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A fundamental property of any ecosystem or habitat is the number of species it contains. Some wetlands contain large numbers of species; some contain few. Within a single wetland, there is similar variation, with some habitats being species rich and other species poor. Such patterns in diversity have long been of keen interest to ecologists (e.g. Williams 1964; Pielou 1975; May 1986; Huston 1994; Gaston 2000) and conservation biologists (Ehrlich and Ehrlich 1981; World Conservation Monitoring Centre 1992). The long-term goal of such work is to determine how many species occur in different parts of the world, and to uncover the factors that predict how many we will find in specified conditions. Since there are good reasons to fear that up to one-fourth of the world's species could disappear in the coming century, it is important to manage wild places, including wetlands, to maximize the number of native species found globally. When species are at risk of extinction – be they quill worts or tigers – managers must create and protect enough habitat to allow their populations to recover. Hence, the study and understanding of diversity occupies a central position in wetland ecology. The objective of this chapter is to survey the number wetland species found in major groups of organisms and then introduce you to some of the critical environmental factors that control them. Often only a couple of factors will determine whether a wetland supports many species or only a few.

9.1 Introduction to diversity in wetlands

Let us begin with the world as a whole. How many species of different types of wetland organisms are there? One source of comparative data is a survey of freshwater animal diversity (Lévêque *et al.* 2005) that used both published sources and museum collections (Table 9.1). The overall conclusion is that some 100 000 animal species require freshwater habitats. Of these, some 50 000 are insects; there are 21 000 vertebrate species, 10 000 crustacean species, and 5000 mollusk species. Among the vertebrates, amphibians occur solely in fresh water, with ca. 5500 species. To this list of freshwater species one would need to add species using coastal wetlands for a global total. Let us look at the diversity of three groups by way of illustration.

9.1.1 Wetlands have many species of fish

The Amazon River has more species of fish (ca. 2000) than any other river in the world, with particularly large numbers of species of characoids and siluroids (Figure 9.1). The former group includes the fruit-eating fish in the genus *Colossoma* (Figure 2.5*d*) that forage in forests during high-water periods. It also includes the carnivorous piranha. The latter group includes the many species of catfish that forage in deeper water. South America as a whole has some 5000 species (Lévêque *et al.* 2005). The next most important rivers for fish biodiversity are the Congo and the Mekong Rivers, the latter having the world's largest freshwater fish, the Mekong giant catfish.

9.1.2 Wetlands have many species of waterbirds

Wetlands often have spectacular numbers of birds. If we begin with about 9000 species of birds in the world, and then take a conservative estimate – that

Table 9.1 The species of freshwater organisms provides a pool from which wetland communities are assembled according to biogeography, physical factors, and biological interactions. There are two sources of uncertainty in these numbers: the total number of species in the groups, and, more seriously, the number of species that occur in wetlands. Note that marine species in coastal marshes are not included

Phylum	Number of freshwater species	Comments
Porifera	197	
Cnidaria	30	
Nemertea	12	
Platyhelminthes	500	
Gastrotricha	250	
Rotifera	1 817	
Nematoda	3 000	
Annelida	>1000	
Bryozoa	70–75	
Mollusca	5 000	
Arthropoda	>65 000	
Branchiopoda	>813	Particularly vernal pools
Ostracoda	3 000	Mostly benthic
Copepoda	2 085	Mostly planktonic
Malacostraca	4 165	Mostly marine
Arachnida	5 000	
Insecta	>50 000	Mainly Diptera and Trichoptera
Chordata	>21 000	
Teleostomi	13 400	
Amphibia	5 504	All but absent from marine
Reptilia	250	
Aves	1 800	
Mammalia	100	

Source: Adapted from Lévêque *et al.* (2005).

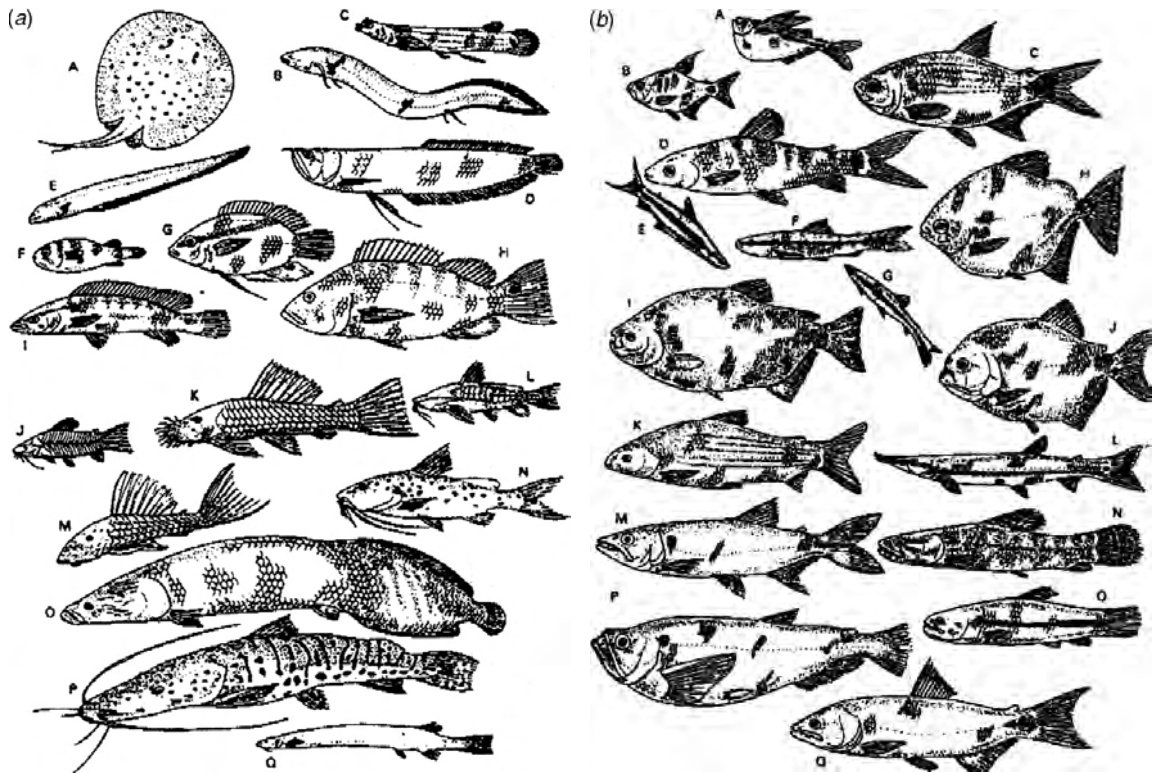


FIGURE 9.1 Some representative siluroid (a) and characoid (b) fish from the Amazon River system. (From Lowe-McConnell 1975.)

20% are wetland dependent – we arrive at an estimate that some 1800 birds may be wetland dependent. Wading birds are one obvious group, as are ducks and kingfishers (Lévêque *et al.* 2005). The Ramsar Convention (The Convention on Wetlands of International Importance; see Section 14.4.3) defines “waterfowl” as species of birds that are “ecologically dependent upon wetlands” and it uses the term “waterbird” as being synonymous with “waterfowl” for the purposes of the application of the Convention (Delany and Scott 2006). According to the fourth edition of *Waterbird Population Estimates* (Delany and Scott 2006), there are 878 waterbird species in 33 families occurring in 2305 biogeographic populations. The largest number of waterbird populations (815) is found in Asia, followed by the Neotropics (554)

and Africa (542). Fewer waterbird populations are found in Oceania (390), North America (384), and Europe (351) (global total does not equal regional population sum because populations are often distributed over more than one region). Data on species trends are not available for about 20% of these populations. About 1% of the populations are extinct, while about one-fourth show a decreasing trend. Oceania is an exception, with 7% extinct, and only 12% decreasing – but Oceania also lacks data on 57% of the species.

At the local scale, the number of birds encountered will often depend upon the amount of forested wetland. In North American wetlands, higher numbers of species occur in riparian forests, swamps, and shrub-dominated wetlands (Figure 9.2).

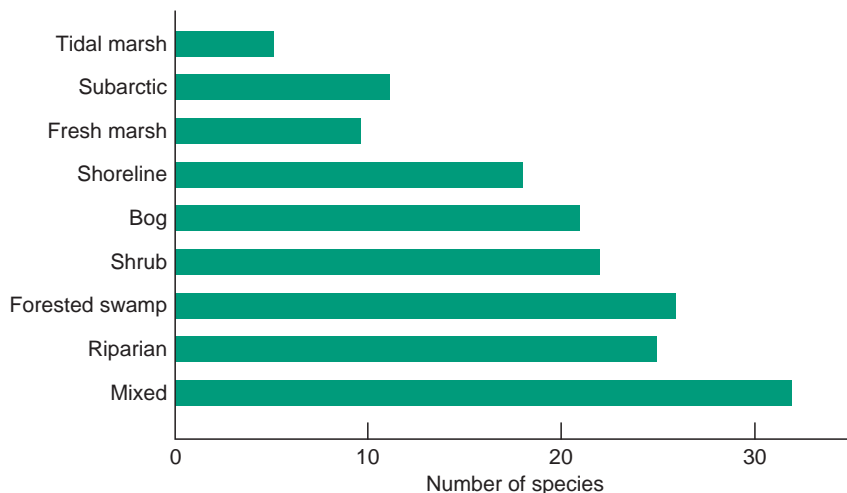


FIGURE 9.2 Median number of species of birds occupying different wetland vegetation types in North America. (After Adamus 1992.)

9.1.3 Most mammals use wetlands occasionally

Only about 100 mammal species have an obligate dependence on wetlands (Lévêque *et al.* 2005), with common examples including nutria, muskrats, beavers, and otters. Some are among the smallest mammals – there are four water-dependent shrews (genus *Sorex*) in North America and ten species in Europe and Asia. Some are also among the largest mammals – the hippopotamus (*Hippopotamus amphibius*) occurs only in Africa as does the pygmy hippopotamus (*Hexaprotodon liberiensis*). There are also semi-aquatic ungulates, the sitatunga (*Tragelaphus spekei*) in Africa, the marsh deer (*Blastocerus dichotomus*) in South America, and the water buffalo (*Bubalus bubalis*) in Asia. The unusual mammal, the duck-billed platypus, an aquatic but

egg-laying species, occurs only in Australia. Many other mammals use wetlands seasonally. More than 120 species of mammals have been recorded from the Pantanal (South America) and the Okavango delta (Africa) (Junk *et al.* 2006). The Sundarbans, part of the Ganges/Brahmaputra River delta, are said to be the largest piece of estuarine mangrove forest in the world. This area is probably best known, however, for supporting the world's largest remaining population of Bengal tigers (Junk *et al.* 2006). The Mississippi River wetlands provide important habitat for large carnivores including the panther and Louisiana black bear (Keddy *et al.* 2009b). In many savanna areas, wetlands provide places of refuge for large herds of mammals during periods of drought (Sinclair 1983; Sinclair and Fryxell 1985). Including these species would considerably lengthen the list of wetland-dependent mammals.

9.2 Four general rules govern the number of species in wetlands

There are some broad general rules that we can build upon – rules that might have been called laws if ecology was as old as physics. Four general rules summarize nearly 200 years of research on the topic (Williams 1964; Pielou 1975; Huston 1994; Rosenzweig 1995). Later in this chapter I will add a few more that are more recent.

9.2.1 The number of species decreases with increasing latitude

The number of species at low latitudes greatly exceeds the number at higher latitudes. This pattern became obvious during the 1800s as global explorers including Wallace, von Humboldt, and even Darwin

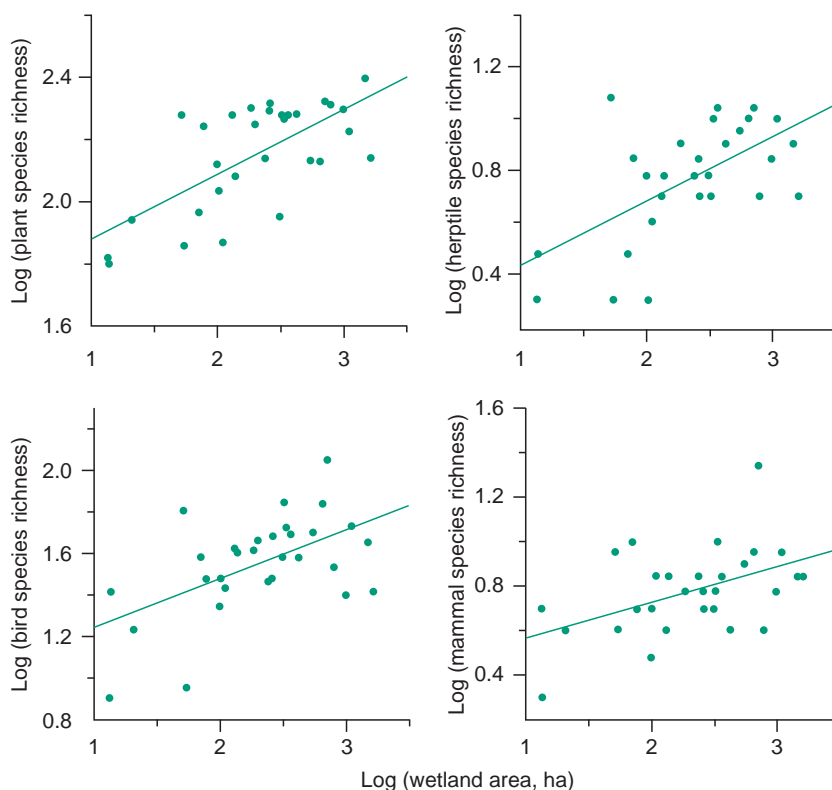


FIGURE 9.3 The relationship between species richness and area for birds, mammals, herpetiles, and plants in southeastern Ontario wetlands. (From Findlay and Houlihan 1997.)

reported on the immense number of new species observed in equatorial regions (Edmonds 1997). While the causes of this latitudinal pattern remain unclear (Rosenzweig 1995; Gaston 2000), it is widespread and well documented, although there may be exceptions within certain restricted groups of species or habitats.

