

Zonation: shorelines as a prism

Given the remarkable diversity of wetland types and the complexities of their processes and composition that we have seen in the first nine chapters, how might we begin systematic scientific study? This is an important issue not only for those of us concerned with wetland ecology, but also for practitioners of ecology in general. Where and how do we start? One is reminded of the old Buddhist story about the blind scholars and the elephant. Asked to describe the elephant, the first scholar, touching the massive side, states "It is like a wall." The second scholar, holding the tail, says "No, it is like a piece of rope." The third, holding the trunk, insists "You're both wrong. It is a kind of snake." And so on. We constantly risk that scholarly understanding of the phenomenon will be distorted by our starting point, or by our own limited frames of reference. Yet, we must start somewhere. Wetlands provide one feature that may assist us in scientific study: they are often arranged along gradients.

10.1 The search for fundamental principles

Anyone who has visited a wetland is likely to have been struck by the power of gradients to produce rapid changes in composition. Whether it is a northern lakeshore, a tree island in the Everglades, a delta on the coast of Louisiana, or a tropical floodplain, minor changes in water depth often produce profound changes in the types of plants and animals that we see. These rapid changes in composition often produce visible bands of different ecological communities, or what is often called **zonation**. These provide a powerful tool for understanding wetlands. They also provide an

opportunity for people working in wetlands to contribute to the larger field of ecology. Gradients function like prisms. Prisms take ordinary light and spread it out into a spectrum for scientific study; a gradient does the same for a complicated ecological community. This spectrum provides us with a pattern we can study. Such patterns are necessary for initiation of scientific inquiry, and zonation provides ready-made patterns. There is a long-established habit of describing wetlands by sketching zonation patterns (Figure 10.1) and as the sketches remind us, zonation patterns

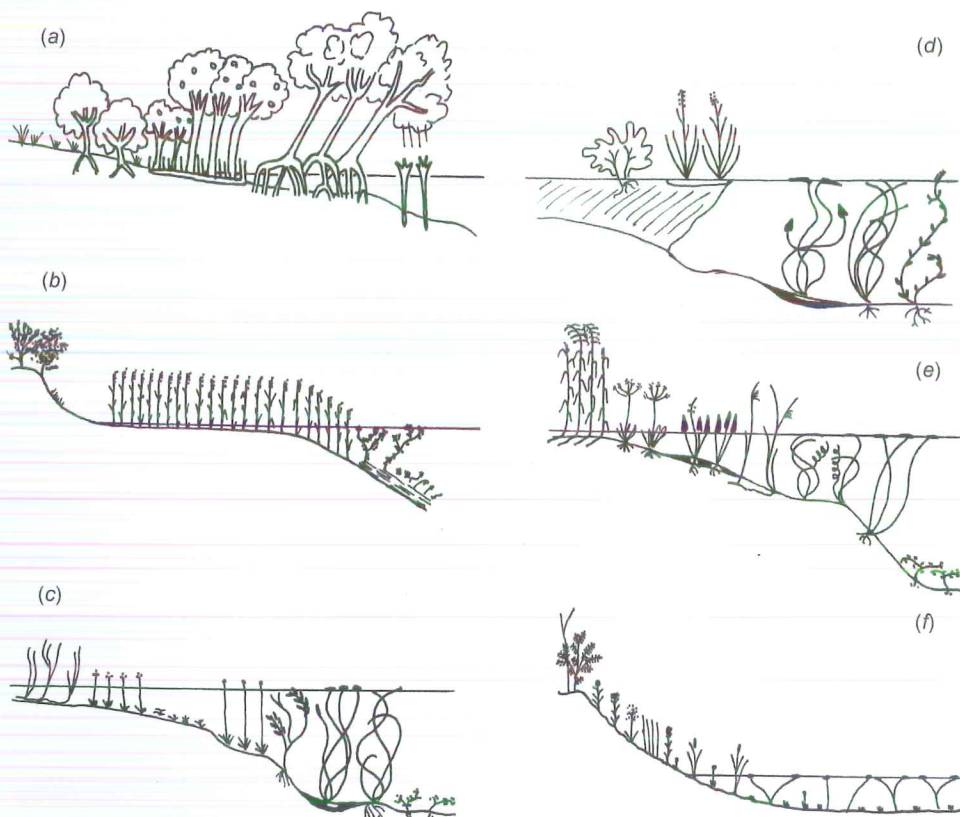


FIGURE 10.1 Some examples of plant zonation: (a) a mangrove swamp of the Caribbean (after Bacon 1978); (b) the eastern shore of Lake Kisajno, northeastern Poland, a typical small-lake phytolittoral (after Bernatowicz and Zachwieja 1966); (c) a sandy shoreline (after Dansereau 1959); (d) a bog (after Dansereau 1959); (e) the St. Lawrence River (after Dansereau 1959); (f) Wilson's Lake, Nova Scotia (after Wisheu and Keddy 1989b).

summarize much of the spatial variation in wetlands. Further, many of our conceptual models in ecology are built around gradients and the distribution of species along them. The oft-repeated admonition by my Ph.D. supervisor, Chris Pielou, was that ecologists should stop trying to find imaginary homogeneous habitats and use the gradients that nature has provided. For all of these reasons, much of my own wetland work has involved the study of gradients.

Wetland zonation can be thought of as a natural experiment (*sensu* Diamond 1983) where nature has set up a pattern of variation for us to

investigate. Most zonation patterns summarize the consequences of differences in water level, from floodplains in Brazil (e.g. Junk 1986) to temperate zone peatlands in Asia (e.g. Yabe and Onimaru 1997) and from salt marshes in Spain (e.g. Garcia *et al.* 1993) to lakeshores in Africa (Denny 1993b). A wetland spread out along a shoreline is not only like a spectrum, it may also be compared to a cadaver neatly spread out and already partly dissected in order to help a struggling medical student. Like medical students, we may find it useful to begin where nature has given a helping hand rather than leaping immediately into unattended surgery.

10.2 Shorelines provide a model system for the study of wetlands

Vegetation on shorelines is closely connected with water levels (e.g. Pearsall 1920; Gorham 1957; Hutchinson 1975). The result is conspicuous zonation. The large rivers and lakes of the world provide extensive areas of such shoreline habitat (Table 10.1). It is natural that our first reaction to zonation is to pull out a field note book and make a sketch of it. Recall the six sketches of zonation patterns from studies in different parts of the world in Figure 10.1. One gains the impression that some wetland ecologists still think that once a sketch of plants has been made, the scientific work is done. In truth, it has barely begun. Primary production, for example, varies among these zones reaching a maximum in shallow water emergent macrophytes (Figure 10.2). The distribution of animals is, in turn, related to the zonation of wetland plants (Figure 10.3).

Zonation of animals in wetlands has received less attention perhaps because animals are less visible and more mobile. But we might expect similar sorts of patterns with them, if only because flooding can directly change food supplies, or indirectly change the habitat by changing the vegetation. For example, Price (1980) has documented zonation patterns of 11 species of foraminifera in salt marshes. Arnold

and Frytzel (1990) found that flooding was an important factor in predicting the distribution of mink, with a strong tendency for them to select large semi-permanent and permanent wetlands with high water levels and irregular shorelines. The distribution of breeding birds also shows zonation, with species showing marked preference for certain vegetation zones in both freshwater marshes (Prince *et al.* 1992; Prince and Flegel 1995) and salt marshes (Weller 1994b).

Each gradient may appear to have its own zonation pattern, depending upon the species that are present. Hence, it may first be useful to review the big picture – to recall that there are typically four wetland types along a gradient of water level and elevation (recall Figure 2.27). Highest on the shore are wooded wetlands. These are only flooded for short periods of time each year and are dominated by trees and shrubs. At lower elevations with more flooding, woody plants give way to wet meadows. Although wet meadows are flooded for much of the year, they are uncovered for several months in each growing season, and so are occupied by plants that show only minimal modification to cope with flooding. As flooding increases further, wet meadows give way to

Table 10.1 Large rivers and lakes that provide extensive areas of shoreline with zoned plant and animal communities

	Country	Average annual discharge at mouth (m ³ /s)
Ten largest rivers of the world		
Amazon	Brazil, Peru	180 000
Congo	Angola, Democratic Republic of the Congo	42 000
Yangtze Kiang	China	35 000
Orinoco	Venezuela	28 000
Brahmaputra	Bangladesh	20 000
Yenisei	Russia	19 600
Rio de la Plata	Argentina, Uruguay	19 500
Mississippi-Missouri	U.S.A.	17 545
Lena	Russia	16 400
Mekong	Burma, Cambodia, China, Laos, Thailand, Vietnam	15 900
		Surface area (km ²)
Ten largest lakes of the world		
Caspian Sea	Russia, Kazakhstan, Turkmenistan, Iran	371 000
Lake Superior	Canada, U.S.A.	83 300
Lake Victoria	Kenya, Tanzania, Uganda	68 800
Aral Sea	Kazakhstan, Uzbekistan	66 458
Lake Huron	Canada, U.S.A.	59 570
Lake Michigan	U.S.A.	57 016
Lake Tanganyika	Burundi, Tanzania, Democratic Republic of the Congo, Zambia	34 000
Great Bear Lake	Canada	31 792
Lake Baikal	Russia	31 500
Lake Nyasa	Malawi, Mozambique, Tanzania	30 500

Source: After Czaya (1983).

emergent marsh, with plants that grow under flooded conditions; these sites may only be uncovered for a short time during drought periods, and as a result, plants show increasing morphological adaptation to flooding. Linear leaves and aerenchyma become conspicuous. Below this, plants occur that are truly aquatic, many with floating leaves.

