

FOURTH EDITION

# Ecology

From Individuals to Ecosystems

Michael Begon, Colin R. Townsend  
and John L. Harper

# ECOLOGY

## From Individuals to Ecosystems

MICHAEL BEGON

*School of Biological Sciences,  
The University of Liverpool, Liverpool, UK*

COLIN R. TOWNSEND

*Department of Zoology, University of Otago, Dunedin, New Zealand*

JOHN L. HARPER

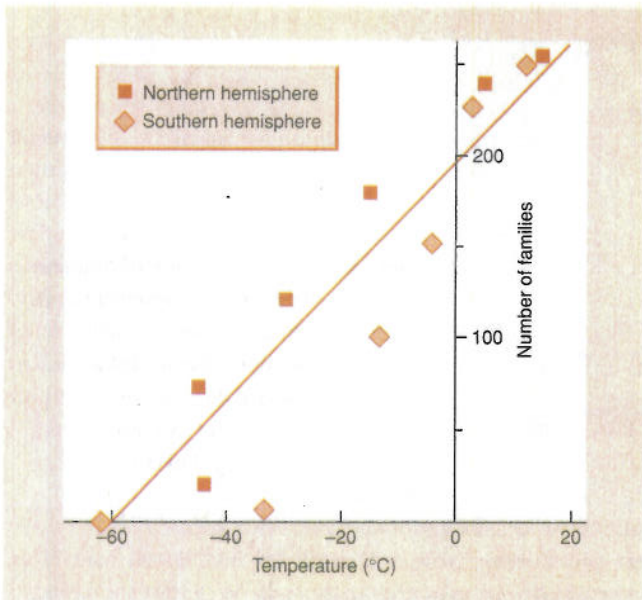
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AR-1453 Page 2 of 16



**Figure 2.13** The relationship between absolute minimum temperature and the number of families of flowering plants in the northern and southern hemispheres. (After Woodward, 1987, who also discusses the limitations to this sort of analysis and how the history of continental isolation may account for the odd difference between northern and southern hemispheres.)

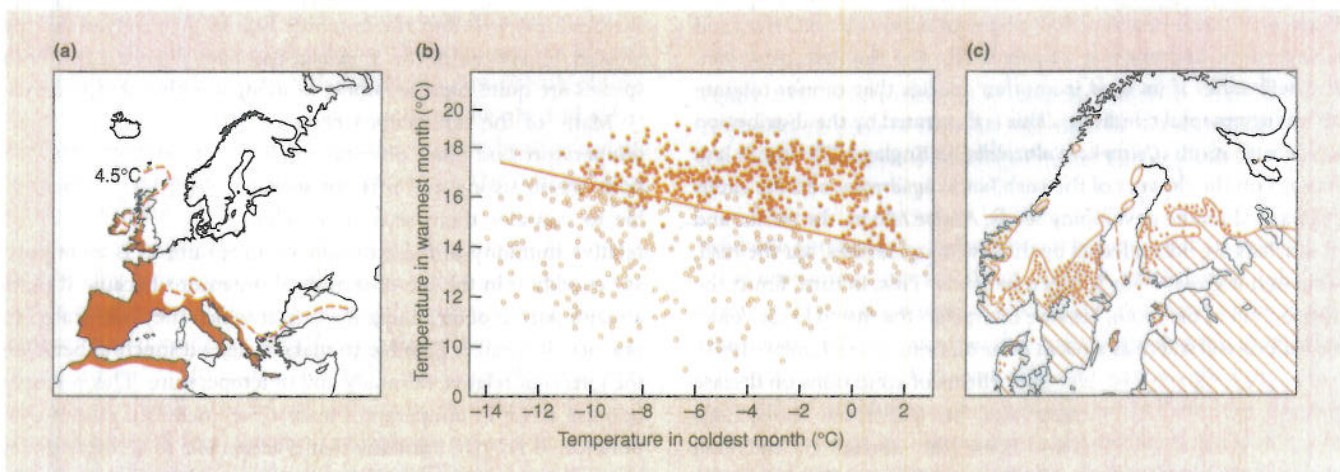
in the shade and, even in a single day, may experience a baking midday sun and a freezing night. Moreover, temperature varies from place to place on a far finer scale than will usually concern a geographer, but it is the conditions in these 'microclimates' that

will be crucial in determining what is habitable for a particular species. For example, the prostrate shrub *Dryas octopetala* is restricted to altitudes exceeding 650 m in North Wales, UK, where it is close to its southern limit. But to the north, in Sutherland in Scotland, where it is generally colder, it is found right down to sea level.

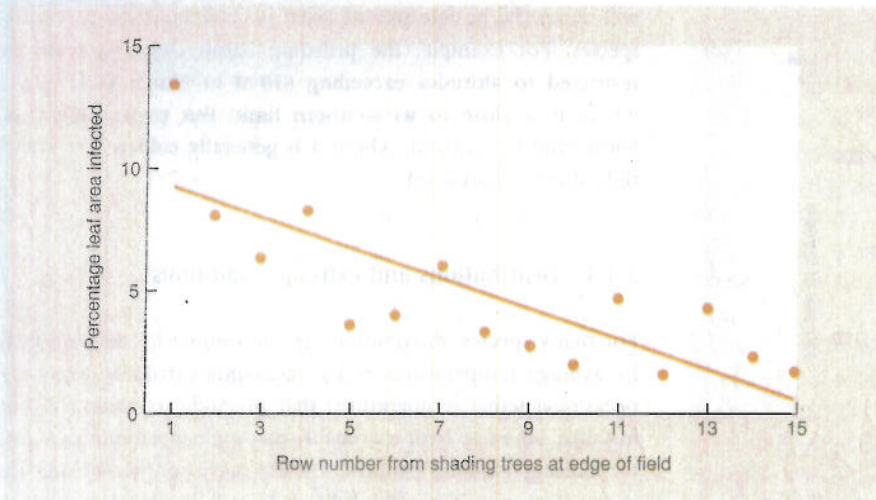
### 2.4.3 Distributions and extreme conditions