Tropical wetlands therefore have more species than temperate wetlands. The Amazon, for example, has more than 1000 species of flood-tolerant trees, whereas the Mississippi River wetlands have about 100 and the peatlands of northern Canada have about ten (Junk *et al.* 2006). Similar patterns occur with most other groups of organisms.

9.2.2 The number of species increases with area

The relationship between species and area sampled can be quantified as

$$S = cA^z$$

where S is the number of species, A is the area, and c and z are constants. This exponential relationship is conveniently turned into a linear one by taking logarithms of both sides:

$$\log S = \log c + z \log A,$$

in which case the constant ($\log c$) represents the intercept of the line and the slope is given by z . This relationship was first quantified using plant species in England (Arrhenius 1921; Williams 1964) and has now been documented for many kinds of plant and animal species (Connor and McCoy 1979; Rosenzweig 1995). In a similar way, the number of species found usually decreases with the isolation of the location (Darlington 1957; MacArthur and Wilson 1967).

This pattern has been shown in wetlands for major groups including plants, reptiles and amphibians, birds, and mammals (Figure 9.3). Similarly, the

Table 9.2 The slope (z) of the species–area relationship $S = cA^z$ for various biota	
Biota	z
Aquatic plants in Adirondack lakes	0.225
Aquatic plants in Danish ponds	0.289
(two districts)	0.266
Fish in Ontario lakes	0.20
Fish in Wisconsin lakes	0.29
Fish in New York lakes	0.24
Mollusks	0.23
Various studies (n = 90)	0.31
Source: After Weiher and Boylen (1994).	

number of fish is related to lake size (Gaston 2000). This has important implications for the design of protected areas – generally, the larger the area protected, the more species the area will support. This is one reason that it is important to protect the world’s largest wetlands (Table 1.3).

Weiher and Boylen (1994) compared an array of published studies from aquatic habitats using the standard regression model $S = cA^z$ (Table 9.2). All slopes fell between 0.20 (fish in Ontario lakes) and 0.29 (aquatic plants in Danish ponds), and were generally lower than those of 90 other studies reviewed by Connor and McCoy (1979). Weiher and Boylen suggest that the lower slopes in lakes may be a result of smaller species pools for freshwater organisms. This first estimate of ca. 0.25 is a useful reference point for other studies.

9.2.3 The number of species increases with topographical variation

In any given area of landscape, the greater the range of elevation, the more different kinds of species there will be. That is, mountainous areas have more species than flat areas. Thus the Andes have more species than any other region in the world. Wetlands tend to be flat, except in the notable cases

of blanket bogs and seepage areas on hillsides. If topography generates diversity, why would wetlands have many species? Is this a contradiction? Perhaps – but flooding creates many subtly different moisture regimes, and each moisture regime also has a characteristic set of species (Figure 9.4). Indeed, studies of zoned communities in the next chapter will show how even minor changes in water affect the distribution of species. A few centimeters of water in a floodplain may simply be the equivalent of many meters of elevation on a mountainside (Nilsson and Wilson 1991). Figures 2.11 and 2.12 also illustrate how many species can occupy a small area of wetland by occupying slightly different water levels.

9.2.4 A few species dominate most samples

In any sample, a few species are common, and many are uncommon. The pattern is obvious to anyone who has spent time looking for wild creatures. At first one finds many new species, but once the common species have been identified, much more time is required to find each new species. Even sorting a grab sample of mud from the bottom of a pond will reveal this phenomenon. In spite of the fact that this pattern is found nearly everywhere, its causes are not yet understood. However, it is a useful general rule. A common way of showing this pattern is the rank–abundance drawing, in which one orders species left to right in order of abundance, and then shows the abundance of each species on the vertical axis. There are many measures of abundance – biomass, number of individuals, cover, frequency, or some combination of these that we might call simply importance. The steeper the curve, the more a few species dominate the sample. Figure 9.5 shows 14 examples of such curves – note that the steepest curve is from a cattail marsh where there are only five species present. Contrast this with the curve immediately to the right from freshwater tidal wetlands – although again there are a few dominant species, there are many more less-common ones.



FIGURE 9.4 Differences in elevation produce much of the diversity found in wetlands, as illustrated by this example of zonation. (See also color plate.)

This pattern of dominance occurs across many scales. At the largest scale it is known as the canonical pattern (Preston 1962a, b; Pielou 1975; May 1981, 1986). At the local scale it is known as the “law of frequency” (Raunkiaer 1908; McGeoch and Gaston 2002; Clark *et al.* 2008). Within a single sample the pattern is generally illustrated with a ranked abundance list or dominance–diversity curve shown above (Peet 1974).

There is no perfect way to describe the dominance and diversity patterns in a group of species. Here are some options. You can simply list all the species – but that ignores the fact that some are much more common than others. You can simply count the number of species – the number you get is often called species richness – but this number says nothing about what kinds of species you found. (There are a confusing number of

names for this property, including species richness, species density, and alpha diversity. Where possible I have used species richness but be aware that other sources may not.) You can prepare a dominance–diversity curve – but some audiences will have trouble interpreting it. You can fit lines to the dominance–diversity curves and describe the equations (e.g. Wilson *et al.* 1996), which is a good deal of work and certainly beyond most audiences. You can calculate a single number called diversity that summarizes the relative abundances of all the species. Formulae for calculating two of these diversity indices are shown below.

The formula for Simpson’s diversity index is:

$$C = \sum_{i=1}^S (p_i)^2$$

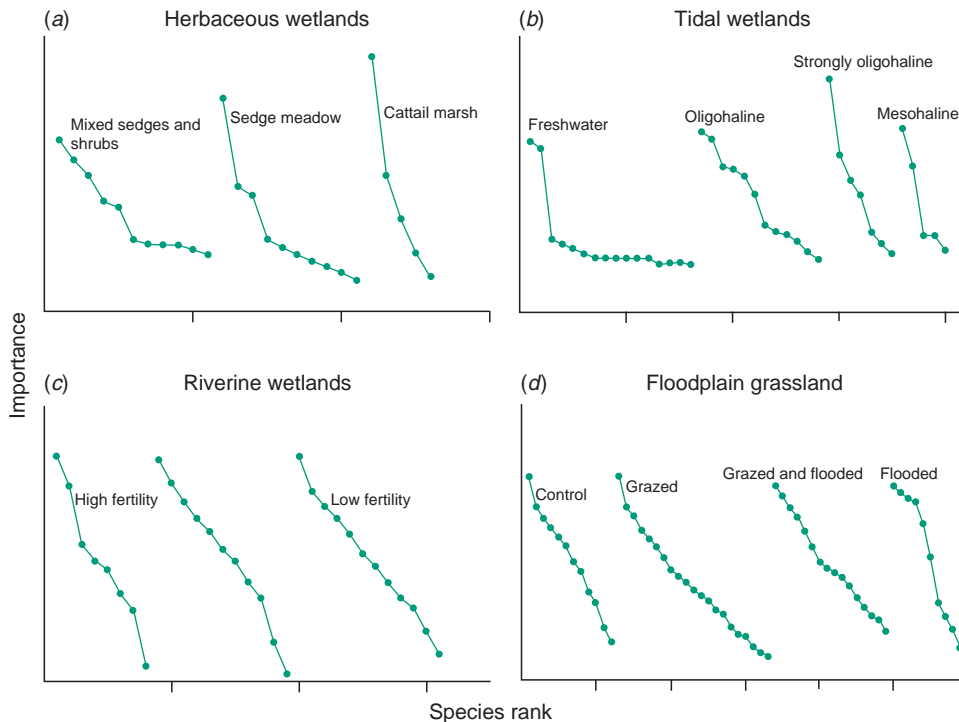


FIGURE 9.5 Ranked abundance lists (dominance–diversity curves) for four different wetlands: (a) herbaceous (after Gosselink and Turner 1978), (b) tidal (after Latham *et al.* 1994), (c) riverine (after Weiher and Keddy 1995), and (d) floodplain grassland (after Chaneton and Facelli 1991).

The formula for the Shannon–Weaver (Shannon–Wiener) diversity index is:

$$H' = - \sum_{i=1}^S (p_i)(\ln p_i)$$

where C and H' are index numbers, s is the total number of species in the sample, and p_i is the proportion of all individuals in the sample that belong to species i .

While it is nice to have a single number (and it is often used, see for example Figures 3.6 and 4.7), a single number also hides much of the information.

As I said, there is no perfect solution. You can read more about measuring diversity elsewhere (e.g. Peet 1974; Pielou 1975). In this book, I have tended to prefer the simplest data – number of species, or species richness (the terms are interchangeable), but have included some data on diversity for completeness.

In spite of the problems with measuring diversity, we are left with a useful general rule – nearly everywhere you go, a few species monopolize the habitat. Dominance is the rule and hence a majority of species are relatively uncommon or even rare.

9.3 Selected examples

The preceding section introduced four general principles. Now let us take a closer look at how they apply in selected groups of

species and selected locations. We will also look for other rules that apply to specific groups or locations.

9.3.1 Factors affecting the number of species of fish

At large geographic scales, climate, salinity and area are predominant factors. “Of the 20,000 recent fish species known to science, over 40 per cent live in freshwaters, and the majority of these live ... within the tropics ...” (Lowe-McConnell 1975, p. 4). The three rivers with the largest fish faunas are the Amazon, Congo, and Mekong Rivers. Each has large areas of wetland. In rivers, the number of fish species is closely related to the area of the river basin (World Conservation Monitoring Centre 1992).

A similar but weaker relationship is found with lake area (Barbour and Brown 1974; Gaston 2000).

In African rivers, river basin area predicts the number of fish species according to the following formula (Welcomme 1979, 1986):

$$S = 0.449A^{0.434}.$$

The Niger River, has, for example, 160 species (the above equation predicts 190). This relationship does not apply to other continents, since similar-sized rivers in South America (e.g. Parana, Orinoco Rivers) have about 370 species and in Asia, the Mekong has some 600.

Returning to the Amazon, something more needs to be said about this fish fauna, the largest in the world. Lowe-McConnell (1987) notes that many of its 1000 tributaries have yet to be surveyed. The majority of the described species are characoids and siluroids. The characoids are mostly laterally compressed, silvery, open-water fish that are active by day. They have undergone spectacular adaptive radiation, include both the fruit-eating *Colossoma* and carnivorous piranha, and are probably “one of the most diverse groups of living vertebrates” (Lowe-McConnell 1975, p. 38). The siluroids (“catfish”), by contrast, are mostly bottom-living and nocturnal. They include piscivores, planktivores, and even parasites. Apart from the characoids and siluroids, the other notable group are the gymnotoids, the nocturnal electrogenic fish. They use electric signals

to sense the environment and communicate with each other, and the electric eel, in addition, uses electricity to defend itself and capture prey.

Perhaps the most unusual group is the fruit-eating characoids, which live in flooded forests and feed upon fruits and seeds (Goulding 1980). This group vividly illustrates the theme of Chapter 2 – that water levels change greatly with season and year. Many of these species, such as *Colossoma*, are commercially important; this species comprised nearly half the 31 000 t landed at Manaus in 1976. It is captured throughout the year with gill nets in flooded forest.

At more local scales, but still within the Amazon, up to 50 species can occur in one water body, although only a subset of these will be common, for as with most other groups, a few species dominate each sample (Lowe-McConnell 1987). There is also turnover along habitat gradients; the fast-flowing Andean streams have a specialized fauna of algal-grazing catfish, whereas the estuarine reaches have largely marine species. Lowe-McConnell also suggests that an added component of diversity can be attributed to the use of forest foods, since this increases both the volume and array of food relative to rivers in which plankton are the main source of primary production.

Leaving the Amazon, and the tropics, for temperate zone lakes, Table 9.3 shows that even at the relatively local scale of 18 small lakes, species richness increases with lake area. Beyond this, the table shows that fish species richness in the summer was significantly related to lake pH ($r = 0.70$) and vegetation structure ($r = 0.69$). Within smaller bog pond lakes, vegetation diversity accounted for more than half of the variation in the summer ($r = 0.84$), but the patterns disappeared during the winter. In larger lakes with cetrachids, winter oxygen and depth were the best predictors ($r = 0.59$), and in the small bog ponds with cyprinids, substrate type and vegetation together were the only significant predictors of the number of fish species.