Even peatlands, which sometimes seem to operate differently from marshes and swamps, are zoned in

a similar manner. Both bryophytes and vascular plants change along elevation gradients (Vitt and Slack 1975, 1984), with the bryophytes being more sensitive to the water table than most vascular plants (Bubier 1995; Bridgham *et al.* 1996). Pools of water have herbaceous aquatic plants, and shallow depressions support emergent sedges. At higher elevations, shrubs become increasingly dominant (Dansereau and Segadas-Vianna 1952; Gorham 1953; Glaser *et al.* 1990; Bubier 1995).

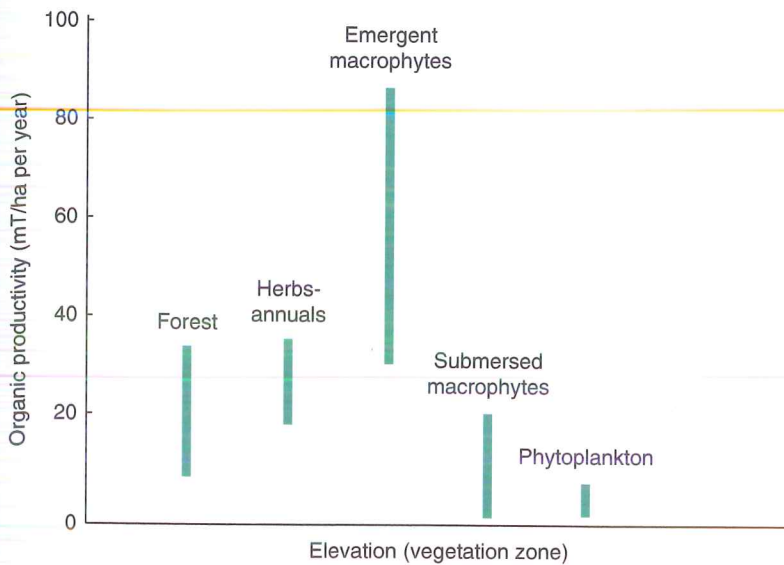


FIGURE 10.2 Changes in primary production with water level. (After Wetzel 1989.)

10.3 Possible mechanisms of zonation

We have recognized the importance of zonation to the study of wetland ecology; now we will move on to explore some of the possible processes behind it.

10.3.1 Ecological succession

Many interpretations of zonation emphasize that plant communities in Figure 10.1 appear to follow a temporal trend, that is, they appear to repeat the sequence of events that would occur as a wetland gradually filled in with detritus and turned into land. "Zonation, therefore, is taken to be the spatial equivalent of succession in time, even in the absence of direct evidence of change" (Hutchinson 1975, p. 497.) This view that zonation patterns are a profile through a successional sequence is widespread: it has been described for peatlands (e.g. Dansereau and Segadas-Vianna 1952) and small marshes along lakes (e.g. Pearsall 1920; Spence 1982). In all these circumstances, organic matter produced by the wetland, combined in some cases with sediment trapped by the vegetation, gradually increases the

elevation of the substrate, turning shallow water into marsh, and marsh into land.

This view – zonation being succession – goes back at least to the early 1800s (Gorham 1953). J. A. De Luc's book, *Geologic Travels*, published in 1810, recognized six discrete stages in the transformation of a lake into a peaty meadowland. Further, De Luc proposed that the rate of succession is greatest on shallow shores; on steep shores the vegetation zones are narrow and the process of change through time nearly non-existent. Walker (1970) also draws attention to Gough's description in 1793 of how lakes are converted to dry land by the accumulation of organic matter, so that "the margin of the pond will be progressively advanced" and the land thereby produced "will, in time, be covered with a bed of vegetable earth," the upper limit of which is set by dry periods because exposure to air will allow decomposition. Such observations were systematized as a successional sequence called a hydrosere by Tansley (1939). As the concept of ecological succession was

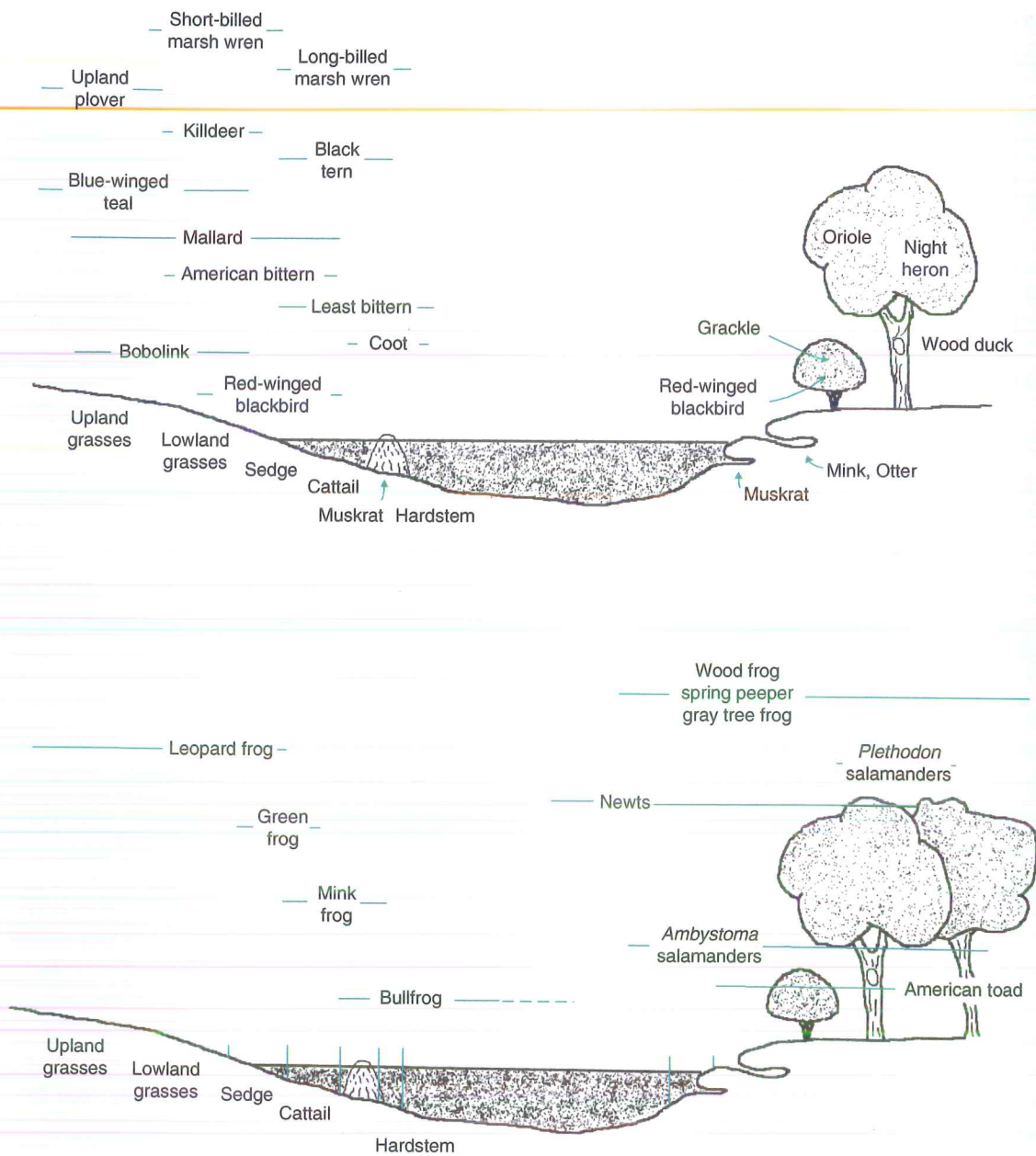


FIGURE 10.3 Zonation in some birds and mammals (top) and amphibians (bottom) in relation to water level and vegetation. (After Weller 1994a.)

popularized with the growth of ecology in the mid-1900s, “pond zonation” was frequently presented as “pond succession” in introductory ecology texts.

Zonation and succession may be closely linked in circumstances such as small ponds and peatlands, where organic matter accumulates, but even De Luc apparently understood that his generalization did

not apply to the steep shores of lakes. With the explosion of ecological studies in the later 1900s, it became clearer that there are many natural forces that delay or even restart such successional sequences. As the effects of fires, floods, storms, and droughts were better documented, many "temporal" successional sequences could perhaps be better understood as dynamic balances between succession and disturbance (e.g. Pickett and White 1985). Simultaneously, population biologists were placing increasing emphasis on the mechanistic interactions among species, leading Horn (1976) to suggest that succession was best understood as a "statistical result of a plant-by-plant replacement process." The importance of disturbance, and the complexity of responses to it, has challenged many of the standard ideas about succession, stability, and predictability in nature (Botkin 1990).

One definitive study examined no fewer than 159 transitions in vegetation types from a series of 20 sediment cores (Walker 1970). In these cores one could find pollen from different vegetation types along a successional path from open water (1) through reeds (5) to peat bog (11). If succession was straightforward and unidirectional, then all 159 transitions should have shown change in the same direction. In fact, there were many exceptions (Figure 10.4, top). Seventeen percent were outright reversals in direction, although these, according to Walker, could well be caused by short-term changes in water level or climate. All successional changes had to pass through a marsh stage dominated by reeds (vegetation type 5 in the table and figure). And, in the end, nearly all ended up in bog (Figure 10.4, bottom). (Note that in Walker's study, mixed marsh was number 12, and simply represented an uncommon and early stage in succession - I have kept his numbering in case you wish to read his original paper.) Hence, we have to accept, at the very least, that even in cases where succession is in progress, many factors, including fires and beaver dams and muskrat grazing, can reverse the direction of change, at least temporarily.