For many species, distributions are accounted for not so much by average temperatures as by occasional extremes, especially occasional lethal temperatures that preclude its existence. For instance, injury by frost is probably the single most important factor limiting plant distribution. To take one example: the saguaro cactus (*Carnegiea gigantea*) is liable to be killed when temperatures remain below freezing for 36 h, but if there is a daily thaw it is under no threat. In Arizona, the northern and eastern edges of the cactus' distribution correspond to a line joining places where on occasional days it fails to thaw. Thus, the saguaro is absent where there are occasionally lethal conditions – an individual need only be killed once.

Similarly, there is scarcely any crop that is grown on a large commercial scale in the climatic conditions of its wild ancestors, and it is well known that crop failures are often caused by extreme events, especially frosts and drought. For instance, the climatic limit to the geographic range for the production of coffee (*Coffea arabica* and *C. robusta*) is defined by the 13°C isotherm for the coldest month of the year. Much of the world's crop is produced in the high-land microclimates of the São Paulo and Paraná districts of



**Figure 2.14** (a) The northern limit of the distribution of the wild madder (*Rubia peregrina*) is closely correlated with the position of the January 4.5°C isotherm. (After Cox *et al.*, 1976.) (b) A plot of places within the range of *Tilia cordata* (●), and outside its range (○) in the graphic space defined by the minimum temperature of the coldest month and the maximum temperature of the warmest month. (c) Margin of the geographic range of *T. cordata* in northern Europe defined by the straight line in (b). ((b, c) after Hintikka, 1963; from Hengeveld, 1990.)



**Figure 2.15** The incidence of southern corn leaf blight (*Helminthosporium maydis*) on corn growing in rows at various distances from trees that shaded them. Wind-borne fungal diseases were responsible for most of this mortality (Harper, 1955). (From Lukens & Mullany, 1972.)

Brazil. Here, the average minimum temperature is 20°C, but occasionally cold winds and just a few hours of temperature close to freezing are sufficient to kill or severely damage the trees (and play havoc with world coffee prices).

#### 2.4.4 Distributions and the interaction of temperature with other factors

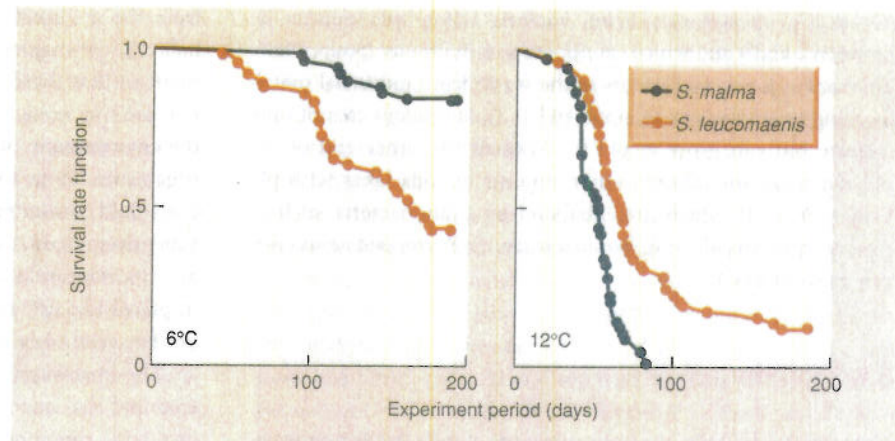
Although organisms respond to each condition in their environment, the effects of conditions may be determined largely by the responses of other community members. Temperature does not act on just one species: it also acts on its competitors, prey, parasites and so on. This, as we saw in Section 2.2, was the difference between a fundamental niche (where an organism *could* live) and a realized niche (where it *actually* lived). For example, an organism will suffer if its food is another species that cannot tolerate an environmental condition. This is illustrated by the distribution of the rush moth (*Coleophora alticolella*) in England. The moth lays its eggs on the flowers of the rush *Juncus squarrosus* and the caterpillars feed on the developing seeds. Above 600 m, the moths and caterpillars are little affected by the low temperatures, but the rush, although it grows, fails to ripen its seeds. This, in turn, limits the distribution of the moth, because caterpillars that hatch in the colder elevations will starve as a result of insufficient food (Randall, 1982).

The effects of conditions on disease may also be important. Conditions may favor the spread of infection (winds carrying fungal spores), or favor the growth of the parasite, or weaken the defenses of the host. For example, during an epidemic of southern corn leaf blight (*Helminthosporium maydis*) in a corn field in Connecticut, the plants closest to the trees that were shaded for the longest periods were the most heavily diseased (Figure 2.15).