Table 9.3 Factors predicting species richness of fish in Wisconsin lakes

	Summer				Winter			
	$y = a + bx$				$y = a + bx$			
Independent variable	r		a	b	r		a	b
All lakes ($n = 18$)								
1. Log (lake area)	0.69	*	1.86	3.50	−0.08	NS	3.14	−0.26
2. Log (maximum depth)	−0.47	*	8.25	−5.50	0.04	NS	2.69	0.34
3. Log (connectedness + 1)	0.60	*	3.58	1.96	−0.30	NS	3.64	−0.67
4. Log (alkalinity)	0.66	*	1.58	3.87	−0.02	NS	2.94	−0.09
5. Log (conductivity)	0.60	*	−7.70	7.20	−0.06	NS	3.82	−0.52
6. pH	0.70	*	−9.98	2.39	0.14	NS	0.58	0.34
7. Log (total dissolved solids)	0.42	NS	−0.58	3.95	−0.07	NS	3.59	−0.45
8. Log (winter oxygen + 1)	−0.42	NS	7.48	−2.83	0.02	NS	2.78	0.11
9. Substrate diversity	−0.08	NS	6.48	−0.66	−0.27	NS	4.04	−1.48
10. Vegetation diversity	0.69	*	2.66	3.93	0.00	NS	2.83	0.00
11. Depth diversity	−0.12	NS	7.33	−1.61	0.19	NS	1.36	1.72
12. Depth and substrate	0.08	NS	4.92	0.72	−0.02	NS	2.98	−0.10
13. Depth and vegetation	0.58	*	−0.47	4.22	0.07	NS	2.30	0.35
14. Substrate and vegetation	0.50	*	0.73	3.67	−0.16	NS	3.98	−0.81
15. Depth, substrate, and vegetation	0.57	*	−2.16	4.25	−0.08	NS	3.58	−0.39

Notes: Correlation coefficients (r , * = $p \leq 0.05$) and linear regressions for summer and winter species richness (y) vs. each of 15 environmental factors (x). Multiple regressions most closely predicting species richness are as follows: summer richness = $3.75 + 4.56 \log \text{area} - 3.84 \text{ substrate diversity}$ ($r^2 = 0.67$, $p \leq 0.05$); winter richness = $-3.15 + 1.14 \text{ pH} - 1.30 \log (\text{connectedness} + 1)$ ($r^2 = 0.24$, $p > 0.05$).

Source: From Tonn and Magnuson (1982).

9.3.2 Factors affecting the number of insects

Determining the number of species of aquatic invertebrates in a wetland is an identification challenge (or perhaps nightmare), since some aquatic larvae can be identified only to genus or order. And, remember, the insects comprise only one small group of aquatic invertebrates. About 2% of insects have aquatic stages, for a total of 50 000 freshwater species worldwide. The dominant groups include the Diptera (flies, more than 20 000 species), Trichoptera (caddis flies, more than 10 000 species), Coleoptera (beetles, more than 6000 species), and Odonata (dragonflies and damselflies, 5500 species). Hence,

diversity is sometimes measured only as the number of genera, which, of course, significantly underestimates the species diversity. Recall, as but one example, that Tarr *et al.* (2005) collected a total of 6202 aquatic invertebrates, which represented 47 genera, with a mean of more than 10 genera per wetland – and these were only large and predatory species. Thus the number of genera of invertebrates in a wetland is usually much greater than the number of species of amphibians, birds, or fish. This is one reason that the invertebrates are poorly known.

Hydroperiod as a key factor. In a set of 42 wetlands in New Hampshire (Tarr *et al.* 2005), the number of genera increased with the length of the hydroperiod

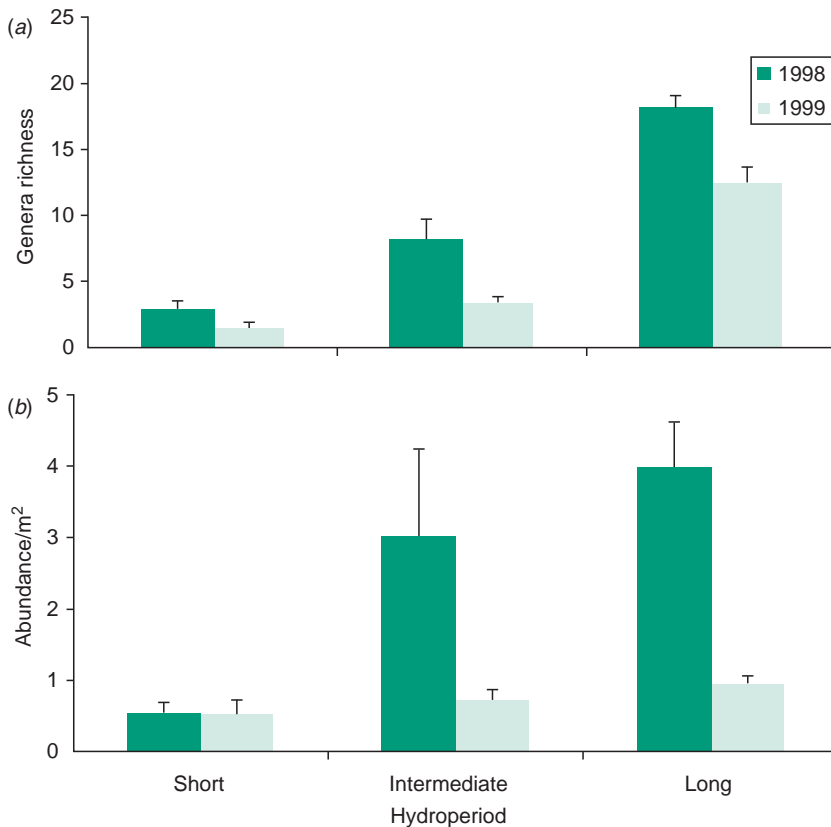


FIGURE 9.6 The number of genera (a) and the overall abundance of predatory macroinvertebrates (b) increases with hydroperiod, from ephemeral ponds (left) to permanent ponds (right). (After Tarr *et al.* 2005.)

(Figure 9.6). Short hydroperiod wetlands had few genera and relatively low abundance of those genera; the dominant genus was *Acilius*, predatory diving beetles. Other groups like *Notonecta* and *Libellula* were largely restricted to and dominated the long hydroperiod wetlands.

The presence of predatory fish species did not significantly influence invertebrate genera richness but did significantly reduce the abundance of invertebrates in the permanent wetlands. The fish also were associated with distinctive invertebrate communities. *Libellula*, *Leucorrhinia*, and *Notonecta* were more likely to occur in wetlands without predatory fish. *Buena*, *Basiaesha*, and *Hydaticus* were more likely to occur in wetlands with predatory fish. Since the presence of fish has a major impact upon amphibians and invertebrates, one should be

cautious about introducing fish to ponds that do not have them. (The many “helpful” people who want to stock goldfish in ponds seem remarkably unaware of the impacts on frogs and invertebrates, or about what will happen if these fish escape into a nearby lake or river, where they can grow to 33 cm in length.)

In coastal areas, hydroperiod is often connected to salinity, particularly in warmer climates where water in pools evaporates and can lead to hypersaline conditions. In the Camargue, the south-flowing Rhone River supplies fresh water to coastal wetlands. The major factors affecting the composition of invertebrates are therefore salinity and hydroperiod (Figure 8.11).

As an aside, students and teachers may find keeping an aquarium with invertebrates to be an enjoyable and educational experience. The diversity of life history types and species that can be found in

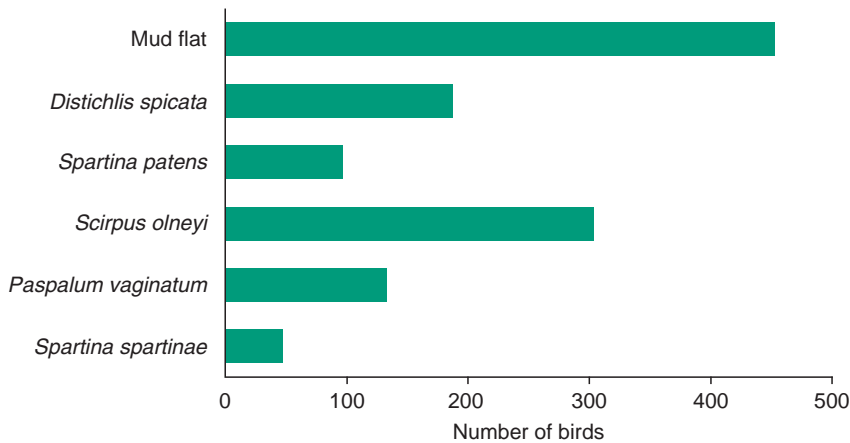


FIGURE 9.7 The number of common birds observed in six vegetation zones along the Texas coast. (From data in Weller 1994b.)

even a small sample of pond mud is remarkable, and the aquarium does not require a great deal of care. Clegg, author of a popular guide to pond life (Clegg 1986) notes that building small ponds is suitable for private gardeners and for schools. Britain, for example, has 44 species of damselflies and dragonflies, and since they can usually be identified with binoculars, they provide a sport equivalent in interest to birdwatching. At one time, wetland managers had to manage wetlands mainly for hunting and fishing. The goal was easy to count: number of ducks, number of pelts, number of fish. The large and growing group of non-consumptive users has shifted the emphasis toward other species including birds and amphibians, and to wildlife viewing rather than killing. The European experience, and the proliferation of field guides to groups like dragonflies (Clegg 1986, Mead 2003) suggests that wetland managers will soon not only have to maintain wetlands for ducks, or for birds and amphibians, but also for other species such as dragonflies and diving beetles. If citizen scientists can be used to monitor species such as dragonflies, the data may provide very sensitive indicators of changes occurring in wetlands.

9.3.3 Factors affecting the number of species of waterbirds

As with fish, amphibians, and reptiles, the bird fauna of the tropics is richer than that of other regions,

with some 85% of all species or subspecies being tropical (Darlington 1957). The number of waterbird populations also varies by geographic region with Asia having almost twice as many as each of the other five regions (Africa, Europe, Oceania, Neotropics, North America; see Section 9.1.2) of the world (Delany and Scott 2006).

At the much smaller scale, the number of birds changes with the type of wetland. Along the coast, salinity is always likely to be an important consideration. Many birds use coastal marshes during migration, and the number of bird species changes among the vegetation types, *Scirpus olneyi* marshes having more species and individuals than other vegetation zones (Figure 9.7). Largely unvegetated mud flats, however, had both the highest number of individuals and species of birds; this is the favored location for shorebirds to forage for invertebrates. This might lead us to suspect that the total number of bird species in a wetland will correspond rather well with the number of vegetation types. This seems to be generally true if the vegetation types also differ in physical structure, less so if the changes are merely in plant species composition. Further, the physical structure appears to have both a vertical and horizontal component. The vertical component refers to structural complexity of the plants, more structural complexity usually generating increased bird diversity (e.g. MacArthur and MacArthur 1961; Huston 1994), in which case

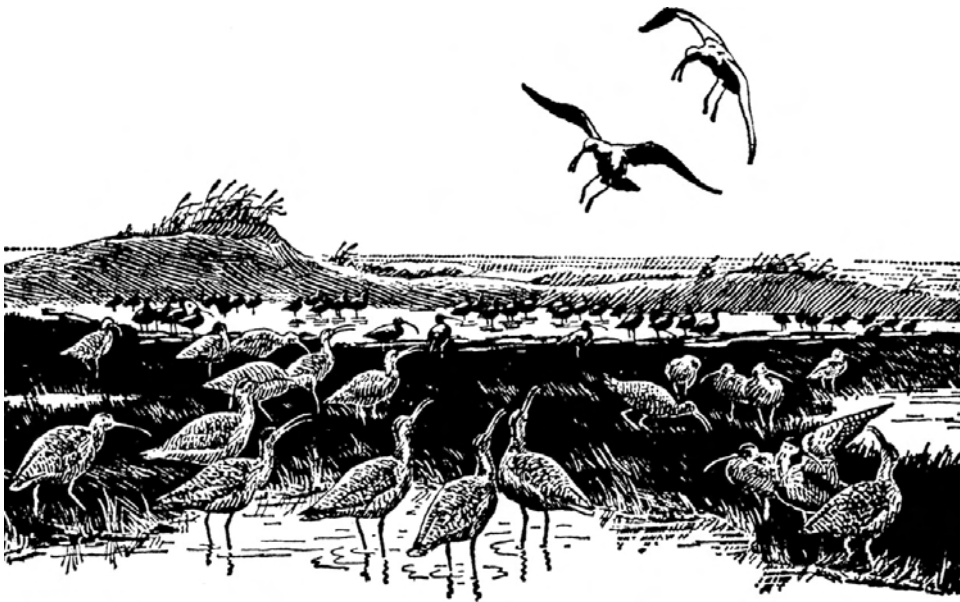


FIGURE 9.8 Although Eskimo curlew were abundant in 1870, it is highly unlikely that anyone reading this book will see one. After market hunters had exterminated the passenger pigeon, they moved on to the Eskimo curlew. (Illustration by T. M. Shortt, from Bodsworth 1963.)

forested wetlands will generally have more species of birds than herbaceous wetlands. Census reports of breeding birds confirm this: forested riparian wetlands have a median of 25 bird species whereas freshwater marshes have only 9.5 (Adamus 1992). The horizontal component of structural diversity refers to the patchiness of habitat. Wetlands with patches of vegetation interspersed with patches of open water are most desirable for waterfowl (e.g. Weller 1978; Kaminski and Prince 1981; Ball and Nudds 1989). The breeding bird census data from Adamus illustrate this horizontal component; vegetation types reported as “mixed” had a median of 32 bird species, the highest number of species reported (Figure 9.2).

Waterbird populations change with time owing to a combination of factors including precipitation, breeding habitat, over-wintering habitat, and hunting pressure. There is as yet no consensus on the relative importance of these factors. Certainly, the cases of outright extinction can often be attributed

to the primary force of over-hunting combined with secondary effects of habitat destruction. Two examples:

The *Labrador duck* once nested in the Canadian Maritimes, and was even painted by artists like Audubon; the last individual was shot on Grand Manan Island, New Brunswick, in April 1871. “The most plausible explanation of its passing seems to be that the already small numbers were singly unable to withstand persecution by man, particularly on its restricted breeding grounds” (Godfrey 1966, p. 74).

