triple bottom line approach that brings together ecological, economic and social perspectives for a sustainable future. Estimates of future greenhouse gas emissions, the concentrations to be expected in the atmosphere, and the resulting changes to global temperature vary considerably. Figure 22.19 shows predicted patterns of increase, and in some cases eventual decreases, based on a variety of scenarios related to conceivable values for population increase, potential changes in the use of various energy sources, and likely technological advances.

. . . and to increasing agricultural development

A further example of predicted global change concerns the significant threats posed to ecosystems around the world by increasing agricultural development. Given the projected increase in human population, the associated impacts of increased erosion, unsustainability of water supply, salinization and desertification, excess plant nutrients finding their way into waterways, and the unwanted consequences of chemical pesticides will all increase over the next 50 years as more land is converted to grow crops and pasture (Figure 22.20). To control the environmental impacts of agricultural expansion, we will need scientific and technological advances as well as the implementation of effective government policies. Once again sustainability requires its three faces – ecology, economics and sociopolitics.

The range of problems facing the human race in the early years of a new millennium are unprecedented, and most of those problems are – in the broadest sense – ecological. Philosophers may have contemplated 'Man's place in the world' for generations, but the question has now taken on a new and much more practical meaning. The luxury of asking 'What does it all mean?' is being replaced by the urgent 'What are we to do?' The closing sections of this book have made the point that ecologists cannot address this question alone – and nobody would let us, even if we wanted to! But equally, the question cannot be addressed without the intimate involvement of those with deep, scientific, ecological understanding. Ecologists of the future face two challenges, equally urgent: to advance our science, and to involve our science thoroughly in local, national and global policies. We must believe that those challenges will be met: to doubt it would only paralyze us.

Summary

In this last of the trilogy of chapters (Chapters 7, 15 and 22), we deal with the application of theory related to succession, food webs, ecosystem functioning and biodiversity.

Managers need to be aware that community composition is hardly ever static. Management objectives that seem to require stasis – the annual production of an agricultural crop, the restoration of a particular combination of species, the long-term survival of an endangered species – are likely to fail unless succession is taken into account.

Every species of concern to managers has its complement of competitors, mutualists, predators and parasites, and an appreciation of such complex interactions is often needed to guide management action in diverse fields including human disease, conservation, harvesting and biosecurity.

Nutrient runoff from agricultural land, together with treated or untreated human sewage, can upset the functioning of aquatic ecosystems through the process of cultural eutrophication, increasing productivity, changing abiotic conditions and altering species composition. One potential solution is the 'biomanipulation' of lake food webs to reverse some of the adverse effects of nutrient enrichment. Moreover, knowledge of terrestrial ecosystem functioning can help determine optimal farm practices, where crop productivity involves minimal input of nutrients. The setting of ecosystem restoration objectives (and the ability to monitor whether these are achieved) requires the development of tools to measure the 'ecosystem health' of terrestrial and aquatic environments.

Much of the planet's surface is used for, or adversely affected by, human habitation, industry, mining, food production and harvesting. Thus, there is a pressing need to use our knowledge of the distribution of biodiversity to design networks of reserved land and water, whether specifically for conservation or for multiple uses, such as harvesting, tourism and conservation combined.

We finish by emphasizing a reality that applied ecologists cannot ignore. The application of ecological theory never proceeds in isolation. First, there are inevitably economic considerations: how can farmers maximize production while minimizing adverse ecological consequences; how can biodiversity and ecosystem functioning be evaluated alongside profits from forestry or mining; how can returns be maximized from limited conservation dollars? Second, there are almost always sociopolitical considerations: what methods can be used to reconcile interested parties; should sustainable management be set in law or encouraged by education; how can the needs and perspectives of indigenous people be taken into account? These issues come together in the so-called triple bottom line of sustainability, with its ecological, economic and sociopolitical perspectives.

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Organism index

Page numbers in *italic* refer to figures; those in **bold** to tables

Subject index

Page numbers in *italic* refer to figures; those in **bold** to tables

Plate 1.1 Arctic tundra, Greenland. (Courtesy of J. A. Vickery.)

Plate 1.2 Coniferous forest: (a) aerial view of conifer forest, Alberta, Canada (© Planet Earth Pictures/Martin King) and (b) a pine forest in the fall, Sweden (© Planet Earth Pictures/Jan Tove Johansson).