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	6	1	1
	7	2	.	.	2	8	2	3	.	17
	8	1	.	1	.	1	2	3	.	8
	9	.	.	.	1	2	.	1	.	.	1	10	.	15
	10	1	.	.	.	1	.	.	.	2	.	.	10	15
	11	1	1	.	1	3
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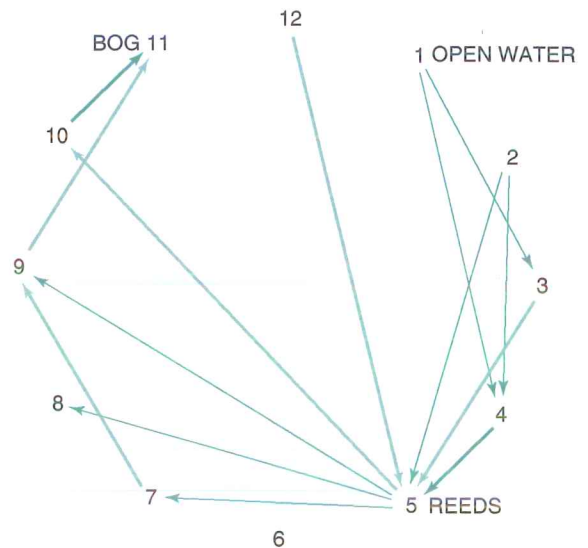


FIGURE 10.4 Frequencies of transition among 12 vegetation stages, ranging from open water (1) through reed swamp (5) to bog (11) to mixed marsh (12), in 20 pollen cores from a range of wetlands including small lakes, valley bottoms, and coastal lagoons in the British Isles. Top, tabulated frequencies; bottom, transition diagram (line thickness shows relative frequency). (After Walker 1970.)

Another source of data that has challenged the succession view is the ubiquity of buried reserves of seeds (Table 4.1). We now understand that disturbance will trigger the re-emergence of species from pools of their buried seeds. Charles Darwin himself had commented on the remarkable number of seedlings that emerged from a spoonful of mud, and increasingly, ponds and potholes were found to be vast repositories of buried seeds (e.g. Salisbury

1970; van der Valk and Davis 1976, 1978). This led van der Valk to propose that many zonation patterns were not successional sequences, but rather represented short-term responses of plant communities to local changes in the environment.

There has therefore been a progression of views on zonation, the past ones emphasizing long-term unidirectional succession, the later ones emphasizing the short-term responses of organisms to changing environmental conditions. Two specific examples nicely illustrate this shift in emphasis. In 1952, Dansereau and Segadas-Vianna could draw zonation profiles of peat bogs in eastern North America (Figure 7.9), and confidently relate them to succession diagrams ending in climax vegetation of *Picea mariana* or *Acer saccharinum* (these being named the Pictum marianae and Aceratum saccharophori associations). The many other vegetation types they named were considered to belong to one of three stages of bog succession: pioneer, consolidation, and subclimax, all leading, by means of peat accumulation, from open water to woodland. In 1996 Yu *et al.* described zonation through a single shoreline swamp at Rice Lake (just north of Lake Ontario), with a zonation sequence not unlike that discussed by Dansereau and Segadas-Vianna. Aided by sediment cores, and by studies of pollen and plant macrofossils, Yu *et al.* found two main stages in the vegetation history. An open marsh stage with sedge genera such as *Carex* and *Eleocharis* persisted for some 2700 years with no successional change, a situation they explain by fluctuating water levels. Then, about 8300 years BP, there was a transition to perennials associated with wet meadows (e.g. *Verbena hastata*, *Lycopus americanus*, and *Carex* spp.) and by about 7500 years BP a transition to cedar (*Thuja occidentalis*) swamp. This change coincided with a regional period of warm and dry climate. The adjoining lake levels dropped and the swamp went dry about 1000 years later. During a cooler and wetter period, lake levels rose and the cedar swamp reappeared. Yu *et al.* conclude: "Paleoecological data for the past 11000 years show that there were no significant successional changes

of marsh communities for about 2700 years . . . When change did occur, it was ultimately controlled by allogenic [external] factors such as climate and water level changes." Further, when the climate changed, "The herbaceous marsh converted directly to cedar swamp without the shrub-marsh and(or) alder-thicket stages."

These two studies illustrate the change in perspective that has occurred over the last 50 years. It would be far too easy, however, merely to conclude (as is often done) that a correct view (dynamics) has replaced a wrong one (succession). Even Dansereau and Segadas-Vianna noted that fluctuating water levels could control vegetation succession, and that fire could cause vegetation to regress. And Yu *et al.* would have to concede that, at Rice Lake, trees are now growing in accumulations of 2 meters of peat and several more of organic silt, thereby elevating the swamp forest above what would otherwise be open water. Whether one therefore focuses upon succession or on short-term dynamics would appear to be somewhat a matter of emphasis and perspective: general patterns as opposed to site histories, large-scale processes as opposed to small-scale dynamics, and classification as opposed to process.

These developments leave us with two questions about zonation. What purpose or advantage is there in relating zonation to succession? If there is some value, then in what circumstances is this a correct parallel to draw? For the purposes of this book, I assume that viewing zonation as succession may be useful in habitats such as peatlands, where unidirectional change driven by the accumulation of peat is a powerful and useful generalization. Even progressive changes in peat accumulation may, however, occasionally reverse themselves (Figure 10.4). In other cases, such as the shores of large lakes or rivers, the connection between zonation and succession is weak, and if anything, confuses rather than clarifies the causes of patterns seen in the vegetation (Figure 2.27). In these cases, it may be best to view the shoreline as a dynamic response to changes in water level, with short-term successional trends (or perhaps

just competition) repeatedly interrupted by flood, drawdowns, ice scour, and fire. Overall, I suggest that succession is a useful concept to keep in our vocabulary, but we should be careful about when and where we use the concept.

10.3.2 Physical factors

The direct effects of physical factors have also been offered as an explanation for zonation on shorelines and for the distribution patterns of most plants. Pearsall (1920) studied plant patterns in wetlands around English lakes, and concluded (p. 181) "sediments become finer as water deepens; since sediments are zoned along lake shores and since they differ in chemical composition, we are justified in assuming that zonation of vegetation is a result of differences in soil conditions." He placed particular emphasis upon soil organic matter, and silt and clay content. Spence's review (1982) added in some extra factors, such as lower light levels in deeper water, but still assumed as a first approximation, at least, that physical factors themselves produced the different distributions of species.

Elsewhere, Myers (1935) described the kinds of zonation he encountered along watercourses in northeastern South America, and offered the explanation of physical factors as controls upon the different kinds of shoreline vegetation. Near the sea, he said, the zonation consisted of mangroves such as *Rhizophora mangle* which mixed with and then, as the water freshened, gradually gave way to *Pterocarpus draco*. "The distance to which the mangrove zone extends upstream is doubtless determined by the influence of brackish water, and this, in its turn, in these uniformly sluggish streams . . . depends chiefly on the size of the river." The sequence from the ocean inland went as follows: (i) *Rhizophora*, (ii) *Pterocarpus* (often mixed with *Pachira aquatica*), (iii) mixed bank vegetation "smothered by a dense curtain of creepers," (iv) swamp forest with no differentiated bank fringe, (v) tall rainforests with no differentiated bank fringe. Myers was of the opinion that the kind of

zonation he saw could be explained by three main causes: the width of the stream, the character of the water, and distance from the sea.

Since then, there has been increased sophistication in the study of plant response to flooding. As we have already seen (Chapter 1), flooding is associated with low soil oxygen levels. Aerenchyma provides one means of avoiding this stress, but in the absence of transported oxygen, the aerobic metabolism of the plant is superseded by the glycolytic pathway, and the products of anaerobic metabolism accumulate (Crawford 1982). These problems are compounded when plants are flooded by saline rather than fresh water.

When you compare species from different habitats, there are certainly metabolic differences among species, as illustrated by the degree to which plants accumulate alcohol dehydrogenase when flooded (Figure 10.5). It is tempting to assume therefore, that the distributions of species in zoned wetlands (whether freshwater or saltwater) are directly a consequence of their abilities to cope with physical constraints imposed by flooding and salinity. Like the view of zonation as succession, it provides a useful one-size-fits-all view of wetlands. But is it correct or useful? One way to explore the importance of physiology is to use field experiments where one explores the possibility of biological interactions. If one can show that factors like competition are producing zonation, then physiological differences alone may not account for the patterns seen in nature.

10.3.3 Biological interactions can cause zonation

So what evidence do we have for biological factors producing zonation? There are fewer examples for us to draw upon, because these sorts of studies require properly designed experiments and often need to run for several years.