The *Eskimo curlew* (Figure 9.8) once numbered in the millions, nesting in northern Canadian wetlands and wintering in South American coastal marshes. After the extinction of the passenger pigeons, sport and market hunters turned to shooting curlews, which were highly valued for their taste. Between 1870 and 1890, they were all but exterminated. “Migrating in flocks, often large ones, numbers could often be killed with a single

shotgun blast. Sometimes the confused and decimated flocks returned to the decoys only to receive another barrage ...” (Godfrey 1966, p. 145). Curlews “were marketed in all eastern cities, and it was not unusual for twenty-five or thirty hunters to bring in as many as 2,000 curlews in a single day” (Johnsgard 1980). Combined with this onslaught was the clearing of North American prairies used during the migration northward. One of the last known Eskimo curlews was shot on Montauk Point on Long Island on September 16, 1932 by Robert Cushman Murphy. A few were seen reliably near Galveston in the 1960s, and one was killed on Barbados in 1964. They are now assumed to be extinct, although occasional reports of sightings persist. The death in Barbados in 1964? Remarkably, in spite of their toll, these archaic hunting practices continue in Barbados. Tens of thousands of shorebirds are shot each year on artificial lakes using lures, caged birds, and amplified bird calls.

9.3.4 Factors affecting the number of species of amphibians

There are 5504 species of amphibians in the world, all of them restricted to fresh water. This includes 4837 Anura (frogs and toads), 502 Caudata (newts and salamanders), and 165 Gymnophiona (caecilians) (Lévêque *et al.* 2005). Since amphibians have moist, permeable skin, and eggs and larvae that are sensitive to desiccation, environmental factors related to moisture should be important predictors of abundance (Darlington 1957) and, at least at large geographical scales, the number of amphibians is strongly related to temperature (Arnold 1972; Gaston 2000). For example, compare two North American studies – 22 ponds having 25 species of amphibians (Snodgrass *et al.* 2000) and 36 ponds having 14 species (Werner *et al.* 2007) – with one reserve in Ecuador combining floodplain and forest which had 75 species of amphibians (Pearman 1997). Other studies have found that species composition

and richness change with precipitation, soil moisture, altitude, and forest structure (Guyer and Bailey 1993; Pearman 1997). Overall, there are several generalizations that emerge.

Larger areas generally support more species (Findlay and Houlihan 1997), although in one set of small ponds on the coastal plain (most less than 10 ha) this pattern did not occur and hydrology was more important (Snodgrass *et al.* 2000). The latter authors also showed that the smallest ponds can have species not found in other ponds.

Longer periods of standing water will often increase diversity (Pechmann *et al.* 1989; Snodgrass *et al.* 2000; Werner *et al.* 2007), so long as predation by fish does not become a factor (Wilbur 1984). Fish populations have a negative effect on the number of species found (Snodgrass *et al.* 2000) as they can eat the eggs, young, and adults. If the fish are eliminated, the number of amphibian species starts to increase again (Werner *et al.* 2007). Predatory insects like diving beetles may also be more common in permanent water bodies (Tarr *et al.* 2005). For some species, short periods of standing water ensure that fish do not occur, but then there is the risk of death by desiccation before emergence – recall the example of the gopher frog.

Forest cover in the surrounding landscape has strong positive effects (Findlay and Houlihan 1997). One of the important reasons for this relationship is the number of amphibian species, from mole salamanders to tree frogs, that over-winter under logs or in trees. In Ecuador, both the richness of amphibians, and the proportion of *Eleutherodactylus* frogs (those that produce young adults from eggs) declined near pastures (Pearman 1997). Forest cover of a pond itself is likely to reduce amphibian diversity (Werner *et al.* 2007). Recall that the index of biotic integrity for streams is also positively correlated with forest cover (recall Figure 7.17). Recall too from Section 8.2 that roads and urbanization have a strong negative effect on amphibians.

9.3.5 Factors affecting the number of species of mussels

Riparian wetlands often contain clear streams with gravel and sand bottoms. These can provide habitat for invertebrates including freshwater mussels. There are estimated to be 840 species of freshwater mussels in the world (Graf and Cummings 2007) with the largest numbers in the Nearctic (302 species) and the Neotropics (172 species). Many are at risk from changes to the freshwater environment. The list of endangered species in the United States, for example, had 62 species of mussels in 2008. Different species of mussels use different sizes of streams and different substrate types, from mud through to gravel. Hence the flow rates and sedimentation rates are critical. Both of these are strongly affected by wetlands. Since mussels disperse by attaching to fish during their glochidial life stage, the presence of a healthy population of the host fish species is also necessary.

Consider one example. The Louisiana pearlshell (*Margaritifera hembeli*), about 10 cm long, is known from only 24 populations in Rapides and Grant Parishes of Louisiana where it occupies sand and gravel bottoms in flowing water. In some habitats, they reach densities of 300/m², and an age of 75 years (Johnson and Brown 1998). It is considered “threatened” by the U.S. Fish and Wildlife Service (1989) and “critically endangered” by the IUCN (Bogan 1996). The host species, brown madtom (*Noturus phaeus*), is widespread. The principal factors that damage mussel populations are changes in water quality, particularly increases in sedimentation. The Louisiana pearlshell populations occur in Kisatchie National Forest, where they are at risk from sedimentation associated with both logging and grazing. Nearby mining is also producing sediment. Beavers can also negatively affect mussels by impounding streams. The growing use of all-terrain vehicles is a further threat to these species, both from the direct impacts of being crushed by vehicles driving through shallow water, and from the

resulting erosion. This one species illustrates how careful management of riparian zones will be critical for the long-term survival of many mussel species, and adds to the list of species negatively affected by roads.

9.3.6 Factors affecting the number of species of plants in freshwater wetlands

Latitude has unexpected patterns. Since it is well documented that the number of species in most groups of organisms including fish, amphibians, birds, and mammals increases with decreasing latitude (Gaston 2000), we would expect the same pattern in plants. In terrestrial plants, this is indeed what we find. For example the average 0.1-ha plot of lowland neotropical forests has from 53 to 265 species, whereas equivalent areas of temperate forest have some 20 to 26 plant species (Grubb 1987; Gentry 1988). Similarly, while Costa Rica has a flora of some 8000 to 10 000 species, the Carolinas, which are four times as large, have a vascular flora of only 3360 (Radford *et al.* 1968). Against this background, Crow (1993) reports a contradictory observation: such patterns do not occur in aquatic plants, and if anything, the flora is richer in the temperate zone. Since this result is quite remarkable, a few more details are necessary. Crow compared the floras of a number of different types of wetlands using published and original data for tropical and temperate regions. New England had 89 species of aquatic plants, and the Carolinas 65, whereas Costa Rica had only 38 and Panama just 35. In the sedge family (Cyperaceae), the same patterns occur: northeastern North America 217 species, the Carolinas 231 and Central America a mere 94. The middle Amazon, by comparison, has only 37 species of Cyperaceae (Junk and Piedade 1994).

The same sort of unexpected diversity trends arise on a habitat-by-habitat basis. Consider marshes first. Palo Verde National Park in Costa Rica, a large

marsh situated along Rio Tempisque, had a flora of 66 species; in contrast, a single marsh of about 1 hectare (2 acres) on the shores of the Great Lakes had a wetland flora of 128 species (Stuckey 1975) and a mere 1800 m² of longleaf pine savanna in the southeastern United States can have 140 species (Peet and Allard 1993). Temporary aquatic habitats in the Guanacaste Province of Costa Rica yielded a flora of 32 species, compared to 42 for vernal pools in southern California. In the recently glaciated peatlands of North America, studies of individual sites yield floras of some 100 species, whereas in the Cordillera de Talamanca only 20 species were found. The same trend occurs in coastal habitats: New Hampshire salt marshes have a vascular flora of 81 species, whereas mangrove habitats in the Caribbean have fewer than three species each. Admittedly, not all the data are strictly comparable, but Crow's compilation suggests that something is fundamentally different about global patterns of species richness in wetland plants.

As noted earlier, elevation is very important, since it controls, among other things, the duration of flooding. This is why topographical variation is so closely related to diversity – the greater the range of elevation, the more kinds of habitats. You can see this on a single shoreline, where the number and kind of species changes with elevation (Figure 9.9). Flooding reduces the number of species at lower elevations, while shrubs reduce the number of species at higher elevations (Figure 2.27). Hence, there is a corridor of diversity in the seasonally flooded zone.

Superimposed upon elevation gradients, small scale microtopographical heterogeneity is an important source of species richness – even a modest hummock (Vivian-Smith 1997) or tussocks of sedge (Werner and Zedler 1997) are emerging as important sources for species richness. A tussock of one species like *Carex stricta* can provide habitat for many other species depending upon the time of year (Figure 9.10). Tree islands in wet savannas and peatlands similarly support many kinds of plant and animals species (Sklar and van der Valk 2002),

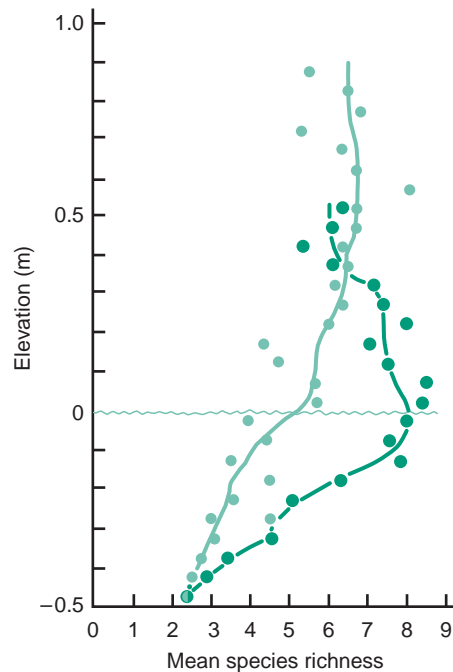


FIGURE 9.9 The number of species (species richness) increases with elevation in a shoreline wetland, although the pattern differs between an exposed shore (light circles) and a sheltered shore (dark circles). (From Keddy 1984.)

thereby increasing the number of species in a wetland. Topographic variation should therefore be included in wetlands under restoration (Keddy and Fraser 2002; Bruland and Richardson 2005).

Disturbance and fertility effects are superimposed on patterns produced by topography. Disturbance and fertility operate by controlling the amount of biomass on a site. Biomass itself is an important predictor of plant diversity. Sites with high biomass often have dense canopies and dense accumulations of litter. As but one example of the negative effects of biomass, Auclair *et al.* (1976a) collected measures of diversity in plots from a riverine marsh, and found diversity was highest where soil nutrients and biomass were low (Figure 9.11).

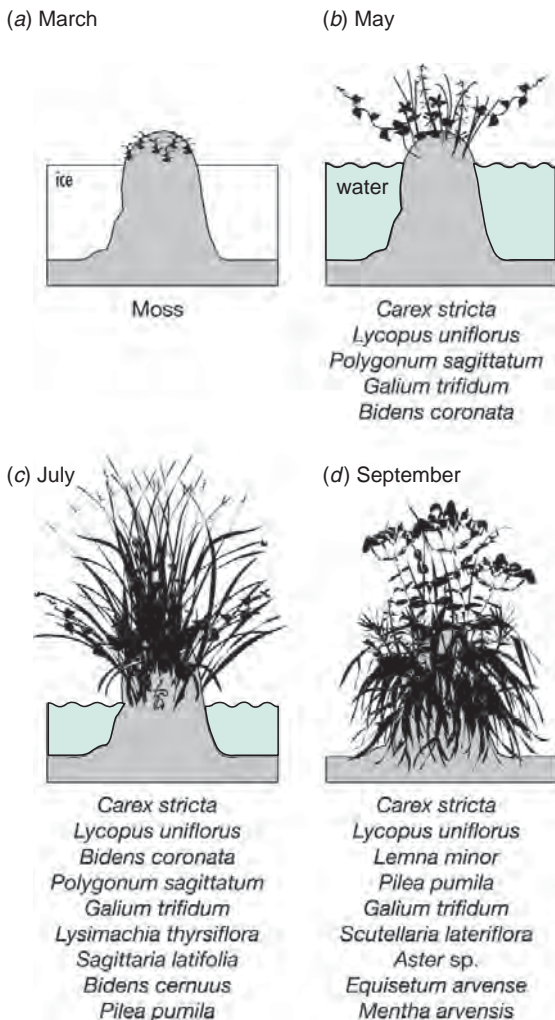


FIGURE 9.10 Even a single tussock of sedge can provide habitat for many other plant species over a growing season. (From Peach and Zedler 2006.)

9.3.7 Factors affecting the number of plant species in peatlands

Overall, plant diversity in peatlands tends to increase with calcium and nutrients in the groundwater (Wheeler and Proctor 2000). Bryophytes appear to be particularly sensitive to calcium levels, while vascular plants are more affected by nutrients. Such gradients are closely connected to landscape

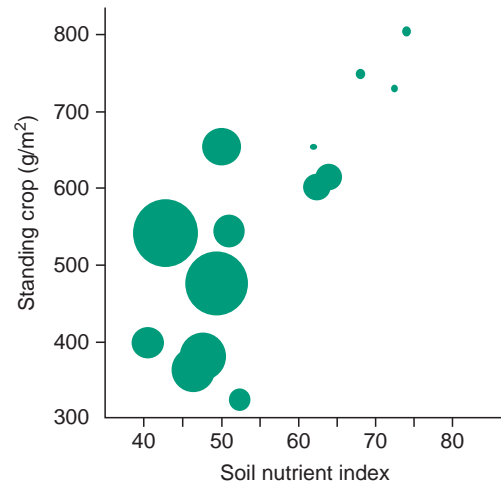


FIGURE 9.11 Plant diversity in a freshwater marsh is higher in locations with lower soil nutrients and lower biomass (standing crop). The circle diameter is proportional to diversity calculated using the Shannon-Weaver index. (After Auclair *et al.* 1976a.)

setting (Godwin *et al.* 2002). At the larger scales, plant diversity generally increases with topographic heterogeneity, growing season, and proximity to the ocean. Local factors such as grazing or mowing may also change the number of species.