Plate 1.3 Temperate forest: (a) mixed woodland in the fall, North Carolina, USA (© The Image Bank/Arthur Mayerson) and (b) late summer in Beechwood, Harburn, Scotland (© Ecoscene/Wilkinson).

Plate 1.4 Savanna. (a) Huge herds of wildebeest and common zebra seen from Naabi Hill, Serengeti, Tanzania. (b) Grassland savanna with scattered trees. Common zebra and wildebeest in the western corridor of the Serengeti, Tanzania. (© Images of Africa/David Keith Jones.)

Plate 1.5 Desert: (a) summertime and (b) spring flowers in Namaqualand, western South Africa. (© Planet Earth Pictures/ J. MacKinnon.)

Plate 1.6 Rainforest. (a, b) Impenetrable forest in southwest Uganda. (© Images of Africa/David Keith Jones.)

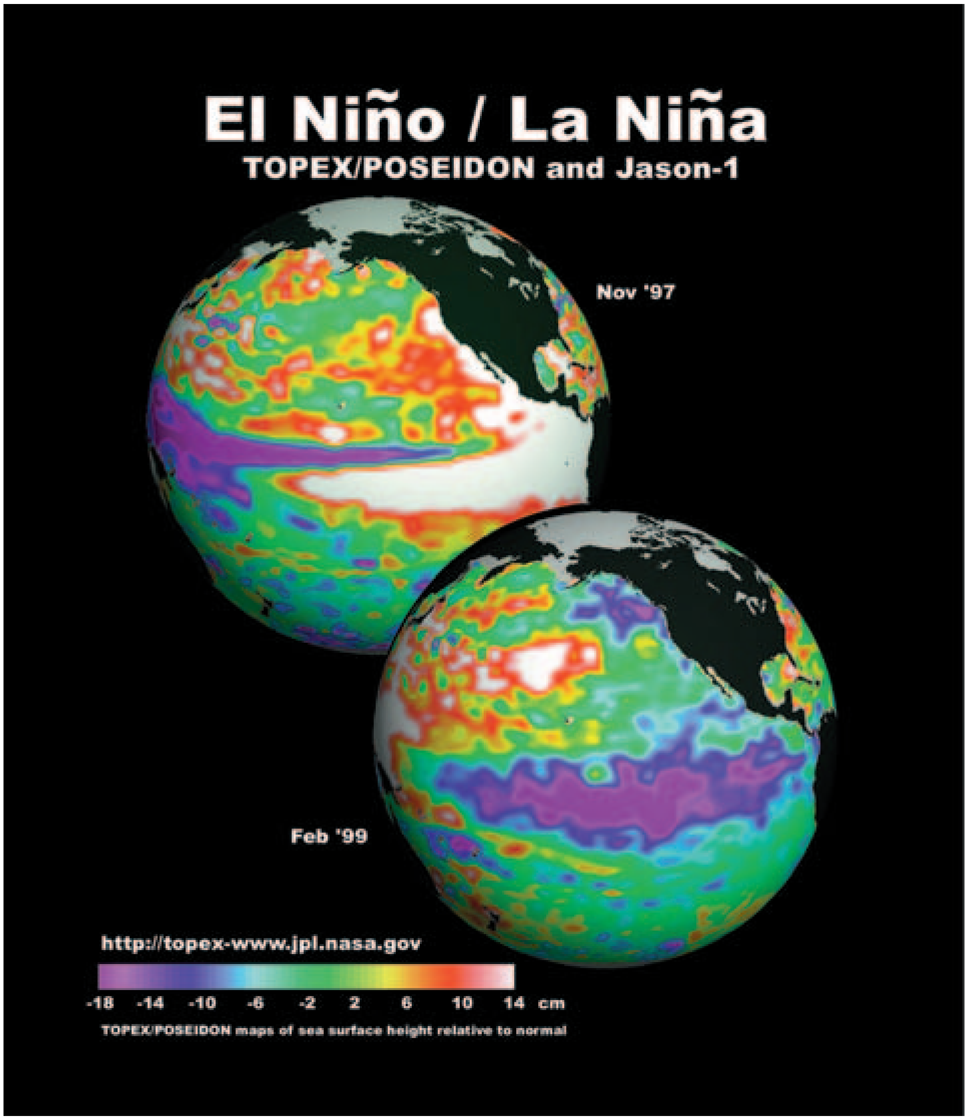

Plate 2.1 Maps of examples of El Niño (November 1997) and La Niña (February 1999) events in terms of sea height above average levels. Warmer seas are higher; for example, a sea height 15–20 cm below average equates to a temperature anomaly of approximately 2–3°C. (Image from http://topex-www.jpl.nasa.gov/science/images/el-nino-la-nina.jpg.) (See Figure 2.11. Courtesy of NASA JPL-Caltech)