Let us begin with an example from salt marshes. In Alaskan salt marshes, the zonation of vegetation is closely connected to flooding (Jefferies 1977; Vince and Snow 1984). Four zones can be delineated with

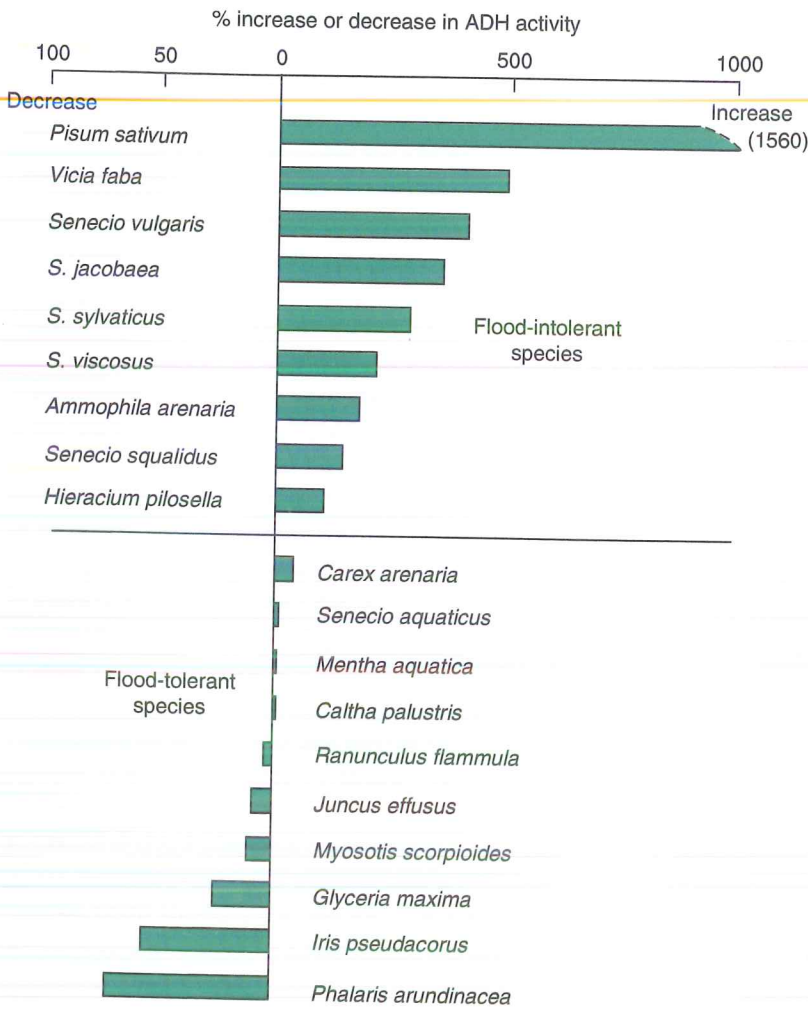


FIGURE 10.5 Alcohol dehydrogenase (ADH) levels in an array of species including flood-tolerant plants (bottom) and flood-intolerant plants (top). (From Crawford and McManmon 1968.)

increasing elevation: outer mud flat (*Puccinellia nutkaensis*), inner mud flat (*Triglochin maritimum*), outer sedge marsh (*Carex ramenski*), and inner sedge marsh (*Carex lyngbyaei*). At one extreme, the outer with *P. nutkaensis* is flooded some 15 times per summer for periods of 2–5 days each, leading to a soil water salinity of some 15–35%. The inner sedge marsh with *C. lyngbyaei* is flooded only twice per summer, when a new or full moon coincides with the perigee (although this single flood may last more than 5 days) and soil salinity is only 6–11%, slightly below the 12% for flooding seawater.

Reciprocal transplant experiments across these four zones (plus a fifth, *Poa eminens*, which grows on riverbank levees), showed that all species could grow in zones when neighboring plants were removed (Snow and Vince 1984). Further, the *P. nutkaensis* from the outer mud flat grew nearly four times larger when transplanted upslope to the inner mud flat than when transplanted to its own zone. The two species from the highest elevations (*C. lyngbyaei* and *P. eminens*) did, however, show reduced growth when transplanted downslope to the outer mud flat. When the same five species were grown at different

salinities in pots, all grew best in waterlogged but low-salinity conditions. Thus, in spite of conspicuous zonation, the limited distributions of these species cannot be accounted for simply by tolerances to salinity or flooding. Zonation therefore must be partly produced by biological interactions; in general, Snow and Vince (1984) suggest, "species occurring in zones along a physical gradient are often limited by physiological tolerance toward one end of the gradient, and by competitive ability towards the other."

A similar set of experiments were applied to study zonation in New England salt marshes (Bertness and Ellison 1987). Although the species were different (*Spartina alterniflora*, *S. patens*, *Distichlis spicata*, *Salicornia europea*), the conclusions were similar: "the performance of each species was lowest in the low marsh and highest on the terrestrial border of the marsh" (p. 142).

Other studies in salt marshes report similar results. For example, on the east coast of North America, the woody species *Iva frutescens* (marsh elder) occurs at higher elevations in marshes. Bertness *et al.* (1992) found that, when these shrubs were transplanted to elevations lower than those they normally occupied, all died within 1 year. Since death occurred in both cleared and uncleared plots, the lower limit of *I. frutescens* is apparently set by physiological constraints rather than competition.

Similar results have been found in freshwater marshes. Grace and Wetzel (1981) studied two common and widespread species of cattails (*Typha latifolia* and *T. angustifolia*); together these species comprised 95% of the biomass at their study site, a small experimental pond in the American Midwest. While both species are relatively tall and spread from extensive mats of rhizomes, the taller of the two, *T. angustifolia*, usually occupies the lower areas of shoreline in the deeper water. Is this just because each species grows exactly where it is best suited by physiology? Both species were transplanted to pots and grown without neighbors at a range of elevations from 15 cm above the waterline to 100 cm below it. The transplants of one species grew well over a greater range of elevations than the natural population,

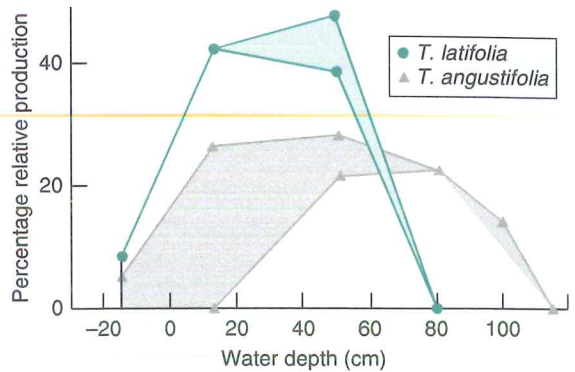


FIGURE 10.6 The growth of two species of *Typha* as a function of water depth; the shaded regions show reduction caused by the presence of the other species. (After Grace and Wetzel 1981.)

suggesting the interaction was strongly one-sided (Figure 10.6). The *T. latifolia* was only marginally affected by *T. angustifolia*, whereas *T. angustifolia* which naturally occurred in the deeper water was apparently excluded from higher elevations by *T. latifolia*. Here is evidence that zonation can be attributed to competition, and that a dominant competitor can exclude a weaker neighbor forcing it into a zone that is physiologically suboptimal.

Another widespread feature of zonation patterns in wetlands is the presence of woody plants at higher elevations (Figure 10.7, left). This produces the characteristic zonation pattern encountered throughout, for example, the northern temperate zone including North America (Keddy 1983), northern Europe (Spence 1964; Bernatowicz and Zachwieja 1966), and Asia (Yabe and Onimaru 1997). Is each species simply responding to the flooding regime, or are biological factors such as competition contributing to these patterns? Experimentally removing these shrubs from many selected areas of shoreline showed that the number of shoreline plants at this elevation increased (Figure 10.7, right).

It is therefore clear that at least some of the herbaceous plants found in flooded conditions can actually grow under considerably drier conditions. This has two possible explanations. It may be that the species that spread up the shore are merely spilling

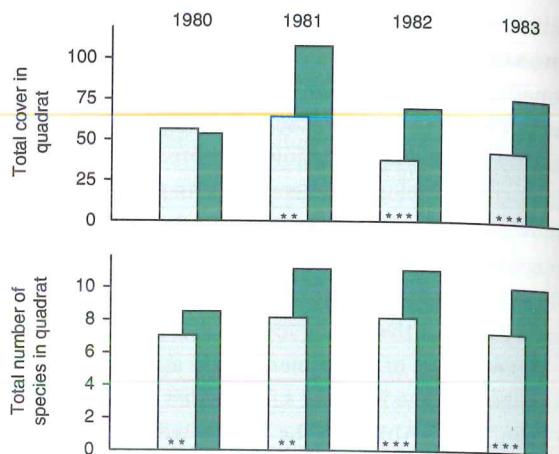


FIGURE 10.7 Shrubs occupy higher elevations in many wetlands (left). Experimentally removing the shrubs increases the cover and number of species of herbaceous wetland plants (right). (From Keddy 1989b.) (See also color plate.)

over from their preferred habitat into marginal conditions created by removing shrubs. It is also possible that these plants are moving to higher elevations which are not marginal, but which actually are better for growth than the lower elevations. Returning to Figure 10.6, *Typha angustifolia* actually can grow better near the water line (where it is naturally absent) than it can in 100 cm of water (where it is naturally present). In nature it apparently occupies a habitat that is less suitable than adjoining drier habitats occupied by neighboring species.

In conclusion, early studies on zonation made the simple assumption that each species grows to the limits permitted by its own physiology. The importance of competition from neighbors in controlling species distributions has since been implied in studies from a wide range of habitats and species (Miller 1967; Mueller-Dombois and Ellenberg 1974; Colwell and Fuentes 1975; Keddy 1989a). Recent experiments demonstrate that neighbors can exert a significant influence upon distributions. That is to say, zonation is an ecological, not just a physiological, phenomenon. Further exploration

of the mechanisms requires the introduction of some new terminology.