As the first example, consider patterns in a set of 65 raised bogs from across eastern North America (Glaser 1992). There were 81 species in total, with from 13 to 50 in individual bogs. Bogs in the southern continental region (north of the Great Lakes) contained fewer than 20 species, whereas bogs in the maritime region had from 32 to 50 species. The most important factors controlling richness were precipitation ($R^2 = 0.605$) and growing season ($R^2 = 0.570$), each of which accounted singly for more than 50% of the variation in species richness among bogs. In another series of bogs, fens, and conifer swamps in boreal Canada (Jeglum and He 1995), plant diversity increased significantly with pH, calcium, and nitrogen. Similar results are reported from Alberta (Vitt and Chee 1990) and Minnesota (Figure 9.12). Overall, fens at high latitudes with

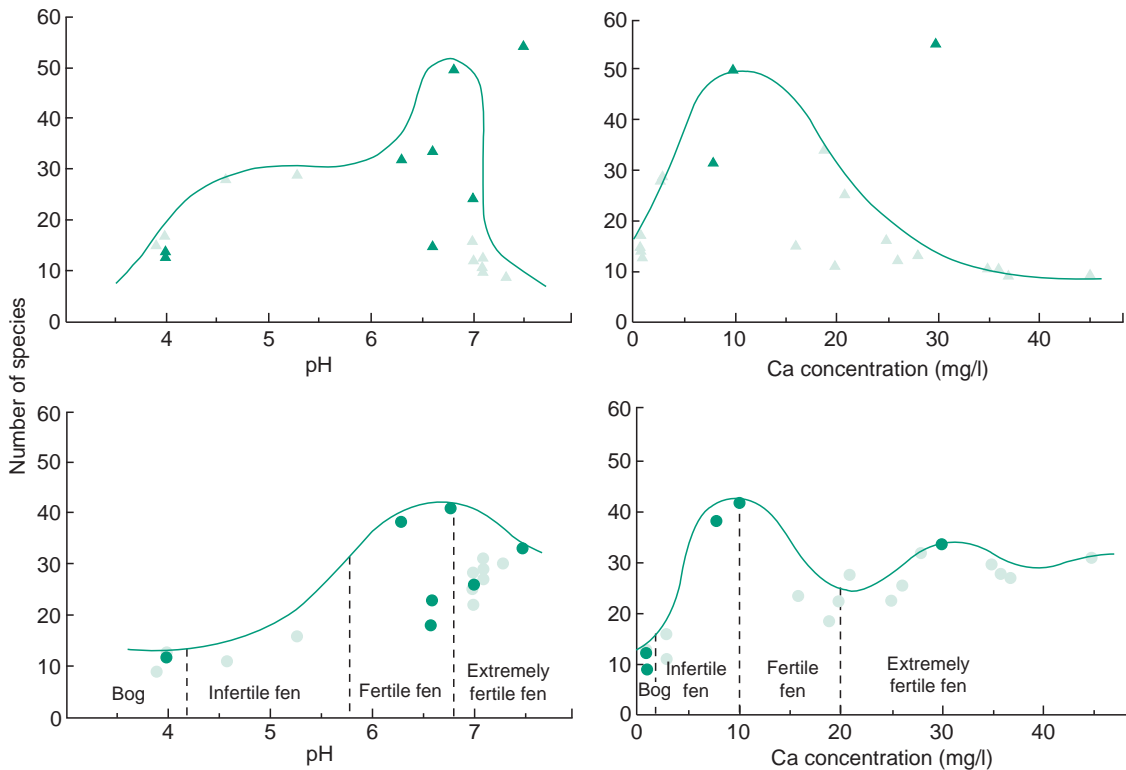


FIGURE 9.12 Plant species richness along chemical gradients in Minnesota peatlands. The top row is bryophytes and the bottom is vascular plants (dark symbols = forested, light symbols = non-forest). (From Glaser *et al.* 1990.)

low temperatures, high microhabitat diversity, and pH about 6.5 have the highest bryophyte and vascular plant diversity (Vitt *et al.* 1995).

Since one of the defining characteristics of peatlands is the abundance of bryophytes, this component of the vegetation can be examined independently of the others. A study of 96 peatlands of continental western Canada found 110 bryophyte species representing three groups: 64 mosses, 26 hepatics, and 20 sphagnums. The number of bryophytes increased with latitude ($R^2 = 0.088$) and decreased with mean annual temperature ($R^2 = 0.145$) (Vitt *et al.* 1995). None of the surface water variables was correlated with richness, and by far the most important factor was the number of microhabitats ($R^2 = 0.455$) as measured by hummocks, pools, and tree bases.

To explore the effects of proximity to the coast, Gignac and Vitt (1990) studied 27 peatlands, from the coastal islands of British Columbia to the interior of Alberta. *Sphagnum fuscum* was the most widespread species, and appeared to be little affected by climate and surface water chemistry. Of the 18 bryophyte species found, seven were limited to oceanic areas (e.g. *S. pacificum*). Some, such as *S. lindbergii*, occurred largely in oceanic sites, but extended inland in infertile fens.

Let us consider one more example, a large wetland complex (>2500 km²) on the edge of the Tibetan plateau at the headwaters of the Yellow River. This, the largest wetland area in China, is a mixture of peatlands and marshes (Tsuyuzaki *et al.* 1990). Here 135 plant species comprised eight major vegetation types. At the lower elevations, frequently

flooded, the dominant species were sedges (*Carex enervis*, *C. meyeriana*) along with *Equisetum limosum* and *Potentilla anserina*. Dryer areas were dominated by *Ranunculus pedicularis*, *Polygonum sphaerostachyum*, and *Trollium ranunculoides*. The mean number of species per quadrat increased along this gradient from 3.5 to 10, illustrating the impact of flooding in restricting particularly the number of forbs. Further west in Tibet, grazing by yaks, sheep, goats, and horses is a common use of wetlands; the mean number of species declined from 8 to 4/m² with increased grazing intensity (Tsuyuzaki and Tsujii 1990).

9.3.8 Factors affecting the number of species of plants in intertidal environments

In Chapter 8, we saw how few plant species could tolerate saline conditions. As a consequence, gradients of salinity are an important factor controlling plant diversity in coastal wetlands, with lower salinity corresponding to higher numbers of species.

The first example comes from the Guadalquivir River delta, some 1500 km² in the southwest of Spain on the shore of the Mediterranean (García *et al.* 1993). The total flora for the site comprised just 87 plant species, including widespread perennial herbaceous genera such as *Scirpus*, *Juncus*, *Phragmites*, *Cynodon*, *Polygonum*, and *Senecio*, some of these genera suggesting near freshwater conditions; at higher elevations, there were many more annuals with scattered stands of chenopoid shrubs. Species richness in 0.25-m² quadrats ranged from 2 to 26. All of the high-richness quadrats occurred at low salinity. Half of the variation in richness could be accounted for by salinity alone; in contrast, biomass of the quadrats could explain only one-fourth of the variation.

Now consider plant diversity along the coast of the Gulf of Mexico. Gough *et al.* (1994) studied the plant diversity in 36 marsh communities.

Most of these plant species were perennial, including widespread genera such as *Aster*, *Eleocharis*, *Scirpus*, and *Spartina*. The best predictor of plant richness was elevation – it alone accounted for 52% of the variation in the number of plant species (Figure 9.13a). At the lowest elevations, there was only slightly above one species per square meter, while at high elevations, the number approached nine. Species richness also decreased with salinity (Figure 9.13b) and biomass (Figure 9.13c), but increased with soil organic matter (Figure 9.13d). Overall, a multiple regression analysis incorporating elevation, salinity, soil organic matter and biomass accounted for 82% of the variation in species richness.

9.3.9 Factors affecting the number of woody plants in swamps

In terrestrial ecosystems, tree diversity decreases with latitude and aridity, but increases with topographic and geological variation (Gentry 1988; Latham and Ricklefs 1993; Specht and Specht 1993; Austin *et al.* 1996). As we have already seen in Chapters 2 and 8, flooding and salinity strictly constrain the growth of woody plants. Keogh *et al.* (1998) collected a data set consisting of more than 250 plots from forested habitats. In tropical areas, terrestrial forests had >120 species per plot, whereas freshwater wetlands averaged only 31 species per plot. Temperate climates, peat substrates, and salinity all further reduced the number of species of trees found (Figure 9.14). Some combinations of constraints, such as northern temperate climate and salinity (salt marsh), were incapable of supporting any trees at all. The additive effects of local environmental constraints are probably the most important factors controlling tree species richness in wetlands. Each constraint appears to reduce the number of species by some two-thirds, with salinity exerting a much stronger effect than peat, cold, or flooding.

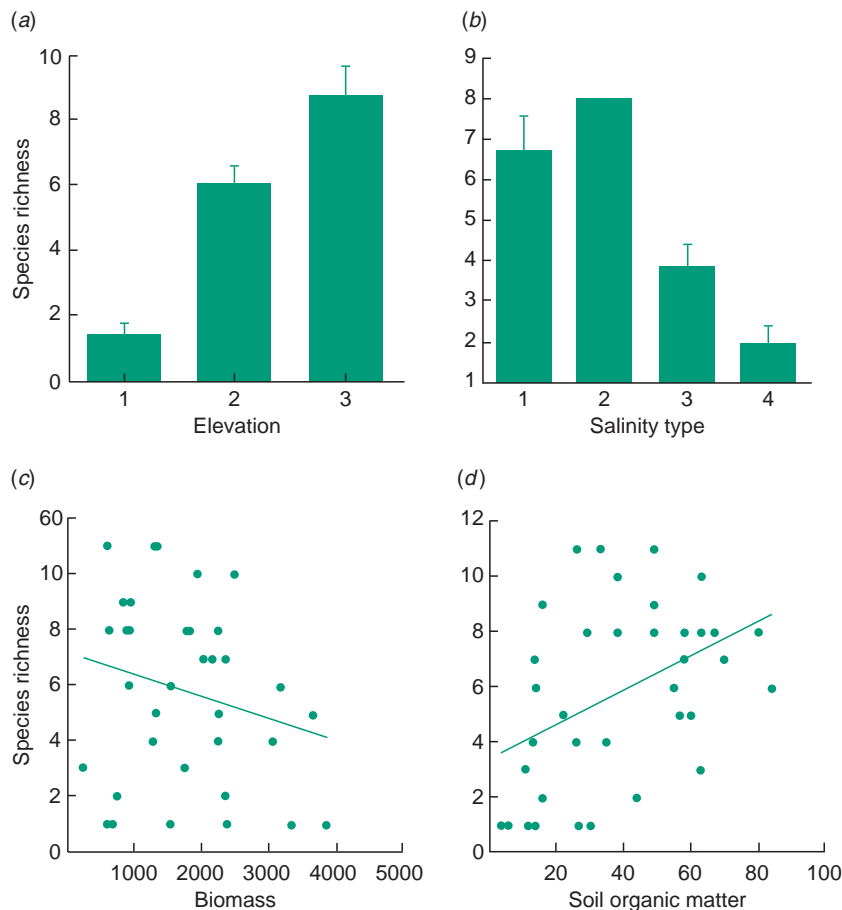


FIGURE 9.13 Plant species richness patterns in Gulf coast wetlands: effects of (a) elevation, (b) salinity, (c) biomass, and (d) soil organic matter. (From Gough *et al.* 1994.)

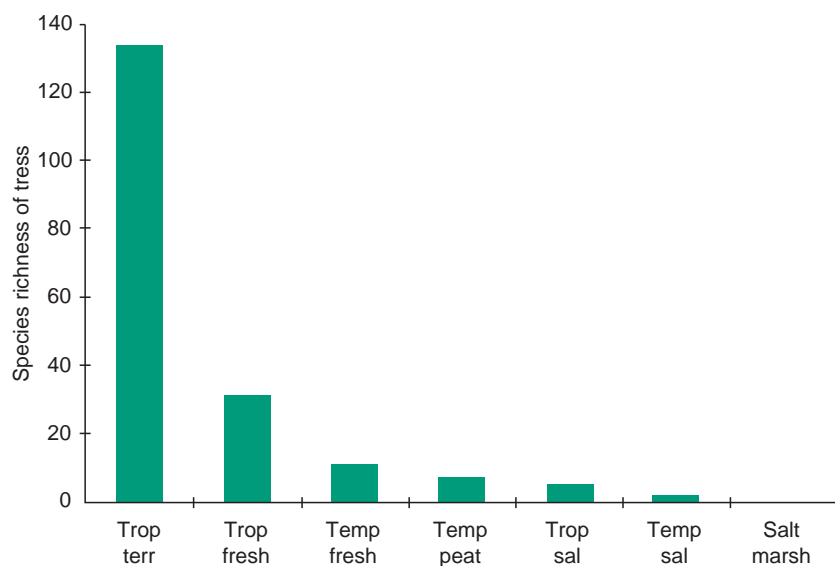


FIGURE 9.14 The species richness of trees in five types of forested wetlands compared to tropical terrestrial forests (left) and salt marshes (right); $n = 257$, Kruskal–Wallis ANOVA, five categories, $p < 0.0001$. (From Keogh *et al.* 1998.)

9.4 Some theory: a general model for herbaceous plant communities

A relatively small number of environmental factors can often successfully predict the numbers of species occupying a wetland. For fish the most important factors are pH, oxygen levels, and vegetation structure. For plants, the factors are elevation, salinity, and fertility. The primary goals in studies of biological diversity are to first uncover these factors controlling species richness, and then to rank them in order of importance. Once such lists are available for a wide array of habitat types and organisms, the task of comparison can begin.