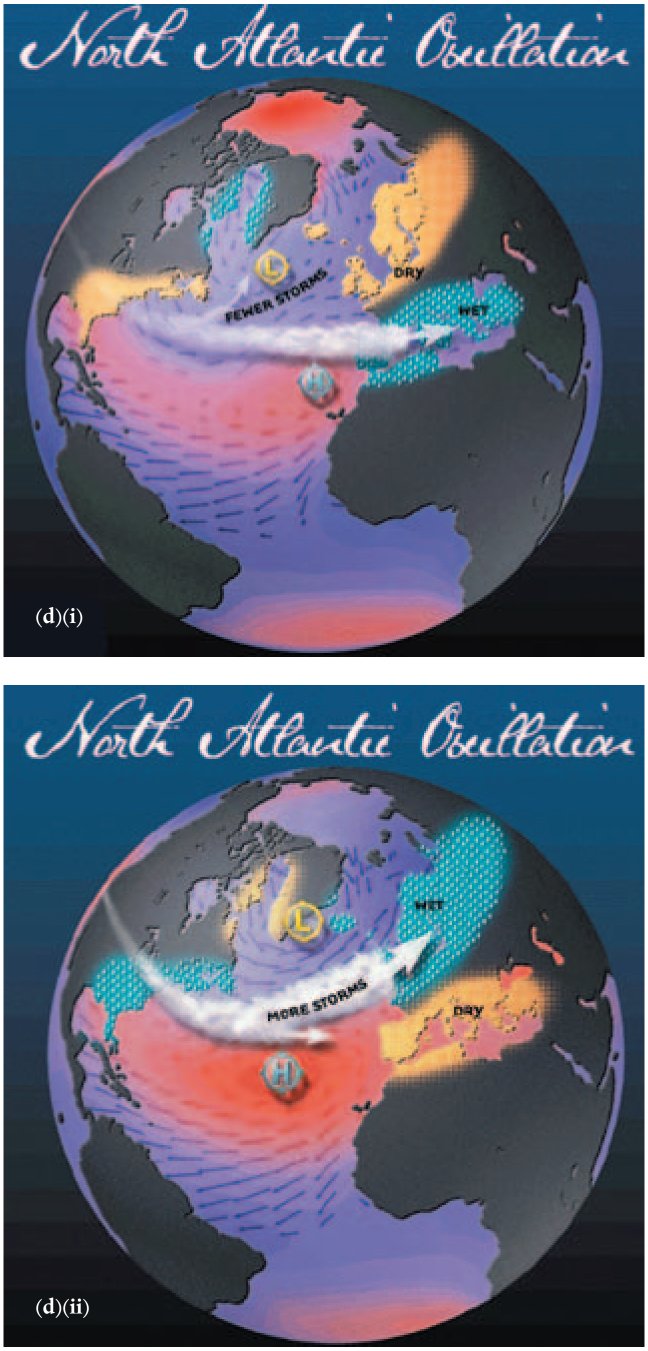

Plate 2.2 Typical winter conditions when the NAO index is positive or negative. Conditions that are more than usually warm (red), cold (blue), dry (orange) or wet (turquoise) are indicated. (Image from http://www.ldeo.columbia.edu/NAO/.) (See Figure 2.11.)