10.3.4 Ecological and physiological response curves in zonation

The terminology of ecological and physiological response curves (Mueller-Dombois and Ellenberg 1974) or, equally, the terms realized and fundamental niches (Pianka 1981) clarify the biological and physiological interactions that produce zonation. The ecological response curve (realized niche) is the distribution pattern of a species in the field with neighbors present. Zonation patterns such as those in Figure 10.1 show only ecological response curves. In contrast, the physiological response curve is the distribution of a species when neighbors are removed, in which case the distribution is presumably explained by the direct effect of physical factors. In the majority of cases studied, the distribution of organisms expands when neighbors are removed – the physiological response curve is usually greater than the ecological response curve. The greater the difference between the two, the

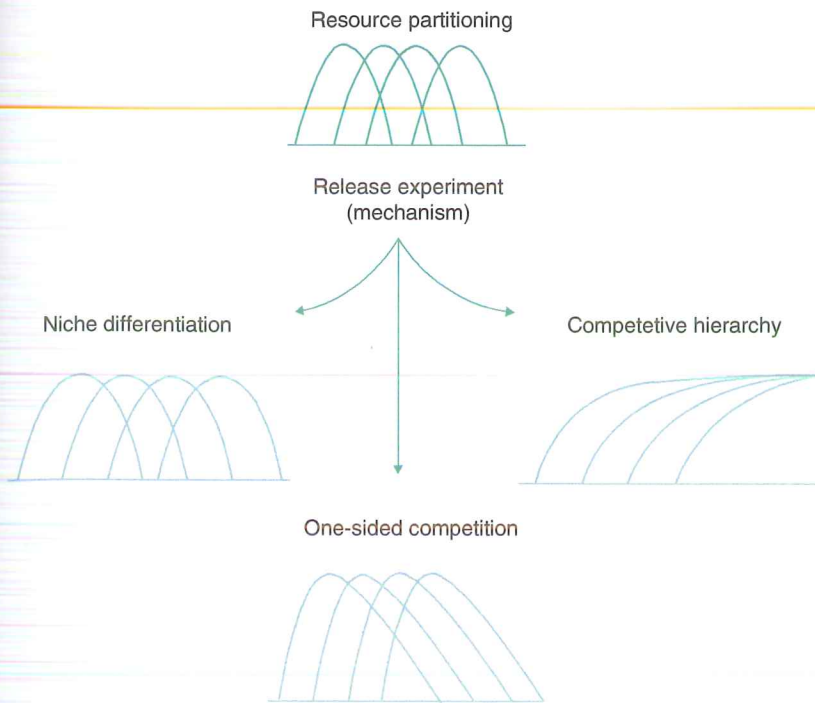


FIGURE 10.8 A zonation pattern (top) can be caused by at least three different competitive mechanisms (bottom). Only experiments can separate among the various mechanisms.

greater the effects of competition from neighbors in producing zonation. (Note that if there are commensal or mutualistic relationships, the removal of neighbors may lead to narrower physiological response curves [e.g. Bertness and Leonard 1997].)

In the zoological literature, zonation and ecological response curves are often referred to as “resource partitioning” (Schoener 1974), and it is generally assumed that ecological and physiological response curves (or, equally, realized and fundamental niches) are very similar. However, in the absence of field experiments, this is pure speculation (Keddy 1989a; Wisheu 1998). When appropriate experiments on partitioning are carried out, two extreme situations are possible. In one case (Figure 10.8, left) the physiological curves remain nearly identical to the ecological (top). In such circumstances, competition plays a minor role in producing zonation patterns. In the other case (Figure 10.8, right), the physiological response curves shift and nest one within another, a situation termed inclusive niches or shared

preference. In such circumstances, competition plays a major role in producing field distributions. Here is a situation where we need fewer ecologists drawing zonation patterns or writing about “ecotones,” and more conducting field experiments.

It may be possible to connect these ideas to the strategy concepts developed by Grime (1977, 1979) and Southwood (1977, 1988). Using their terminology, one group of species can be classified as stress tolerators. Stress tolerators occupy habitats that are chronically unproductive, and they occupy those sites not because they are better competitors, but simply because they can tolerate the extremely undesirable conditions better than other species. There appear to be many examples of wetland species occupying marginal habitats that are beyond the physiological tolerance limits of most other species, including *Zostera* (eelgrass) in salt marshes, and umbrids (mudminnows) in low-pH bog ponds.

Perhaps, then, many emergent and submersed plants are stress tolerators. That is to say, they are excluded by

competition to a marginal habitat that is unsuitable for other species. Although they tolerate flooded habitats, they actually grow better under less stressful conditions. In order to tolerate the extreme conditions, they must reduce rates of photosynthesis or divert photosynthate away from foraging, growth, and reproduction into those adaptations crucial to tolerating the stress. Deeply buried rhizomes, aerenchyma, and reduction in leaf surface area could all be interpreted as costs imposed by conditions. A further cost of such traits could be inherently low growth rates – recall that aquatic plants have inordinately low assimilation rates, usually less than $10 \text{ mol CO}_2/\text{m}^2$ per second (Sand-Jensen and Krause-Jensen 1997).

It may seem to be outrageous to suggest that wetland plants would generally grow better in drier areas. But there is a long list of costs associated with flooding. The biomass invested in petioles increases steadily with depth in all floating-leaved plants that are rooted; this biomass could instead be allocated to leaves or seeds if the plants were growing in shallower water or on mud flats. There are lesser but surely measurable costs associated with the production of aerenchyma; even if aerenchyma could be produced nearly without costs, the presence of aerenchyma confirms the metabolic constraints imposed by flooded soils. One could therefore postulate a scenario in which wetland plants tolerate extremes of flooding but do not physiologically require them. In this scenario, flooding has the primary role of killing the terrestrial plants that would otherwise invade the site and exclude the wetland species. That is, the requirement for flooding may be as much ecological as physiological.

The assumption that organisms are best adapted to the sites they occupy still is often automatic, particularly in physiological studies, but there is growing evidence that many species occupy habitats that are physiologically suboptimal in order to escape the higher costs of occupying habitats where better competitors are already established. We have already seen data suggesting that wetland plant species would grow better under less flooded conditions than those in which they are naturally found (e.g. Figures 10.6,

10.7). And, while competition is an important and pervasive force in wetlands (e.g. Keddy 1990a; Gopal and Goel 1993), a number of recent experiments suggest that competition is relatively less important in areas that are permanently flooded (e.g. McCreary *et al.* 1983; Wilson and Keddy 1991), leading Grace (1990) to conclude independently that deep water offers a refuge for weaker competitors. Postulating that wetland plants would all have shared preference for mud flats or wet meadows may be an unrealistic extreme, but a third alternative is possible, one-sided competition (Figure 10.8, bottom). Here each species' physiological response curve is shifted in the same direction relative to its ecological response curve. In the case of wetland zonation, one may postulate that, in the absence of neighbors, each species would extend landward of its field distribution. Were this to be the case, wetland plants might be sorted into competitive hierarchies where the best competitors have excluded other species into progressively deeper water, forcing such species to adopt increasingly costly adaptations to tolerate flooding.

The problem with exploring such issues is the size and scale of the field experiments needed to study them. Studies with single species are helpful, but we never know how far we can generalize. To surmount this problem we recently grew ten different wetland plant species representing a wide array of growth forms along an elevation gradient in the absence of any neighboring species. That is, we removed competition (or mutualism) as a source of zonation. The species included widespread wetland grasses (*Panicum hemitomon*), emergents (*Peltandra virginica*, *Pontederia cordata*), and sedges (*Cladium jamaicense*, *Schoenoplectus americanus*). Over 3 years, these wetland species all grew better in areas with little flooding (Figure 10.9). Now there are minor differences among species – it appears that *Acorus calamus* grew better at lower elevations than *Sagittaria lancifolia*, but overall the pattern appears clear: most of these species show preference for moist soils, all are damaged by prolonged flooding, and if flooded for more than half the growing season, they die. Hence, other factors, such as differential