Competition between species can also be profoundly influenced by environmental conditions, especially temperature. Two stream salmonid fishes, *Salvelinus malma* and *S. leucomaenis*, coexist at intermediate altitudes (and therefore intermediate temperatures) on Hokkaido Island, Japan, whereas only the former lives at higher altitudes (lower temperatures) and only the latter at lower altitudes (see also Section 8.2.1). A reversal, by a change in temperature, of the outcome of competition between the species appears to play a key role in this. For example, in experimental streams supporting the two species maintained at 6°C over a 191-day period (a typical high altitude temperature), the survival of *S. malma* was far superior to that of *S. leucomaenis*; whereas at 12°C (typical low altitude), both species survived less well, but the outcome was so far reversed that by around 90 days all of the *S. malma* had died (Figure 2.16). Both species are quite capable, alone, of living at either temperature.

Many of the interactions between temperature and other physical conditions are so strong that it is not sensible to consider them separately. The relative humidity of the atmosphere, for example, is an important condition in the life of terrestrial organisms because it plays a major part in determining the rate at which they lose water. In practice, it is rarely possible to make a clean distinction between the effects of relative humidity and of temperature. This is simply because a rise in temperature leads to an increased rate of evaporation. A relative humidity that is acceptable to an organism at a low temperature may therefore be unacceptable at a higher temperature. Microclimatic variations in relative humidity can be even more marked than those involving temperature. For instance, it is not unusual for the relative humidity to be almost 100% at ground level amongst dense vegetation and within the soil, whilst the air immediately above, perhaps 40 cm away, has a relative humidity

**Figure 2.16** Changing temperature reverses the outcome of competition. At low temperature (6°C) on the left, the salmonid fish *Salvelinus malma* outsurvives cohabiting *S. leucomaenis*, whereas at 12°C, on the right, *S. leucomaenis* drives *S. malma* to extinction. Both species are quite capable, alone, of living at either temperature. (After Taniguchi & Nakano, 2000.)



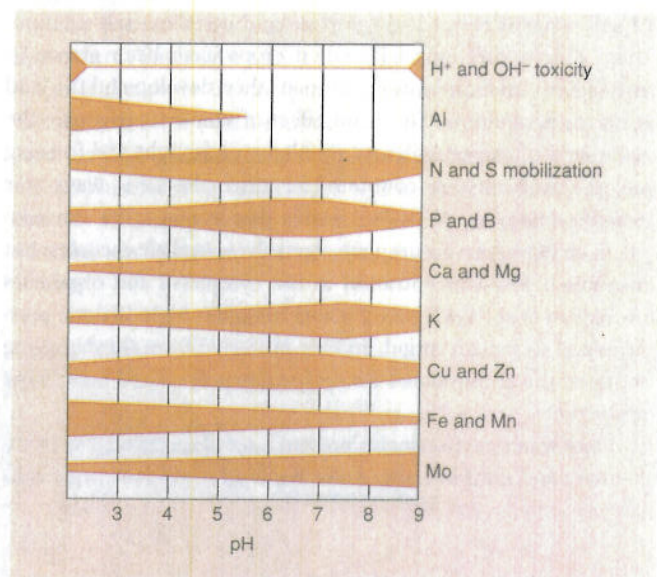
of only 50%. The organisms most obviously affected by humidity in their distribution are those 'terrestrial' animals that are actually, in terms of the way they control their water balance, 'aquatic'. Amphibians, terrestrial isopods, nematodes, earthworms and molluscs are all, at least in their active stages, confined to microenvironments where the relative humidity is at or very close to 100%. The major group of animals to escape such confinement are the terrestrial arthropods, especially insects. Even here though, the evaporative loss of water often confines their activities to habitats (e.g. woodlands) or times of day (e.g. dusk) when relative humidity is relatively high.

## 2.5 pH of soil and water

The pH of soil in terrestrial environments or of water in aquatic ones is a condition that can exert a powerful influence on the distribution and abundance of organisms. The protoplasm of the root cells of most vascular plants is damaged as a direct result of toxic concentrations of  $H^+$  or  $OH^-$  ions in soils below pH 3 or above pH 9, respectively. Further, indirect effects occur because soil pH influences the availability of nutrients and/or the concentration of toxins (Figure 2.17).

Increased acidity (low pH) may act in three ways: (i) directly, by upsetting osmoregulation, enzyme activity or gaseous exchange across respiratory surfaces; (ii) indirectly, by increasing the concentration of toxic heavy metals, particularly aluminum ( $Al^{3+}$ ) but also manganese ( $Mn^{2+}$ ) and iron ( $Fe^{3+}$ ), which are essential plant nutrients at higher pHs; and (iii) indirectly, by reducing the quality and range of food sources available to animals (e.g. fungal growth is reduced at low pH in streams (Hildrew *et al.*, 1984) and the aquatic flora is often absent or less diverse). Tolerance limits for pH vary amongst plant species, but only a minority are able to grow and reproduce at a pH below about 4.5.

In alkaline soils, iron ( $Fe^{3+}$ ) and phosphate ( $PO_4^{3-}$ ), and certain trace elements such as manganese ( $Mn^{2+}$ ), are fixed in relatively



**Figure 2.17** The toxicity of  $H^+$  and  $OH^-$  to plants, and the availability to them of minerals (indicated by the widths of the bands) is influenced by soil pH. (After Larcher, 1980.)

insoluble compounds, and plants may then suffer because there is too little rather than too much of them. For example, calcifuge plants (those characteristic of acid soils) commonly show symptoms of iron deficiency when they are transplanted to more alkaline soils. In general, however, soils and waters with a pH above 7 tend to be hospitable to many more species than those that are more acid. Chalk and limestone grasslands carry a much richer flora (and associated fauna) than acid grasslands and the situation is similar for animals inhabiting streams, ponds and lakes.