Since many wetland managers have to manage vegetation, we should look in more depth at factors influencing plant biomass and plant diversity. Let us begin this story with Grime's (1973) observation in British grasslands that habitats with intermediate levels of biomass appeared to have the largest numbers of plant species. He postulated that there is a general relationship in vegetation between species richness and standing crop, of the form shown in Figure 9.15. Moreover, he postulated that at one end of the gradient, species richness is low because of high levels of stress or disturbance, whereas at the other end, species richness is low because of dominance by a few strong competitors.

This pattern was first documented in wetlands in English fens subjected to different types of management (Figure 9.16a). These fens were located in the Norfolk Broadland, some 3300 ha of fen along watercourses draining into the sea at Great Yarmouth. This work raised the promising possibility that one could develop a general predictive model that would relate species richness to biomass. In the next extension, Wisheu and Keddy (1989a) tested whether this "intermediate diversity" model applied to wetlands on another continent, and further tested whether the pattern was the same in four different vegetation types. A somewhat similar pattern emerged (Figure 9.16b), but the

coefficients of the regression lines also varied among the four habitats. Thus, while the overall shape of the relationship had broad generality, the specific shape was apparently less consistent. The absence of high-biomass sites was thought to be responsible for failure to detect a decrease in species richness at high biomass; Figure 9.16c shows that when high-biomass sites were added, the typical Grime-type curve emerged.

The level of biomass associated with high species richness is of particular interest. Does it vary among vegetation types? That is, even if the shape of the curves vary somewhat, does the region of high diversity always occur at similar biomass levels? Table 9.4 compares a series of published studies; the results are similar enough to hold promise, but not as consistent or tidy as one might hope. Perhaps a much larger data set with many more quadrats is necessary.

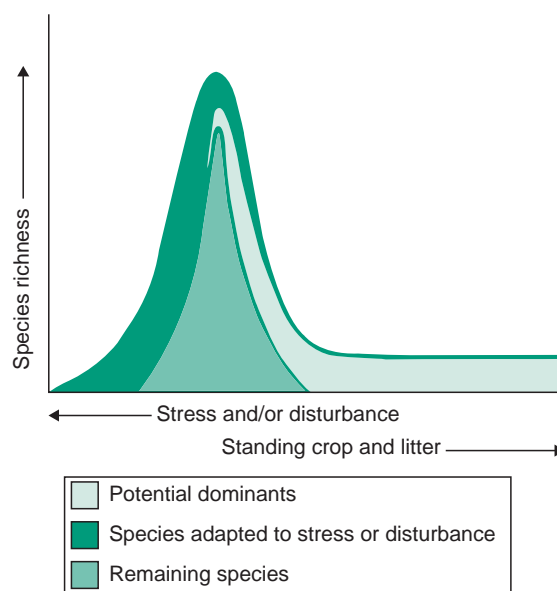


FIGURE 9.15 Species richness along a gradient of standing crop and litter: the concept. (Adapted from Grime 1979.)

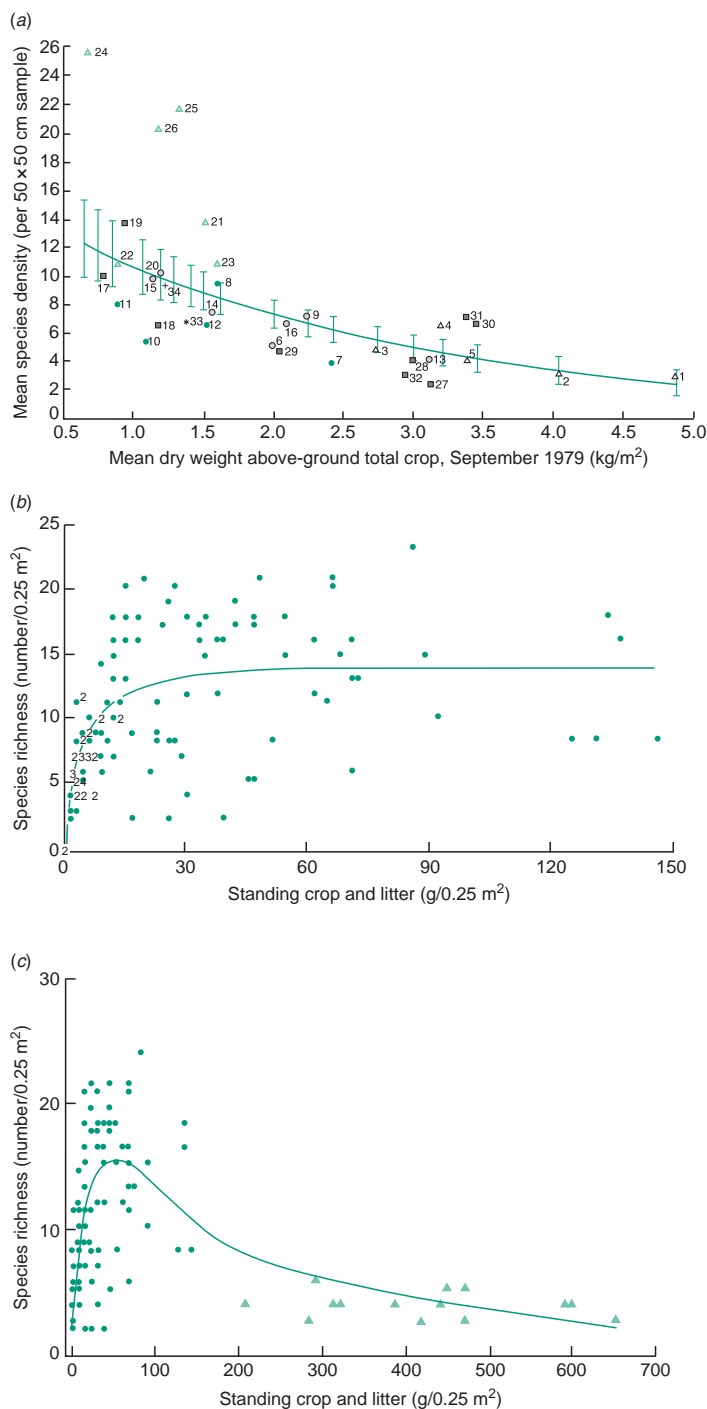


FIGURE 9.16 Plant species richness along gradients of standing crop and litter: (a) fens (From Wheeler and Giller 1982), (b) lakeshores in Nova Scotia (From Wisheu and Keddy 1989a), and (c) lakeshores in Nova Scotia (dots) and high biomass *Typha* marshes in Ontario (triangles) (From Wisheu and Keddy 1989a).

Table 9.4 Standing crop and litter values associated with maximum species richness in an array of wetlands. Note that standing crop and litter are expressed as g/m² and not g/0.25 m². Maximum richness occurs at approximately 500 g/m² in terrestrial vegetation

Site	Habitat type	Standing crop and litter (g/m ²) at maximum species richness
Wilsons Lake, NS, Canada	Occasionally flooded gravel lakeshore	200
	Occasionally flooded boulder lakeshore	140
	Frequently flooded gravel lakeshore	260
	Frequently flooded boulder lakeshore	80
Eastern Canada	Marshes and wet meadows	60–400
Axe Lake, ON, Canada	Lakeshore	50–300
Ottawa River, ON, Canada	Riverine wetland	300
Green Swamp, NC, USA	Pine–wiregrass savannas	280
Gelderse Vallei, the Netherlands	Reed swamp, grassland, road verges	400–500
Westbroekse Zodden, the Netherlands	Fens	400–500
	Wet grassland	425
Norfolk Broadland, UK	Herbaceous fen	1500
Northeast Europe	Chalk grasslands	150–350

Source: From Wisheu and Keddy (1989a).

Data from more than 400 quadrats in Eastern North America (Figure 9.17a) show that wetlands with biomass in the range of 50 g/0.25 m² had the highest diversity across a wide range of wetland sites. Figure 9.17b shows, moreover, that if rare species alone are considered, the vast majority of nationally rare wetland species occur in the very low standing crop habitats, less than 100 g/0.25 m². Similar patterns are found in fens – across 86 herbaceous fens, the number of species ranged from 2 to 50 in 0.25-m² quadrats, and standing crop and litter ranged from 80 to >2900 g/m². The plot of species richness against biomass was very similar to that in Figure 9.15, heavily skewed to the left with maximum species richness around 1000 g/m² (Wheeler and Shaw 1991). The highest biomass and lowest species richness occurred in sites dominated by *Phragmites australis*, and sites with high biomass had few if any rare species. Wheeler and Shaw conclude: “Maintenance of low-growing swards of

herbaceous fen vegetation is particularly important for the conservation of many rare fen species.” At this large scale (wetlands representing a broad range of habitats) the pattern is clear and consistent. Of course, the particular rare species that occur at low biomass change from one region to the next.

How do tropical wetlands fit this pattern? Rejmankova *et al.* (1995) sampled marshes from floodplains and depressions in northern Belize; these marshes are usually mostly flooded all year long, but are occasionally disturbed by fire and desiccation. In general, plant diversity was remarkably low, with a mean of some five plant species in 5 × 5 m quadrats. Plant species richness still reaches a maximum at intermediate levels of biomass in *Typha domingensis* marshes (Figure 9.18). Further, if one adds in high biomass reference sites from the Everglades (indicated with *), the decline in species richness at high biomass levels becomes evident. Thus, a similar pattern to temperate zone marshes emerges, with two

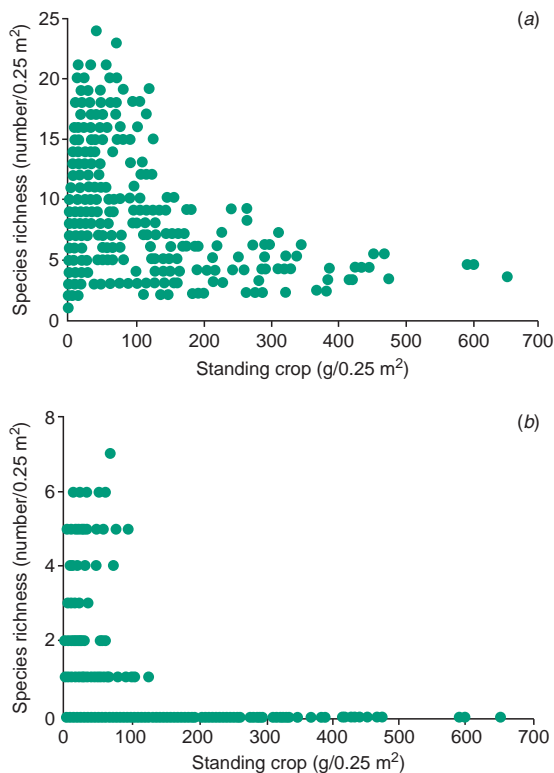


FIGURE 9.17 Plant species richness along gradients of standing crop (a) for 401 0.25-m² quadrats in eastern North America; (b) same quadrats but nationally rare species only. (From Moore *et al.* 1989.)

key exceptions: overall species richness is strikingly lower, and the region of highest species richness is shifted to the right. Similarly, large clonal perennials such as *Eleocharis mutata* and *Typha domingensis* form extensive nearly pure stands in floodplain marshes along the Rio Tempisque in Costa Rica (Crow 1993). This tendency for dominance by a few such species is, suggests Crow, one possible explanation for the low diversity of herbaceous wetland plants in the tropics.

There remains a great deal of scatter around the lines in Figure 9.17. There are at least three ways to try to reduce variance and increase precision. First, one could try to reduce the residual variance by adding in a second predictor variable besides biomass. If biomass is a crude measure of productivity, then disturbance might be an appropriate second factor to use. There is no easy way to measure disturbance, but Shipley *et al.* (1991a) used the proportion of species that were functional annuals as a surrogate, in which case the proportion of flora being perennials becomes an inverse surrogate of disturbance. Using both biomass and the proportion of plants that are perennial it was possible to predict plant species richness with greater success (Figure 9.19).

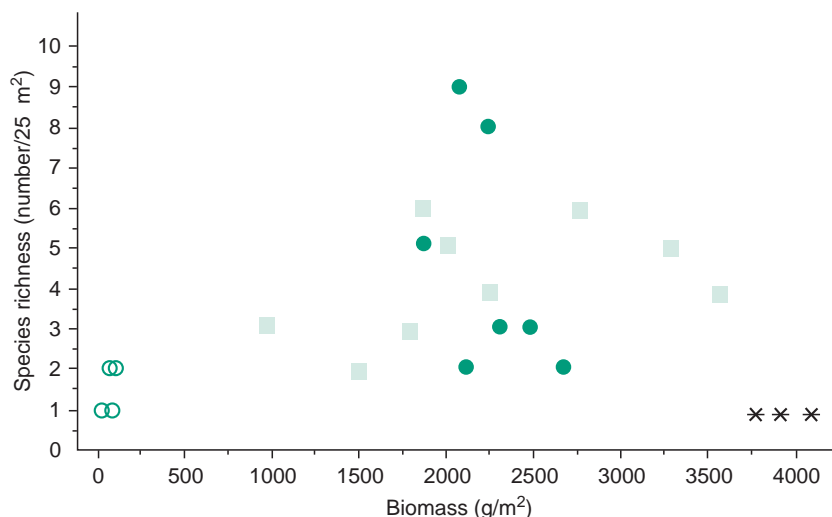


FIGURE 9.18 Plant species richness plotted against biomass for marshes in Belize. Circles are *Eleocharis cellulosa*, squares are *Cladium jamaicense*, and dots are *Typha domingensis*. *Typha domingensis* stands in the Everglades (asterisks) are added for comparison. Plots are 5 × 5 m². (From Rejmankova *et al.* 1995.)