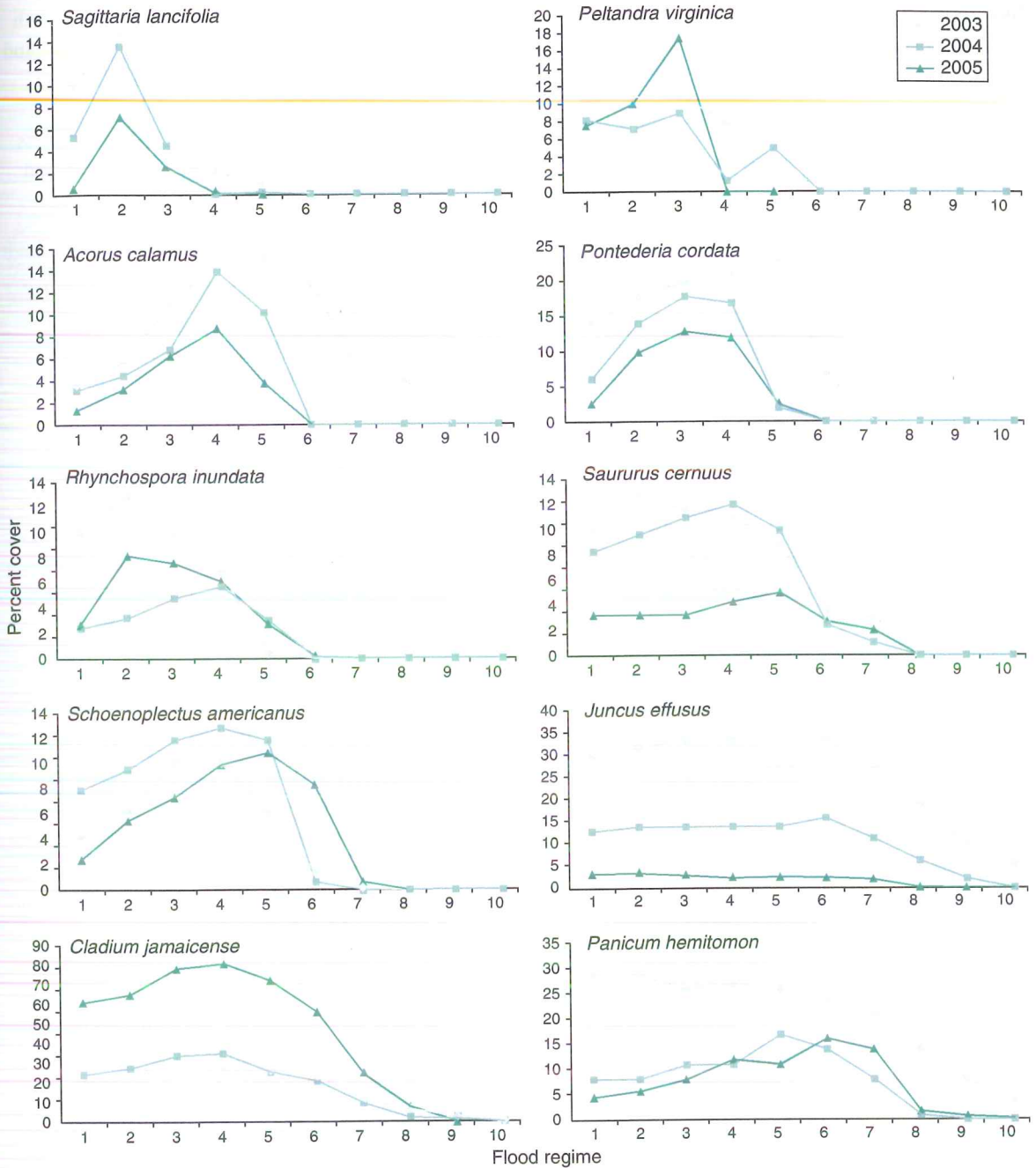


FIGURE 10.9 The effects of flooding regime upon ten species of North American wetland plants over 3 years (2003–2005). All plants were grown without any other species present. The flooding regime ranged from never flooded (left) to continually flooded (right) in an experimental pond in Louisiana. (P. A. Keddy, unpublished data.)

tolerances to competition or grazing, need to be invoked to explain their distributions.

10.3.5 Zonation in arid zone salt marshes

The controls on salt marsh zonation may be quite different in more arid climates. Here, high rates of evapotranspiration produce a salinity gradient that increases with elevation. Hence flooding and salinity are uncoupled as controlling factors. It appears that in Mediterranean-type salt marshes, it is less likely that there is an elevation gradient with one end that is benign and one end that is stressful. Consider an example from southern California, for example, where three zones can be recognized: a low zone with *Salicornia virginica*, a middle zone with *Arthrocnemum subterminale*, and an upper hypersaline salt flat. Transplant experiments using *S. virginica* and *A. subterminale* showed that the intermediate elevations were the most suitable for growth of both species, presumably because lower flooding combined favorably with lower salinity (Pennings and Callaway 1992). The two species were therefore crowded into one region favorable to both: since the border between *Salicornia* and *Arthrocnemum* occurs in prime habitat for both, the competitive interactions were not one-sided but rather represented a stand-off: each species excluded the other from the portion of the superior habitat in which it was the dominant competitor. These marshes therefore differ from the examples we saw earlier, in that the intermediate zone was the less stressful. However, the example also shows that there may be one elevation for which there is a physiological shared preference, with biological interactions therefore producing the final zonation pattern.

10.3.6 Positive interactions also affect zonation in salt marshes

Positive interactions may also influence zonation. Here are three examples. The anoxic soil conditions at low elevations may be alleviated by oxygen

transported by aerenchyma, stimulating the growth of neighbors (Bertness and Ellison 1987; Bertness and Shumway 1993). High soil salinities may be ameliorated by neighbors, allowing seedlings of species such as *Iva frutescens* to establish (Bertness and Hacker 1994). *Juncus gerardi* both shades and aerates intertidal soils, stimulating the growth of neighboring species (Hacker and Bertness 1999). Such positive effects can lead to higher biological diversity on shorelines (Hacker and Gaines 1997). Overall, then, the zonation found in salt marshes appears to result from both positive and negative interactions (Figure 10.10).

When you remove species experimentally to test for competition, you are in fact able to test simultaneously for mutualism. Recall that if a species grows better in cleared plots, this provides evidence of competition; equally, if it grows worse in cleared plots (relative to appropriate controls, of course) then there is evidence for mutualism. If you look back to the competition experiment in Figure 5.9, and look in the top panel at total competition intensity along the gradient, you will see a group of three points with negative competition intensity. These may indicate plots where the effects of neighbors were in fact beneficial – which might make sense in a stressed sandy site that is exposed to waves. Hence, removal experiments allow us to test for biological factors in general. Only when individuals with and without neighbors have identical performance are you justified to assume that biological interactions are negligible. But note that this neutrality is something that you have to demonstrate with an experiment. The assumption that biological factors are negligible – that organisms are only reacting to the physical environment – is no longer acceptable as a starting point in wetland ecology.

10.3.7 Experimental evaluation of zonation and fertility

Zonation patterns may be modified by fertility. The striking changes in plant zonation with changing soil

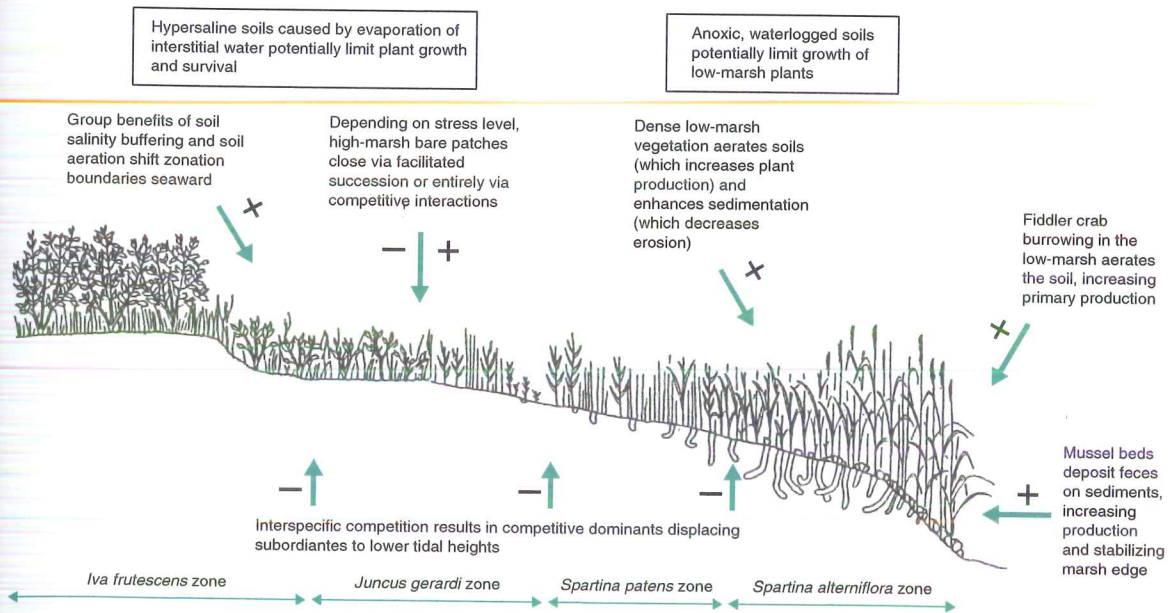


FIGURE 10.10 Some positive and negative interactions in southern New England coastal marshes. (From Bertness and Leonard 1997.)

fertility have been best documented on freshwater shorelines (e.g. Pearsall 1920; Keddy 1983), but the best experimental test comes from coastal marshes. Levine *et al.* (1998) fertilized a series of competition experiments involving typical salt marsh plants: *Spartina alterniflora*, *S. patens*, *Juncus gerardi*, and *Distichlis spicata*. The competitive interactions in fertilized treatments were the reverse of those in the controls. It appeared that *S. alterniflora*, which normally occupied the low elevation zone closest to the ocean, was able, when fertilized, to invade higher areas of the shoreline to exclude both *S. patens* and *J. gerardi*.

10.3.8 Plant species richness and resource specialization

It has long been believed that, all other things being equal (which, of course, they rarely are), higher numbers of species can coexist if they each use a narrower range of resources (e.g. MacArthur 1972; Schoener 1974; Pianka 1981). Certainly, when you

look at a zonation pattern, it seems reasonable: does it not seem probable that more kinds of plants or animals could coexist in a wetland if each occupied a narrower zone of water depths? The test seems simple: measure the range of elevations occupied by each species, and the number of species, and test for a relationship over a large number of sites. This has been done, using a lake in Nova Scotia with an exceptionally rich flora and large numbers of rare species. Some gravel shorelines are **spectacular** in their species richness (Figure 1.7b), while others are rather deficient. Yet, when you measure the mean width occupied by the species, there is no evidence for greater specialization of species on the shorelines with the most species (Figure 10.11). Indeed, the evidence seems to be that the shorelines with large numbers of species have gentle slopes made of a unusual glacial till, and regular disturbance from waves. Similar results were found in Keddy (1983). Such results suggest that coexistence in plants is likely to be explained by factors other than specializations along water depth gradients.