Some prokaryotes, especially the Archaeobacteria, can tolerate and even grow best in environments with a pH far outside the range tolerated by eukaryotes. Such environments are rare, but occur in volcanic lakes and geothermal springs where they are

## Chapter 7

# Ecological Applications at the Level of Organisms and Single-Species Populations: Restoration, Biosecurity and Conservation

### 7.1 Introduction

environmental problems resulting from human population growth ...

The expanding human population (Figure 7.1) has created a wide variety of environmental problems. Our species is not unique in depleting and contaminating the environment but we are certainly unique in using fire, fossil

fuels and nuclear fission to provide the energy to do work. This power generation has had far-reaching consequences for the state of the land, aquatic ecosystems and the atmosphere, with

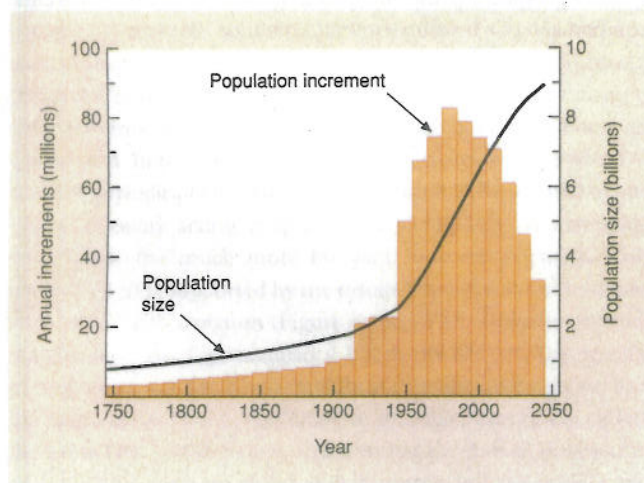


Figure 7.1 Growth in size of the world's human population since 1750 and predicted growth until 2050 (solid line). The histograms represent decadal population increments. (After United Nations, 1999.)

dramatic repercussions for global climate (see Chapter 2). Moreover, the energy generated has provided people with the power to transform landscapes (and waterscapes) through urbanization, industrial agriculture, forestry, fishing and mining. We have polluted land and water, destroyed large areas of almost all kinds of natural habitat, overexploited living resources, transported organisms around the world with negative consequences for native ecosystems, and driven a multitude of species close to extinction.

An understanding of the scope of the problems facing us, and the means to counter and solve these problems, depends absolutely on a proper grasp of ecological fundamentals. In the first section of this book we have dealt with the ecology of individual organisms, and of populations of organisms of single species (population interactions will be the subject of the second section). Here we switch attention to how this knowledge can be turned to advantage by resource managers. At the end of the second and third sections of the book we will address, in a similar manner, the application of ecological knowledge at the level of population interactions (Chapter 15) and then of communities and ecosystems (Chapter 22).

Individual organisms have a physiology that fits them to tolerate particular ranges of physicochemical conditions and dictates their need for specific resources (see Chapters 2 and 3). The occurrence and distribution of species therefore depends fundamentally on their physiological ecology and, for animals, their behavioral repertoire too. These facts of ecological life are encapsulated in the concept of the niche (see Chapter 2). We have observed that species do not occur everywhere that conditions and resources are

... require the application of ecological knowledge, ...

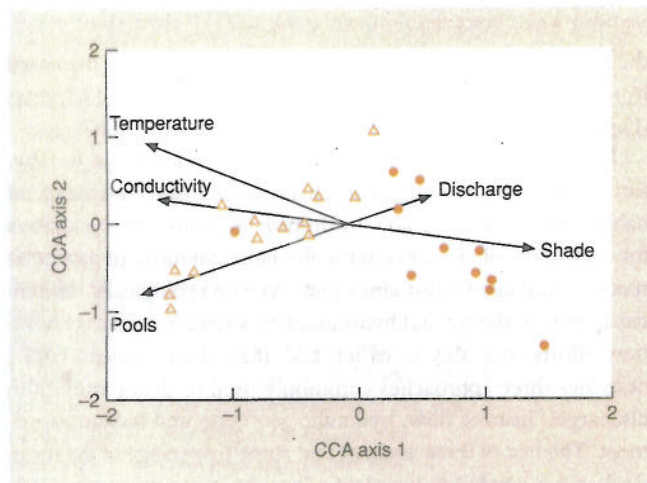
... niche theory, ...

inflection point is sometimes used as a basis for setting a minimum discharge. Finally, habitat assessment methods are based on discharges that meet specified ecological criteria, such as a critical amount of food-producing habitat for particular fish species. Managers need to beware the simplified assumptions inherent in these various approaches because, as we saw with the pikeminnows, the integrity of a river ecosystem may require something other than setting a minimum discharge, such as infrequent but high flushing discharges.

## 7.2.2 Dealing with invasions

a technique for displaying species niches . . .