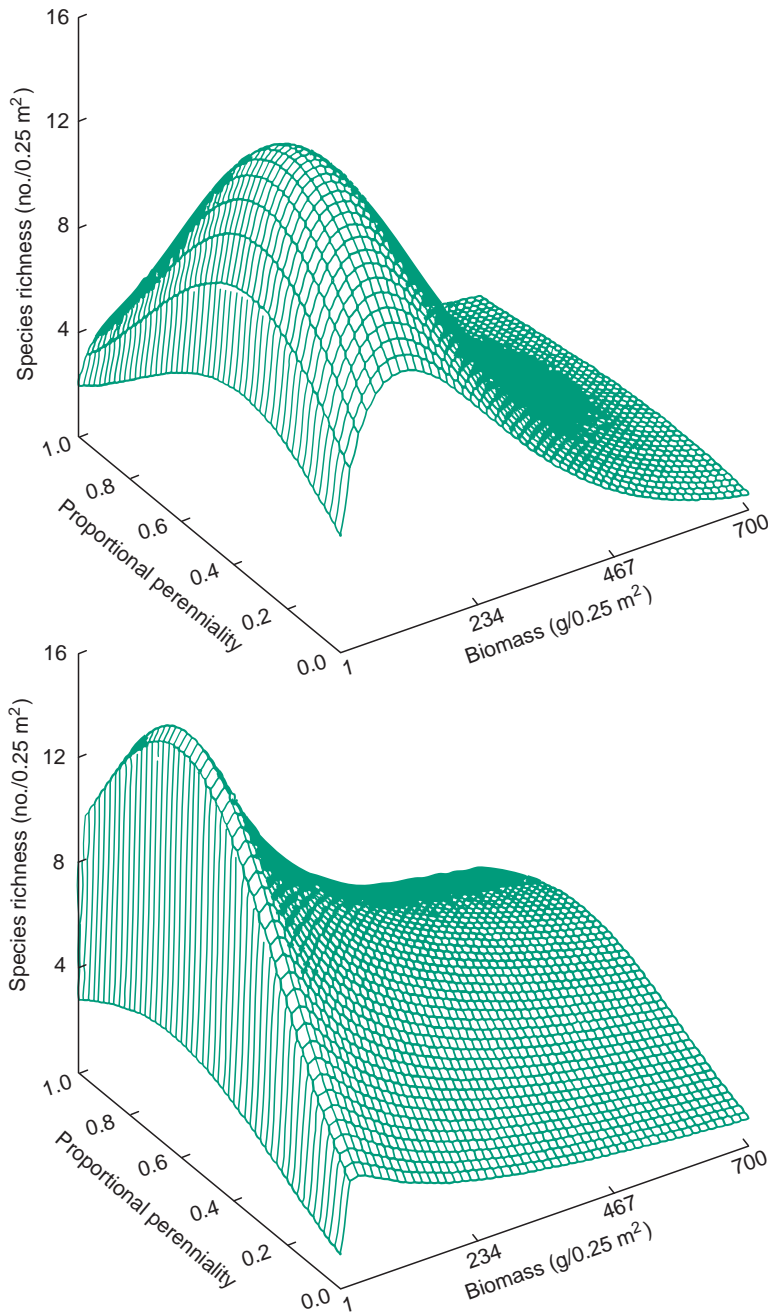


FIGURE 9.19 Plant species richness as a function of both biomass and the proportion of species that are perennial for two geographic locations, Quebec (top) and Ontario (bottom). (From Shipley *et al.* 1991a.)

Seventy-five percent of the variance could be accounted for in a set of 48 quadrats from Quebec, and 45% of the variation in a larger data set of 224 quadrats from southern Ontario.

A second approach to greater precision would be to try reducing unexplained variation by dividing the data into smaller units. Instead of comparing across many vegetation types, one might look for better

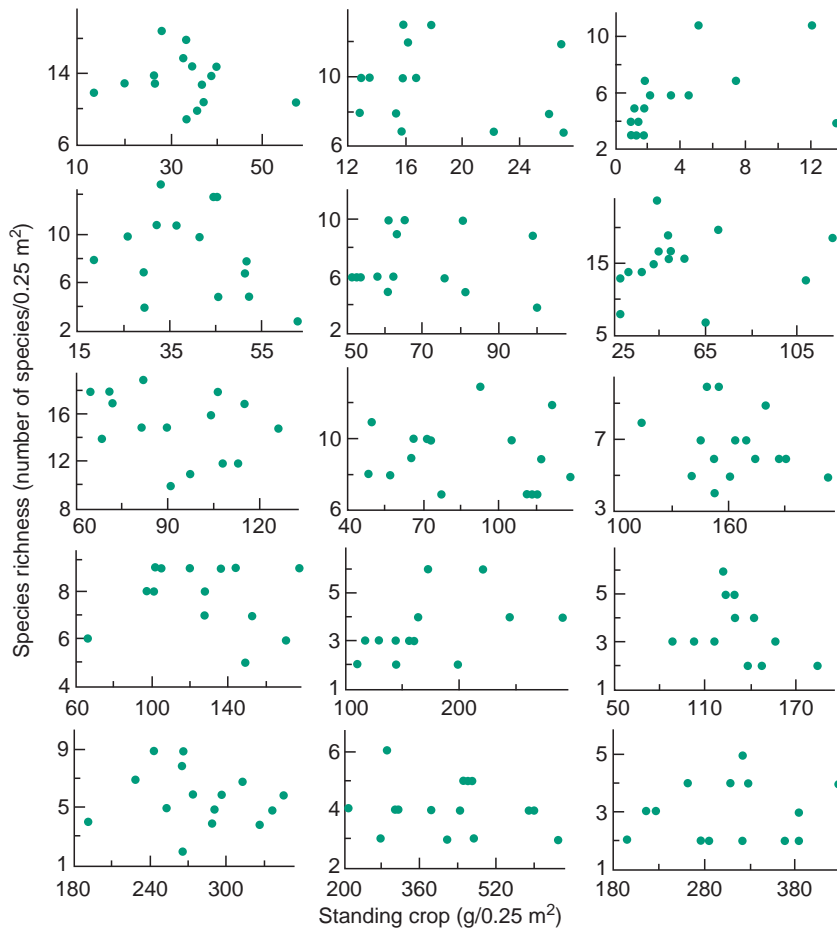


FIGURE 9.20 Plant species richness as a function of standing crop within 15 vegetation types. (From Moore and Keddy 1989.)

relationships within single vegetation types. In many cases this would also shorten the biomass gradient because long biomass gradients are usually the result of comparison across many vegetation types. If the data are divided this way, the intermediate biomass model cannot be detected at all (Figure 9.20). Apparently the factors and processes that produce the intermediate diversity pattern occur only in large-scale comparisons across vegetation types.

A third approach to greater precision requires reconsidering the statistical methods. In his original work, Grime (1973) proposed that the relationship applies to *potential* species diversity. A significant problem with this verbal formulation is that “potential diversity” cannot be measured. Most workers have used curve-fitting techniques

which assume that all observed data points have equal weighting. However, taking the original wording precisely, Grime proposed that there is an outer envelope or upper limit to species richness. It was only the outer limit of the relationship he drew in Figure 9.15. There is a growing set of tools called quantile regression which is useful for studying the edges of data sets (Cade *et al.* 1999; Cade and Noon 2003), a procedure that prescribes envelopes within which data points will lie. Figure 9.21 uses a hand-drawn line to delineate the species richness envelope. This technique is now being used to re-explore patterns in wetland data sets (e.g. Schröder *et al.* 2005). Moving our attention from patterns in means to patterns in edges changes the type of questions we might ask. Instead of trying to

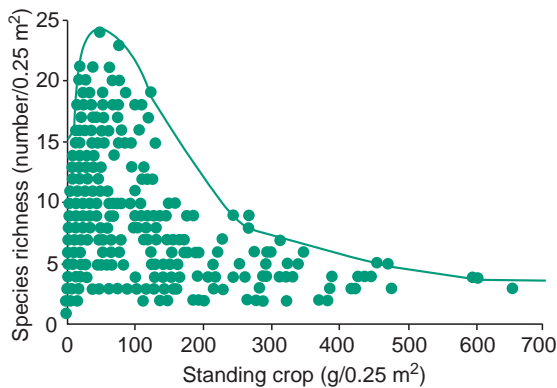


FIGURE 9.21 A boundary line or envelope marks the upper limit of species richness in herbaceous wetlands. (After Moore *et al.* 1989, in Wisheu *et al.* 1990.)

account for scatter around the line, as Shipley *et al.* (1991a) attempted to do, if one begins with an edge, the challenge is to explain why many sample units fall below the line.

Saline marshes may be an exception to this model, at least at relatively small scales. The patterns in Figure 9.13 seemed to demonstrate that physical factors were more important than biomass. If one excludes certain extreme environments – lowest elevations, saline and brackish marshes – a much stronger relationship between species richness and biomass emerges, one accounting for 34% of the variance. Even so, the pattern is simply one of decreasing species richness with increasing biomass, with no evidence of a curvilinear component. The explanation given by Gough *et al.* (1994) is that physical factors control potential richness by controlling the pool of species available (that is, the set having the appropriate physiological tolerance limits: Figure 8.7) and this control may be

so strong that it overrides most other processes. Hence, we will next have to look more closely at the topic of species pools (Section 9.5).

Experiments may also help to clarify causal relationships. Hacker and Bertness (1999) extended these descriptive studies of salt marshes by setting up competition experiments in several zones in a New England salt marsh. In this system, plant species number is low in the high and low intertidal and high in the middle intertidal. They established plots with and without plant neighbors, finding that competition was more important in the high intertidal while physical factors were most important in the low intertidal. In the middle zone, direct positive interactions apparently influenced species richness – three of the four species died (*Atriplex patula*, *Iva frutescens*, and *Solidago sempervirens* but not *Limonium nashii*) without neighbors but had minimal mortality with neighbors. These positive effects were due to one particular facilitator species, *Juncus gerardi*, which ameliorated the soil conditions that develop in its absence. It shaded the soil, decreasing evaporation and resulting salt accumulation, and oxygenated the soil with its aerenchyma. They concluded that the higher species richness in the middle intertidal is dependent on three co-occurring conditions – the absence of a competitive dominant, less harsh physical conditions than the lower intertidal, and the presence of a facilitator species. Hence, the model first described by Grime may apply rather well to the vertical gradient encountered along coastlines. Moreover, positive interactions may increase plant diversity in such stressed habitats (Hacker and Gaines 1997). The entire topic of zonation on shorelines will be the focus of the next chapter.

9.5 More theory: the dynamics of species pools

We have looked at many different scales in this chapter, from large global-scale relationships to patterns in single wetlands. It is important to realize that the patterns one finds will depend upon the scale

of a study. Thus, the intermediate biomass model of Section 9.4 concentrated on predicting the number of species in small areas or small pieces of habitat. But when planning parks and nature reserves, there is

less interest in the number of species per sample unit, the focus being the total number of species protected in a reserve system.

This distinction among the number of species in a sample unit, the number in one park, and the number in a pool, is important for both theoretical and applied purposes. As we increase the size of each sample unit (e.g. quadrat), or as we increase the number of such units, more species will be encountered.

The relationship has been well documented, and is generally asymptotic – that is to say, the number of new species encountered declines with sampling effort until, in theory, all of the species have been encountered and tallied (e.g. Pielou 1975). The asymptote is a good estimate of the number of species in the habitat type. In practice, if sample units become large enough, or numerous enough, new habitats are encountered, in which case the number of species tends to continue increasing with the sampling effort. Further, as the scale of sampling is expanded, the controlling processes are likely to change, with local processes such as competition being eclipsed by processes such as landscape history or speciation (Ricklefs 1987). It is therefore important to specify in advance exactly what habitat type or geographic locale is being inventoried. The word **pool** then describes the complete list of species for that habitat, park, or geographic locale.

Eriksson (1993) has provided a simple model to help explore the relationships between community richness (the number of species in a local community), and the number in the pool. Let the number of species in a particular community, S , be a function of local colonization and extinction, just as the number of species in the pool, N , is a function of speciation and extinction. The local colonization rate is then proportional to the number of species in the species pool, N , minus the number of species already present in the community, S – that is, the number of potential colonizers left in the pool. The local extinction rate, however, is a function only of the number of species already present. Adding in two proportionality constants for the rates of

colonization, c , and extinction, e , S changes with time (t) as follows:

$$\frac{dS}{dt} = c(N - S) - eS,$$

and at equilibrium the value of S is

$$S^* = N(c/c + e).$$

This simple expression yields some predictions.

First, if the local extinction rate, e , is very low, then S^* will be close to N ; that is, the local community will contain most of the species in the pool. Second, if the rates of colonization and extinction are equal, that is $c = e$, then $S^* = 1/2N$; the local community will have one half of the species in the pool. Third, if extinction rates are much higher than colonization rates, the community will be species poor and yet the number of invading species per unit time will be relatively high. One simple explanation, then, for communities having many species is the existence of a large species pool; that is to say, S is large because N is large. Eriksson calls this the species pool hypothesis. Depending upon the values of e and c , however, a variety of other scenarios can be postulated.