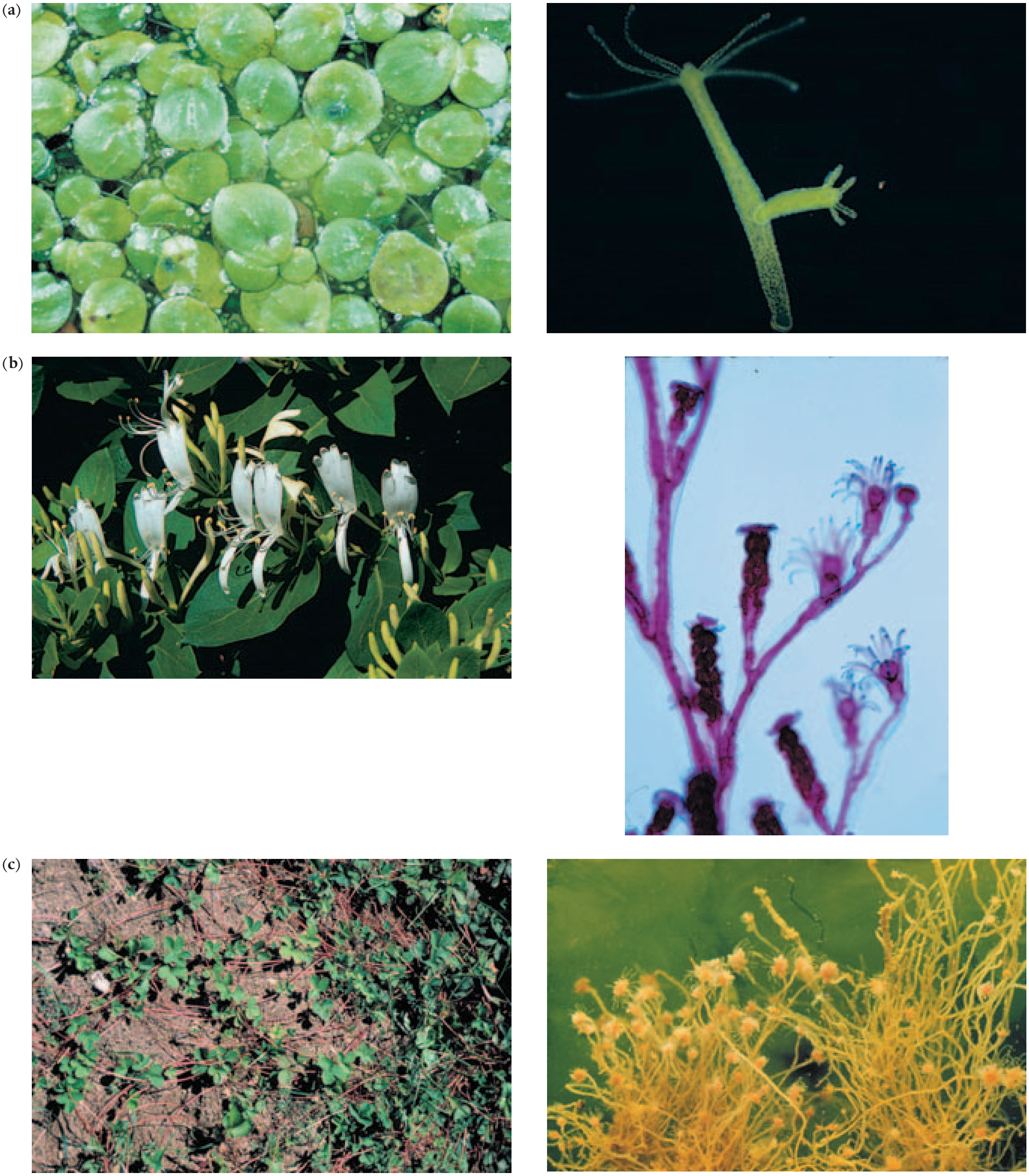
(a)
(b)
(c)

Plate 4.1 Modular plants (on the left) and animals (on the right), showing the underlying parallels in the various ways they may be constructed. (*previous page*) (a) Modular organisms that fall to pieces as they grow: duckweed (*Lemna* sp.) and *Hydra* sp. (b) Freely branching organisms in which the modules are displayed as individuals on 'stalks': a vegetative shoot of a higher plant (*Lonicera japonica*) with leaves (feeding modules) and a flowering shoot, and a hydroid colony (*Obelia*) bearing both feeding and reproductive modules. (c) Stoloniferous organisms in which colonies spread laterally and remain joined by 'stolons' or rhizomes: a single plant of strawberry (*Fragaria*) spreading by means of stolons, and a colony of the hydroid *Tubularia crocea*. (*above*) (d) Tightly packed colonies of modules: a tussock of the spotted saxifrage (*Saxifraga bronchialis*), and a segment of the hard coral *Turbinaria reniformis*. (e) Modules accumulated on a long persistent, largely dead support: an oak tree (*Quercus robur*) in which the support is mainly the dead woody tissues derived from previous modules, and a gorgonian coral in which the support is mainly heavily calcified tissues from earlier modules.

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