It is not straightforward to visualize the multidimensional niche of a species when more than three dimensions are involved (see Chapter 2). However, a mathematical technique called *ordination* (discussed more fully in Section 16.3.2) allows us to simultaneously analyze and display species and multiple environmental variables on the same graph, the two dimensions of which combine the most important of the niche dimensions. Species with similar niches appear close together on the graph. Influential environmental factors appear as arrows indicating their direction of increase within the two dimensions of the graph. Marchetti and Moyle (2001) used an ordination method called canonical correspondence analysis to describe how a suite of fish species – 11 native and 14 invaders – are related to environmental factors at multiple sites in a regulated stream in California (Figure 7.3). It is clear that the native and invasive species occupy different parts of the niche space: most



**Figure 7.3** Plot of results of canonical correspondence analysis (first two CCA axes) showing native species of fish (●), introduced invader species (▲) and five influential environmental variables (arrows represent the correlation of the physical variables with the canonical axes). (After Marchetti & Moyle, 2001.)

of the native species occurred in places associated with higher mean discharge ( $\text{m}^3 \text{s}^{-1}$ ), good canopy cover (higher levels of percent shade), lower concentrations of plant nutrients (lower conductivity,  $\mu\text{S}$ ), cooler temperatures ( $^{\circ}\text{C}$ ) and less pool habitat in the stream (i.e. greater percent of fast flowing, shallow riffle habitat). This combination of variables reflects the natural condition of the stream.

The pattern for introduced species was generally the opposite: invaders were favored by the present combination of conditions where water regulation had reduced discharge and increased the representation of slower flowing pool habitat, riparian vegetation had been removed leading to higher stream temperatures, and nutrient concentrations had been increased by agricultural and domestic runoff. Marchetti and Moyle (2001) concluded that restoration of more natural flow regimes is needed to limit the advance of invaders and halt the continued downward decline of native fish in this part of the western USA. It should not be imagined, however, that invaders inevitably do less well in 'natural' flow regimes. Invasive brown trout (*Salmo trutta*) in New Zealand streams seem to do better in the face of high discharge events than some native galaxiid fish (Townsend, 2003).

Of the invader taxa responsible for economic losses, fish are a relatively insignificant component. Table 7.2 breaks down the tens of thousands of exotic invaders in the USA into a variety of taxonomic groups. Among these, the yellow star thistle (*Centaurea solstitialis*) is a crop weed that now dominates more than 4 million ha in California, resulting in the total loss of once productive grassland. Rats are estimated to destroy US\$19 billion of stored grains nationwide per year, as well as causing fires (by gnawing electric wires), polluting foodstuffs, spreading diseases and preying on native species. The red fire ant (*Solenopsis invicta*) kills poultry, lizards, snakes and ground-nesting birds; in Texas alone, its estimated damage to livestock, wildlife and public health is put at about \$300 million per year, and a further \$200 million is spent on control. Large populations of the zebra mussel (*Dreissena polymorpha*) threaten native mussels and other fauna, not only by reducing food and oxygen availability but by physically smothering them. The mussels also invade and clog water intake pipes, and millions of dollars need to be spent clearing them from water filtration and hydroelectric generating plants. Overall, pests of crop plants, including weeds, insects and pathogens, engender the biggest economic costs. However, imported human disease organisms, particularly HIV and influenza viruses, cost \$7.5 billion to treat and result in 40,000 deaths per year. (See Pimentel *et al.*, 2000, for further details and references.)

The alien plants of the British Isles illustrate a number of points about invaders and the niches they fill

... shows why native fish are replaced by invaders

a diversity of invaders and their economic costs

species niches and the prediction of invasion success

Table 7.2 Estimated annual costs (billions of US\$) associated with invaders in the United States. Taxonomic groups are ordered in terms of the total costs associated with them. (After Pimentel *et al.*, 2000.)

Type of organism	Number of invaders	Major culprits	Loss and damage	Control costs	Total costs
Microbes (pathogens)	> 20,000	Crop pathogens	32.1	9.1	41.2
Mammals	20	Rats and cats	37.2	NA	37.2
Plants	5,000	Crop weeds	24.4	9.7	34.1
Arthropods	4,500	Crop pests	17.6	2.4	20.0
Birds	97	Pigeons	1.9	NA	1.9
Molluscs	88	Asian clams, Zebra mussels	1.2	0.1	1.3
Fishes	138	Grass carp, etc.	1.0	NA	1.0
Reptiles, amphibians	53	Brown tree snake	0.001	0.005	0.006

NA, not available.

(Godfray & Crawley, 1998). Species whose niches encompass areas where people live and work are more likely to be transported to new regions, where they will tend to be deposited in habitats like those where they originated. Thus more invaders are found in disturbed habitats close to transport centers and fewer are found in remote mountain areas (Figure 7.4a). Moreover, more invaders arrive from nearby locations (e.g. Europe) or from remote locations whose climate (and therefore the invader's niche) matches

that found in Britain (Figure 7.4b). Note the small number of alien plants from tropical environments; these species usually lack the frost-hardiness required to survive the British winter. Shea and Chesson (2002) use the phrase *niche opportunity* to describe the potential provided in a given region for invaders to succeed – in terms of a high availability of resources and appropriate physico-chemical conditions (coupled with a lack or scarcity of natural enemies). They note that human activities often disrupt conditions