In many cases, ecologists have data not on the entire community, but only on the number of species in a series of samples from that community, such as the number of species in a set of quadrats, traps, nets, or transects. The total number of species encountered in the sampling therefore becomes a working estimate of the pool; the greater the sampling effort, the more reasonable the assumption becomes. Describing all these possible sample types as a “sample unit” for the sake of linguistic convenience, we can ask what relationships might exist between the number and composition of sample units and the species pool. In the extremely unlikely case where all sample units are identical in composition, then the species richness of any one sample unit will be the same as the pool. The greater the compositional difference between each pair of sample units, the greater pool

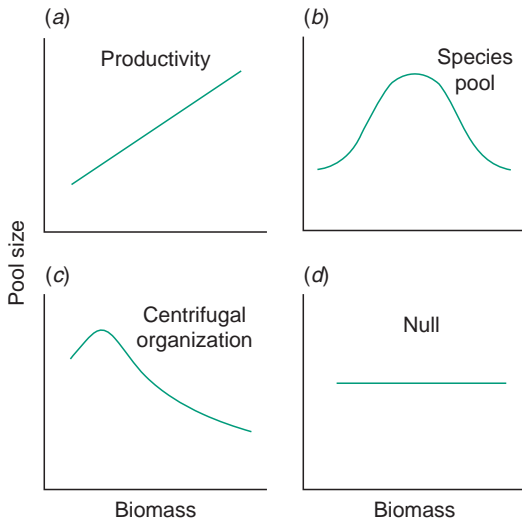


FIGURE 9.22 Four possible patterns in pool size along a biomass gradient. (After Wisheu and Keddy 1996.)

size will be relative to the number of sample units. We have already seen (Section 9.4) how species richness (or number of species per sample unit) varies along biomass gradients. Suppose we now take the same gradient, but ask instead how pool size varies along it.

Several relationships between pool size and environmental conditions might be postulated. From one point of view (e.g. Connell and Orias 1964), pool size may be highest in high-biomass wetlands because these have the most energy to allocate among species (Figure 9.22a). Alternatively, pool size may simply mirror species richness (Figure 9.22b), high pool diversity occurring where the number of species in plots (also called species density or alpha diversity) is also high (e.g. Preston 1962a, b; Taylor *et al.* 1990; Eriksson 1993). Although this latter hypothesis may perhaps seem the most likely, particularly based upon what we know about global diversity patterns, it is founded upon the assumption that the degree of similarity among quadrats does not differ along gradients. If the average difference between quadrats is greater in low-biomass

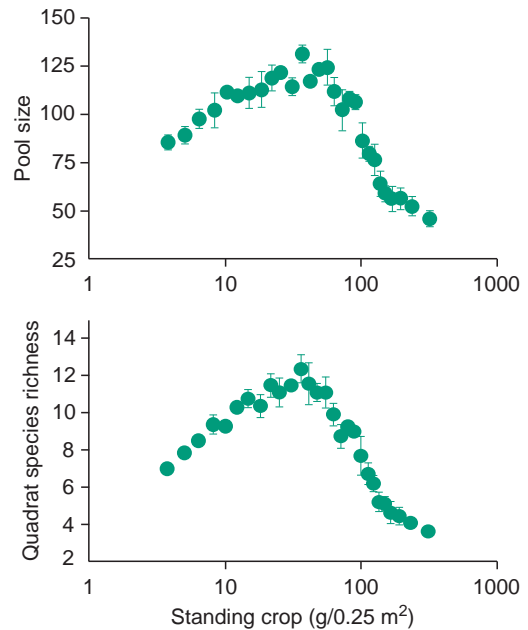


FIGURE 9.23 Actual patterns in the number of species at two scales: pool size (top) and species richness plots (bottom). (After Wisheu and Keddy 1996.)

conditions, then the pool size curve will be shifted to lower biomass habitats (Figure 9.22c). This would likely be the case with centrifugal organization (Keddy 1990a). Wisheu and Keddy (1996) tabulated data for 640 quadrats from shoreline marshes across eastern North America, plotting both species richness and pool size against biomass (Figure 9.23). Both reached maxima in similar habitats with approximately $50 \text{ g}/0.25 \text{ m}^2$. The number of species in plots was a nearly constant percentage of pool diversity, irrespective of the biomass of the sites examined.

The ecological processes that cause this pattern in pool size remain unclear. We cannot even say with certainty which mode of causation operates. Is the pool pattern (produced by large-scale evolutionary processes) causing the well-known intermediate diversity pattern? Or is the alpha diversity pattern (produced by local ecological processes such as stress, disturbance, and competition)

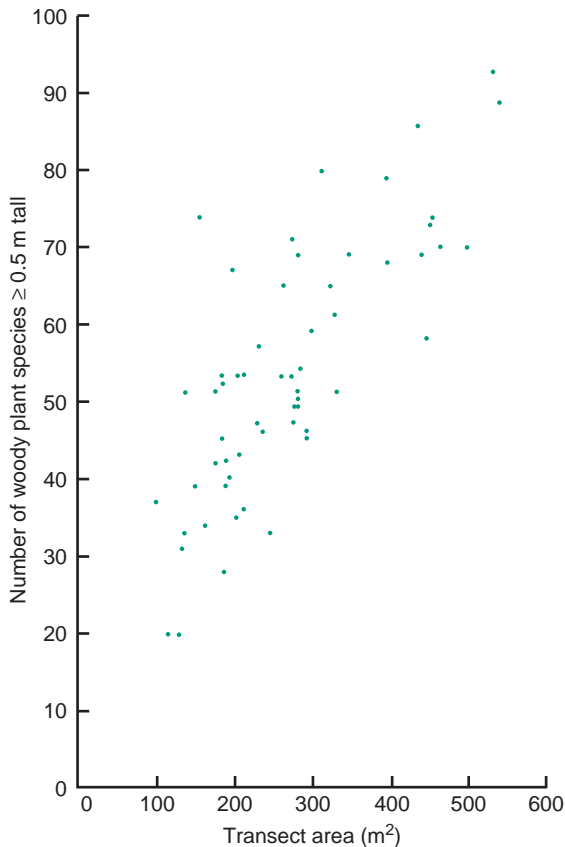


FIGURE 9.24 Pattern of species richness of woody plants occurring in tropical riparian forests – species richness increases with sampling scale and with no sign of an asymptote. (From Meave *et al.* 1991.)

causing the pool pattern? These sorts of basic questions have important consequences for the way in which we both design and manage nature reserve systems.

Comparable data for other wetlands are not available, so we do not know how general the patterns in Figure 9.23 are. Pool sizes in tropical bottomland forests must be remarkable, since Meave *et al.* (1991) found that the number of plant species continued to climb linearly as quadrat size approached 500 m² (Figure 9.24). Such tropical riparian floodplain forests may be extremely important centers for the protection of biological diversity (Salo *et al.* 1986; Meave and Kellman 1994). This stands in sharp contrast with Crow's (1993) observations on the restricted size of species pools in aquatic vascular plants. Riparian corridors in general appear to have high numbers of plant species and may support a significant proportion of the entire flora of an area; Nilsson and Jansson (1995) found that just four free-flowing rivers supported 366 plant species, or 18% of the entire Swedish flora of vascular plants. Meave and Kellman (1994) report 292 plant species from a mere 1.6 ha, and suggest that riparian corridors may have provided reservoirs of diversity for rainforest plants during periods of drier climate.

9.6 Conservation of biological diversity

There is a very important, and still frequently misunderstood, connection between local species diversity and pool size. Conserving “biodiversity,” which is an important conservation goal (e.g. World Conservation Monitoring Centre 1992; Reid *et al.* 1993; Noss 1995), requires us to think about the full species pool for an area. At the largest scale, our challenge is to maintain the species pool of the entire planet or at least of a region, a topic to be more

fully addressed in Chapter 14. But most managers must focus on maintaining or increasing diversity at only one location. It is entirely possible that our attempts to increase local diversity can actually reduce biodiversity, that is, reduce the species pool. To understand this apparent paradox, consider the following two examples.

Altering the hydrology of salt marshes with dikes increased the number of birds found (Figure 2.6) and

it doubled bird species richness. This might at first appear to be a worthy contribution to conservation of biological diversity. The added birds in impoundments, however, were generally birds that occurred in other freshwater wetlands, whereas the birds in the natural salt marshes were more specialized species such as clapper rails and sharp-tailed sparrows. Impounding a salt marsh may simply increase numbers of common birds and decrease uncommon ones. From the global perspective, diversity is decreased.

A similar management outcome can be seen when infertile wetlands (Figure 3.3) become more fertile. As a specific example, consider the New Jersey Pine Barrens, where there are many rare plants, in part because the habitats are very infertile. This infertility means that carnivorous plants are particularly well represented in the flora. Human activities often increase the fertility of sites. Sites that are thus enriched support nearly three times the number of species as pristine sites (Table 9.5). Enrichment therefore increases local diversity, but this increase is almost entirely accounted for by the invasion of exotic species better adapted to higher nutrient levels. Infertile sites, in contrast, have floras that are 88% composed of native species, 12% of which

Table 9.5 Species occurring at pristine and enriched coastal plain sites in the New Jersey Pine Barrens

	Number of species	Percent carnivorous	Percent non-native
Pristine sites	26	12	12
Enriched sites	72 ^a	0	96

^a Actual count was 73. One species was unidentifiable as to being native or non-native.

Source: From Wisheu and Keddy (1992), after Ehrenfeld (1983).

are carnivorous. Again, the local increase in diversity occurs because common species are added at the expense of uncommon ones.

The general rule, then, is that if increasing local diversity is achieved by increasing populations of globally common species, or decreasing globally rare ones, the local management is being counter-productive. Measuring species richness or diversity is no substitute for thinking. Management for maintaining “biodiversity” only makes sense if one takes a global perspective as the context for evaluating local actions.

CONCLUSION

Often our first step in the study of a wetland is to determine which species occur there. There are often good data on birds and amphibians, with poorer data on invertebrates and plants. Partly this is because there are so many more kinds of invertebrates and plants. There are some general rules that allow us to judge how many species an area is likely to have: I have shown you four of them. In addition, there are other rules that apply more specifically to individual groups. Amphibians, as we saw, are positively affected by adjoining forest, and negatively affected by adjoining roads. Plant diversity tends to be higher in infertile habitats with low biomass.

Overall, the task of protecting species requires us to set aside large areas with large species pools and minimize the detrimental effects of humans upon them. We now have good maps of which parts of the world have the most species – the world’s biological hotspots (Myers *et al.* 2000). We also know that each of these needs to have large protected areas with well-designed buffer zones (Noss and

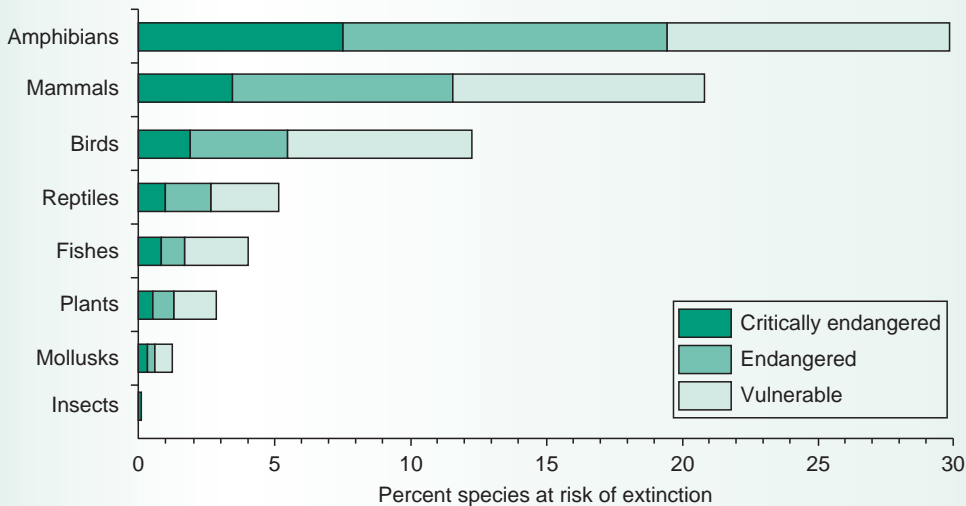


FIGURE 9.25 At the global scale, many species have become so rare that they face extinction. The IUCN *Red List* documents species at risk of extinction in three categories: critically endangered (extremely high risk), endangered (very high risk), or vulnerable (high risk). Note that more than one in four amphibians is vulnerable (IUCN 2008).

Cooperrider 1994; Noss 1995). This is an important priority for reversing the processes that are driving species to extinction.

With regard to future research, it would be useful to understand better why diversity varies in the way it does. A vast majority of the examples discussed in this chapter used descriptive approaches, experimental studies being much less common. I have described a few experiments elsewhere in this book (e.g. Figures 3.12, 4.4, 5.9). These illustrate the potential of properly designed field experiments to inform us of factors controlling species richness, but they also illustrate the limitations of experimentation. Most existing experimental studies suffer from two restrictions. The first is their small scale, usually small quadrats or microcosms, although much larger-scale experiments are possible. The second is their dependent variable, often the abundance of a few selected species, in which case overall consequences for diversity cannot be ascertained. The study of diversity requires a wise mixture of descriptive and experimental studies.

Overall, we can conclude that we have some encouraging general principles about factors like area, heterogeneity, and fertility and their effects on diversity. Still, there is a need for humility – humans need to approach wetland management with caution, given the real risk of making things worse rather than better. The mistaken assumption that increasing local diversity must be good (even when it decreases global diversity) is a perfect example of widespread misapplication of theory in management.

Overall, we are in an era when diversity is declining, certainly at the global scale (Wilson 1993) and often at the local scale as well. The number of species at risk of extinction, as documented by the *Red List* maintained by the IUCN, is high (Figure 9.25) and continues to rise alarmingly. It is doubtful that anyone will ever see an Eskimo curlew again. Hence, there seems to be a great need to apply wisely our existing information on diversity in wetlands.