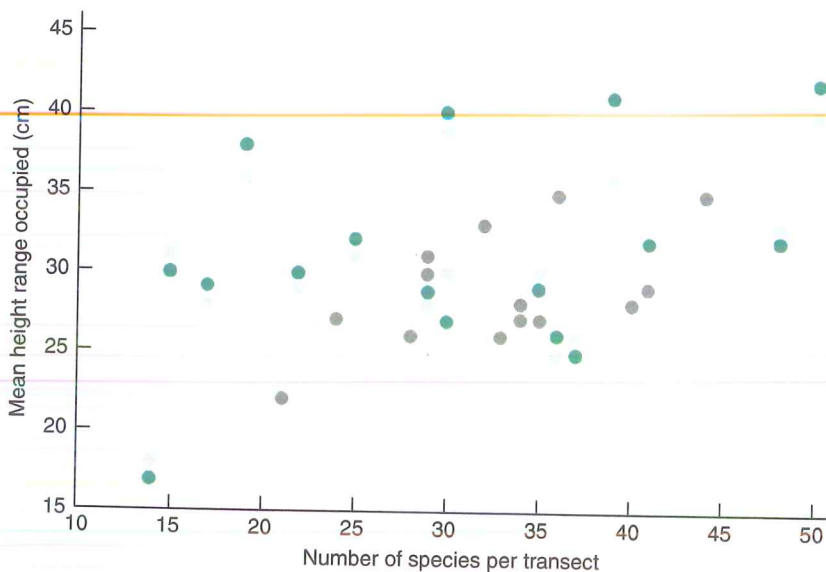


FIGURE 10.11 The mean elevation range occupied by a plant species plotted against species richness in 30 lakeshore transects. Light dots include all lakeshore species; dark dots are shoreline species alone; gray dots indicate both species groups. (From Keddy 1984.)

10.4 Zonation and changing sea level

Sea levels rise and fall through time. The amount of water locked in continental glaciers is one of the most important factors affecting sea level. Over the past century, we have been experiencing rising sea levels, at the rate of 1.8 mm/yr (Figure 7.19).

If global temperatures rise enough to melt the Greenland ice cap, this could cause a change of 6.5 meters (Table 10.2). There is debate not only about how likely this event is, but how fast it will happen (Dowdeswell 2006; Kerr 2006). Recall that thresholds are events where a small change in a causal factor (say mean global temperature) produces a large change in a response variable (say glacier size). Recall too that the transition from ice to water is a classic threshold, since it takes only a small change to produce the phase transition from solid to liquid, or vice versa. While we should always be cognizant of how much sea levels have changed in the past, the data assembled by Douglas (shown in Figure 7.19) make it clear that we are currently in an era of rising sea levels. A good source of evidence is the location of mooring rings in old harbors – once well above sea level, many are

now submerged (Figure 10.12). And no, it is not that the land is sinking, since many of these sites occur in areas that were once glaciated and are still rising in a process known as post-glacial rebound. The sea is simply rising faster than the land.

In the past, shorelines were free to migrate inland when sea levels rose. An added problem in interpreting the effects of rising sea levels for coastlines is the presence of human cities, farms, or roads inland from marshes. A thousand years ago, the marsh would have slowly moved inland, and its area would have remained more or less constant. Now many marshes are pinned between rising oceans and human infrastructure, so as sea levels rise, the wetland slowly disappears.

Where there is natural landscape along the coast, a characteristic zonation pattern occurs. This is typified by a zone of dead forest. A forest does not move inland (like Birnam Wood did in Shakespeare's play *Macbeth*). Rather, the individuals nearest the sea die. Hence, the zone of dead trees is one of the obvious features along receding coasts (Figure 10.13). The marsh then slowly moves inland as herbaceous

Table 10.2 The estimated potential sea level rise that would be caused by melting of present-day glaciers and ice sheets

Location	Volume (km ³)	Potential sea level rise (m)
East Antarctic ice sheet	26 039 200	64.80
West Antarctic ice sheet	3 262 000	8.06
Arctic peninsula	227 100	0.46
Greenland	2 620 000	6.55
All other ice caps, ice fields, and valley glaciers	180 000	0.45
Total	32 328 300	80.32

Source: U.S. Geological Survey (2000).



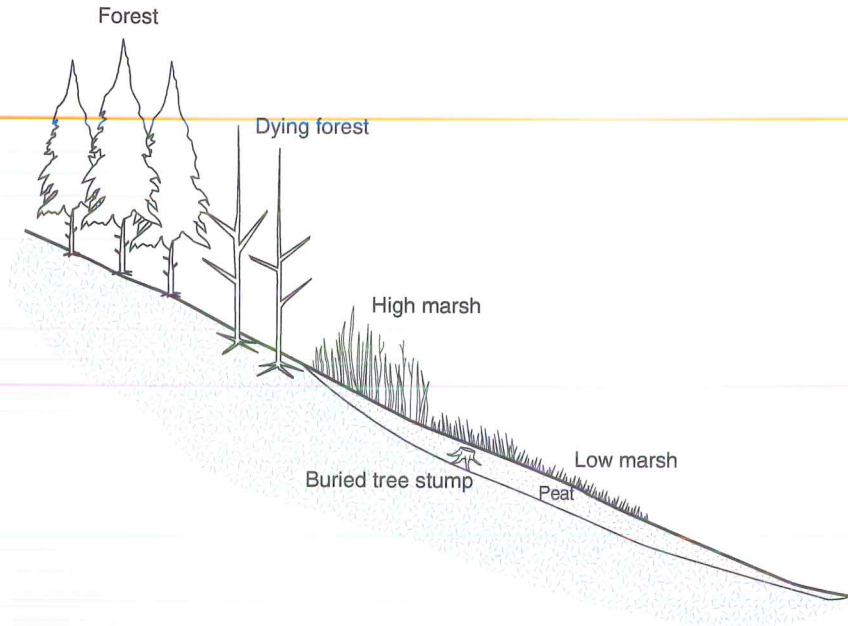
FIGURE 10.12 Construction of the fortress of Louisbourg (left, photo by A. Fennell of painting by L. Parker, from Johnston 1983) was begun in 1719; (right) this old mooring ring was above high tide then – and now it is well below (Taylor *et al.* 2000).

species spread under the dead trees. The exact profile of the shoreline, and the depth of peat, will depend upon a set of factors including rate of rising sea level, rate of primary production, rates of decomposition, rate of herbivory, and frequency of pulses such as hurricanes. A shoreline may not retreat gradually but leap inland with each major storm.

Although low coastal areas like Louisiana and Bangladesh are receiving the most attention, the

steady rise of sea level is an issue in many other places. In northeastern North America (Nova Scotia and New Brunswick), sea levels are rising in the range of 30 to 40 cm per century (Begin *et al.* 1989), thereby causing a regression of forest, and sometimes also creating areas of wetland between the forest and the ocean. Along the coast of New Brunswick, for example, sand dunes are moving upland with rising sea levels, and burying peatlands and spruce forests.

FIGURE 10.13 As sea levels rise, coastal marshes slowly migrate landward, leaving a trail of peat behind them in deeper water. Dead trees on the edge of the upper marsh are the most obvious clue that this process is occurring.



Between the forest and dunes there are frequently areas of shallow water or marsh; this flooding reduces tree growth rates and regeneration. As sea levels continue to rise, these trees in turn are killed and buried by the migrating dunes. Depending upon topography and drainage, the area of marsh changes with time. A complex system of forest, peat bog, sand dunes, and freshwater lagoons therefore occurs, with the dunes and lagoons revealing their origin through the still rooted stumps and standing dead trees emergent amidst them. The presence of conifer stumps in a coastal wetland, like mooring rings under water, is rather obvious evidence that coastlines are changing.

Overall, we have three choices for adapting to these events. Planned retreat recognizes the inevitable, and involves abandoning areas closest to the shoreline. Accommodation involves constructing human features to minimize risk. Ports could be built on shorelines, but human dwellings might be restricted to higher elevations inland. There is also the protection option, reinforcing the shoreline

with sea walls or artificially enhanced dunes or wetlands (Nicholls and Mimura 1998; Vasseur and Catto 2008).

What does this mean for zonation? On one hand, we need to view zonation as a biological phenomenon largely driven by competition, as you have seen from the experiments above. On the other hand, we need to realize that when water levels change, these affect the biological interactions. We have already seen in Chapter 2 how zonation patterns change in the Great Lakes with fluctuations in water levels. It appears that many coastal marshes will appear like Figure 10.13, as biological interactions like competition rebalance in the face of rising sea levels. Although Figure 10.13 is a good starting point, the outcome and shape of our coasts will be influenced by a combination of factors depending upon rates of rise, rates of sedimentation, rates of peat formation, and frequency of storms, producing an array of potential zonation patterns and shoreline profiles (Brinson *et al.* 1995).

10.5 Statistical studies of zonation

Although there are vast numbers of papers with sketches of species distributions along gradients, virtually none has taken the next logical step: the quantitative study of zonation and its control by environmental factors. Such studies are even rarer than experiments. There are at least four reasons for the statistical properties of zonation. (i) Although there are many pictures and a vast literature describing zonation, there is no way to compare such studies without measurable properties. (ii) The zoological literature abounds with theories of resource use (e.g. Miller 1967; MacArthur 1972; Pianka 1981), and zoned communities provide an exquisite opportunity to test hypotheses about such phenomena. (iii) The issue of whether ecological communities are continuous or discrete has raged on for decades without resolution, and there is no way to slay this dragon except to actually measure the manner in which communities change along gradients. (iv) Science requires measurable properties. Without actually measuring species distributions along gradients, we can only tell entertaining tales about them.