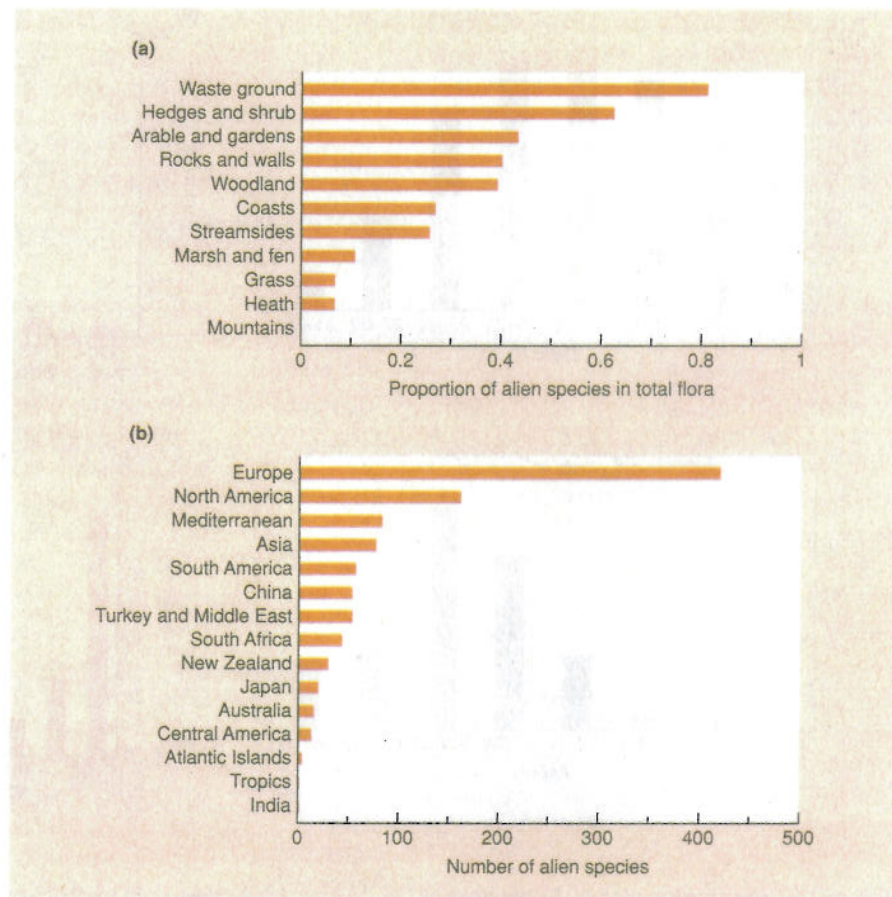


Figure 7.4 The alien flora of the British Isles: (a) according to community type (note the large number of aliens in open, disturbed habitats close to human settlements) and (b) by geographic origin (reflecting proximity, trade and climatic similarity). (After Godfray & Crawley, 1998.)



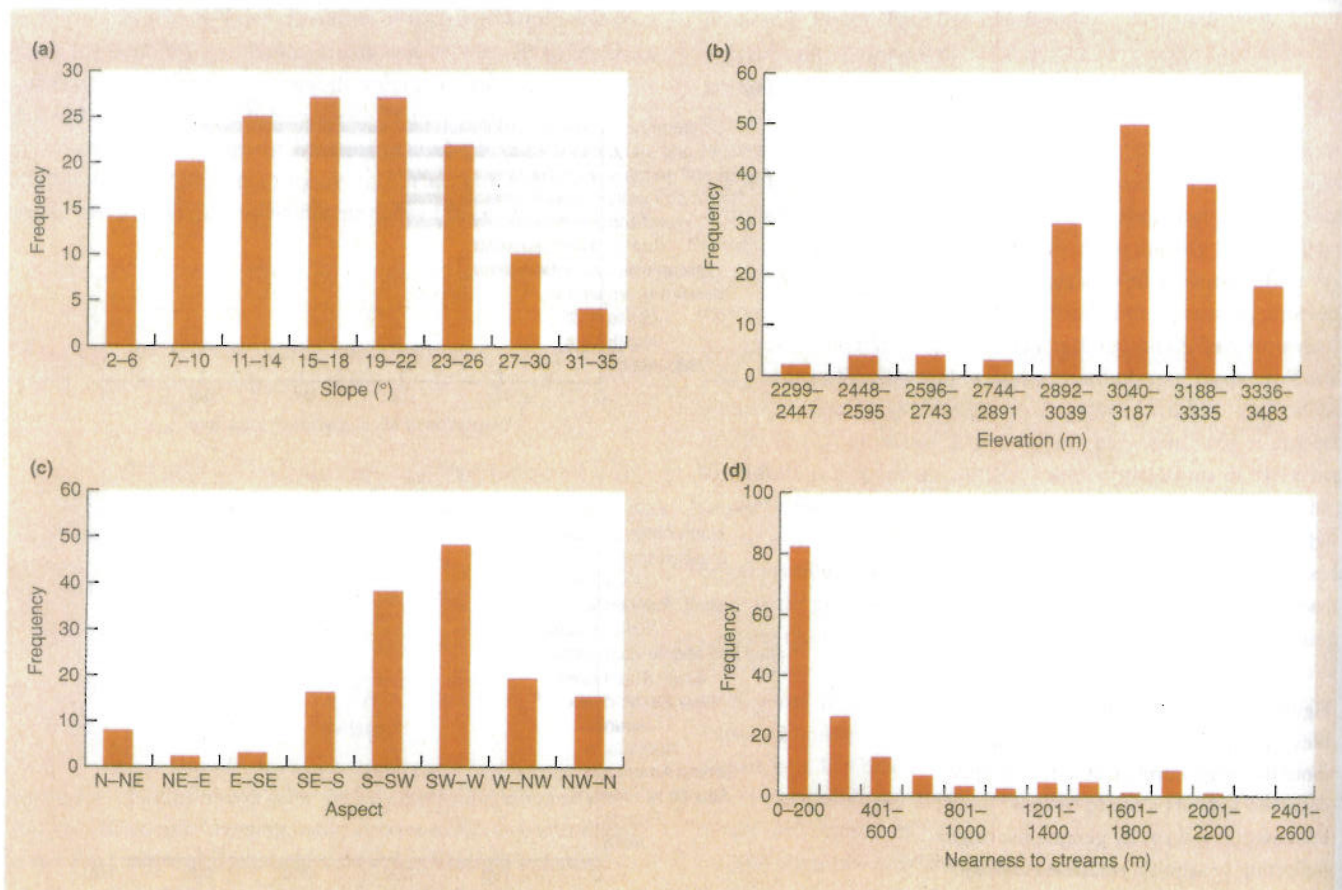
in ways that provide niche opportunities for invaders – river regulation is a case in point. Not all invaders cause obvious ecological harm or economic loss; indeed some ecologists distinguish exotic species that establish without significant consequences from those they consider ‘truly invasive’ – whose populations expand ‘explosively’ in their new environment, with significant impacts for indigenous species. Managers need to differentiate among potential new invaders both according to their likelihood of establishing should they arrive in a new region (largely dependent on their niche requirements) and in relation to the probability of having dramatic consequences in the receiving community (dealt with in Chapter 22). Management strategies to get rid of invading pests usually require an understanding of the dynamics of interacting populations and are covered in Chapter 17.

### 7.2.3 Conservation of endangered species


The conservation of species at risk often involves establishing protected areas and sometimes the translocation of individuals to new locations. Both approaches should be based on considerations of the niche requirements of the species concerned.

The overwintering habitat in Mexico is absolutely critical for the monarch butterfly (*Danaus plexippus*), which breeds in southern Canada and the eastern United States. The butterflies form dense colonies in oyamel (*Abies religiosa*) forests on 11 separate mountains in central Mexico. A group of experts was assembled to define objectives, assess and analyze the available data, and to produce alternative feasible solutions to the problem of maximizing the protection of overwintering habitat while minimizing the inclusion of valuable land for logging (Bojorquez-Tapia *et al.*, 2003). As in many areas of applied ecology, ecological and economic criteria had to be judged together. The critical dimensions of the butterfly’s overwintering niche include relatively warm and humid conditions (permitting survival and conservation of energy for the return north) and the availability of streams (resource) from which the butterflies drink on clear, hot days. The majority of known colony sites are in forests on moderately steep slopes, at high elevation (>2890 m), facing towards the south or southwest, and within 400 m of streams (Figure 7.5). According to the degree to which locations in central Mexico matched the optimal habitat features, and taking into account the desire to minimize

niche ecology and  
the selection of  
conservation reserves



**Figure 7.5** Observed frequency distributions of 149 overwintering monarch butterfly colonies in central Mexico in relation to: (a) slope, (b) elevation, (c) aspect and (d) proximity to a stream. (After Bojorquez-Tapia *et al.*, 2003.)



## 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

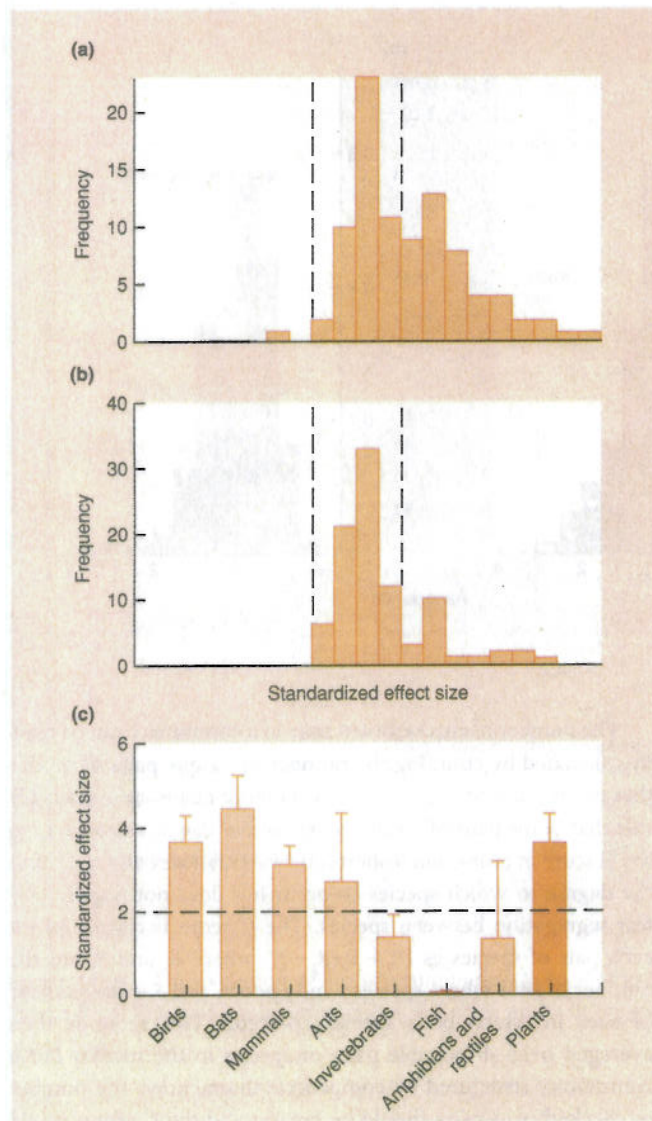
It is important to distinguish between *species richness* (the number of species present in a defined geographical unit – see Section 16.2) and *biodiversity*. The term biodiversity makes frequent appearances in both the popular media and the scientific literature – but it often does so without an unambiguous 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



**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 anemone 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.

A basic distinction can thus be made between *equilibrium* and *nonequilibrium* theories. An equilibrium theory, like the one concerned with niche differentiation,

**equilibrium and nonequilibrium theories**

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.



## 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.

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

#### the question of scale: macroecology

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.

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).

a model incorporating niche breadth, niche overlap and resource range

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).

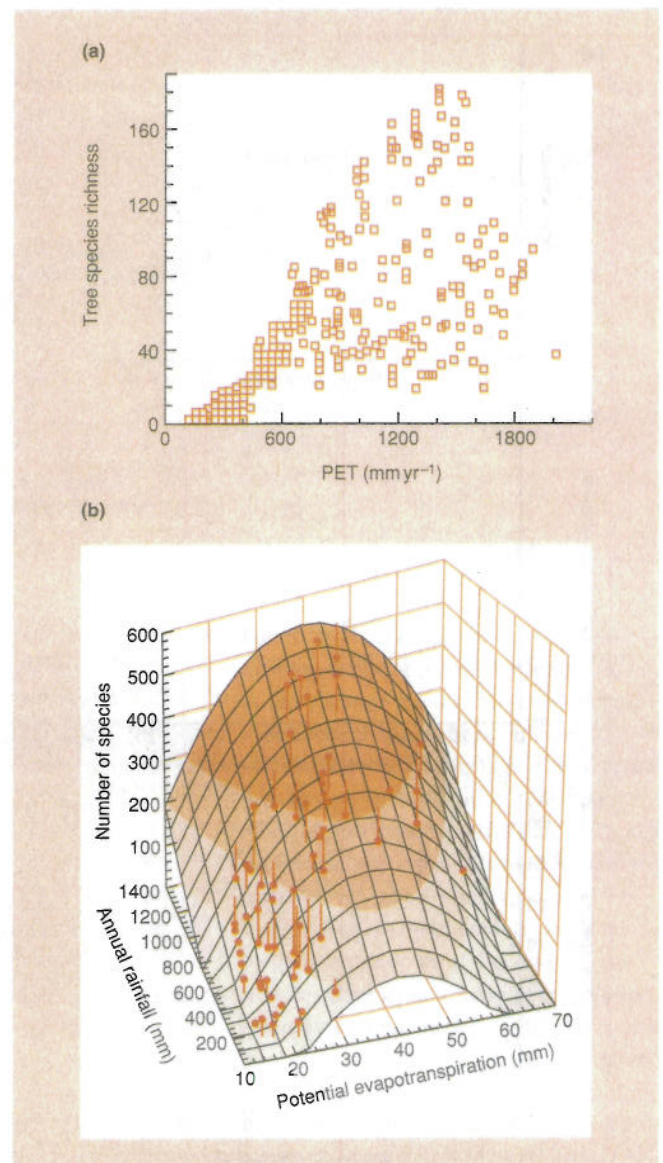
increased  
productivity might  
lead to . . .  
. . . increased  
richness . . .

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.

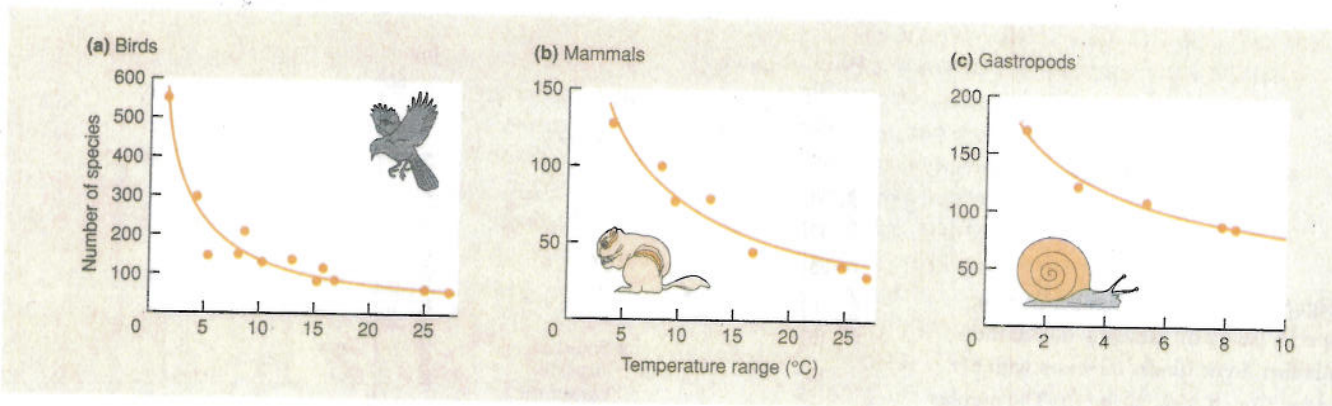
When the North American work (Figure 21.3a) was extended to four vertebrate groups, species richness was found to be correlated to some extent with tree species richness itself. However, the best correlations were consistently with PET (Figure 21.4). Why should animal species richness be positively correlated 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,



**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<sup>2</sup> 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.)

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 21.9** 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  $\delta$  is smaller, see Figure 21.1c).

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.

... but there is no good evidence either way

### 21.4.2 Environmental age: evolutionary time

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).

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

variable recovery from an ancient disturbance?

unchanging tropics and recovering temperate zones?



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