What properties might we measure on zonation? Here are four, with a brief rationale for each.

- (i) The degree to which species distributional limits are clustered ("boundary clustering"). At one extreme (Figure 10.14, left) they may be

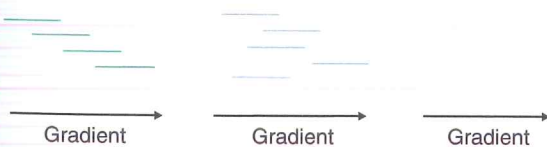


FIGURE 10.14 Species may be distributed along gradients in a manner that is overdispersed (left) like shingles on a roof, random (middle), or underdispersed (right) like pages of a book. Underdispersed boundaries are usually called clustered boundaries. Statistical tests can distinguish among these possibilities.

overdispersed, like the shingles on a roof; at the other extreme (Figure 10.14, right) they may be clustered (Pielou 1975; Underwood 1978). The middle case is a random distribution. Since one can analyze landward and waterward (or upper and lower) distributional limits independently, there are actually two properties here.

- (ii) The range of elevation that each species occupies in a transect. This is a crude measure of realized niche width for a species; averaged over all species, one obtains a measure of mean niche width on that gradient.
- (iii) Species richness. Some shorelines have many species on them, others have very few. By counting the number of species in transects of standard width, one can relate species richness to other properties.
- (iv) Exposure. It has been widely observed that zonation patterns change with exposure to waves (e.g. Pearsall 1920; Bernatowicz and Zachwieja 1966; Hutchinson 1975). By measuring the position of transects along gradients of exposure to waves, one can determine how properties (i) to (iii) are affected by waves and ice scouring.

Given the great theoretical interest in the effects of disturbance upon ecological communities (e.g. Connell 1978; Grime 1979; Huston 1979), it seems remarkable that more studies have not made use of these circumstances.

We now have at least four quantitative properties that we can measure along gradients: boundary clustering, niche width, species richness, and exposure. The next step is to explore some relationships among them.

The first example, Pielou and Routledge (1976), examined data on species distributions in five sets of salt marshes at different latitudes in eastern North America. In many of the transects, species boundaries were significantly clustered, that is, there were zones

composed of sets of species with similar distributional limits. Salt marsh zonation, therefore, looks similar to the right side of Figure 10.14. Moreover, the upper limits were more clustered than the lower limits, irrespective of latitude (Figure 10.15). This pioneering study showed that with proper sampling methods and appropriate null models, it was possible to find measurable patterns in zoned communities.

The causes of such patterns cannot be deduced solely from statistical analyses. None the less, Pielou and Routledge did find evidence that biological interactions were responsible for some of the species distributions. Their logic was as follows. If these patterns were solely the result of physiological responses to salinity and inundation, then distributional limits of species would be independent. If, however, one species set the limits of another through competition, then there would be a tendency for distributional limits to coincide. That is, species distributional limits would tend to abut one another.

In terms of physiological and ecological response curves, Pielou and Routledge (1976, pp. 102–6) suggest that physiological and ecological factors will create different kinds of zonation patterns. Using a set of 40 transects near Halifax, Nova Scotia, they found that distributional limits tended to coincide ($p < 0.001$). Therefore, they concluded that competition produces some of the observed clustering of zonation in salt marshes. Regrettably, the test was too crude to test for changes in the intensity of competition among latitudes.

A subsequent attempt to explore patterns among these properties used data on zonation from a small sandy lake typical of many near the Great Lakes. This lake had an array of zonation patterns including those associated with open sand beaches, sheltered fertile bays, and floating bog margins (Keddy 1981, 1983). The flora of this lake, and the array of vegetation types, appear in many ways typical of the northern temperate zone. The following patterns were found:

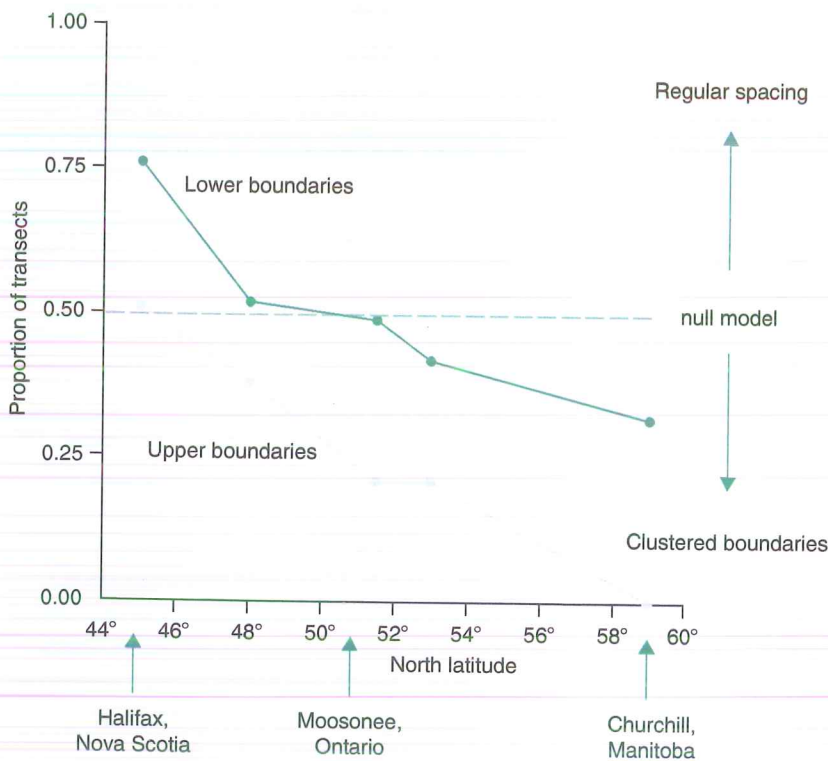


FIGURE 10.15 The clustering of species distributions in salt marshes plotted against latitude. Notice that the lower the measure of clustering, the more species distributional limits coincide. (After Pielou and Routledge 1976.)

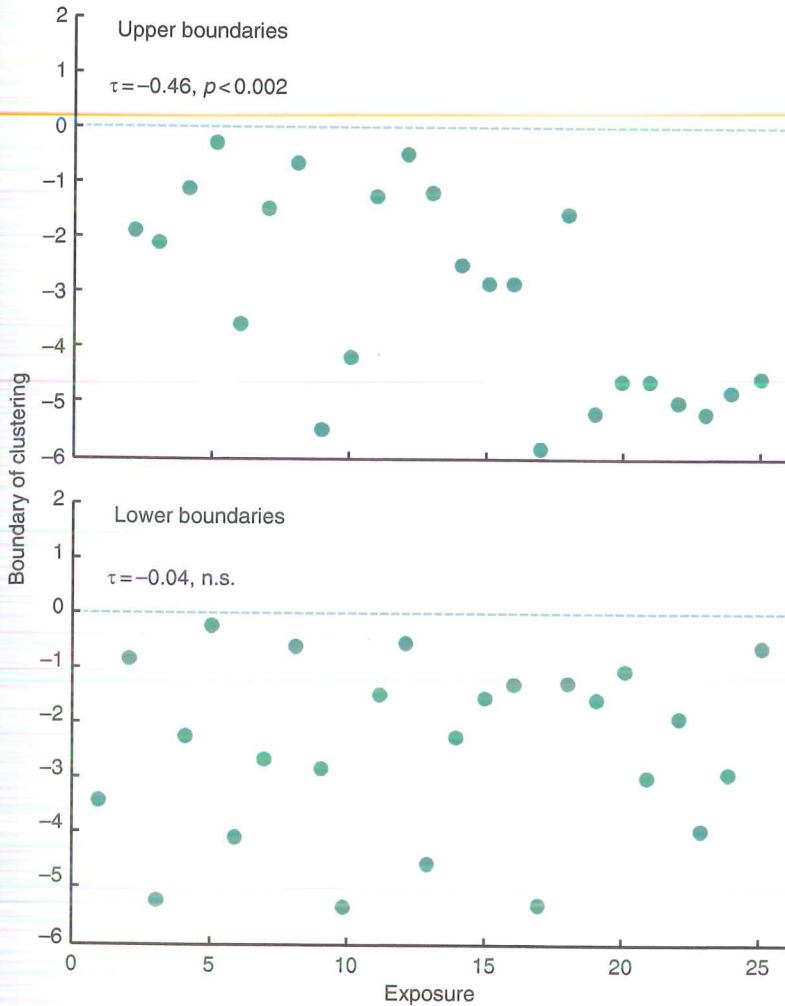


FIGURE 10.16 The clustering of species boundaries plotted against exposure to waves in a small lake. The dashed line presents the null model. (From Keddy 1983.)

- (i) Both the upper and lower boundaries of species were clustered. That is, just as Pielou and Routledge (1976) showed, there were certain elevations where more species reached their distributional limits than would be expected by chance alone. This is shown in Figure 10.16 where the measures of boundary of clustering for each of 25 transects fall below zero.
- (ii) The degree to which species distributions were clustered (that is, the intensity of the zonation on a shoreline) increased with exposure to waves. This occurred because exposure to waves increased the clustering of upper boundaries (Figure 10.16, top); lower boundaries were unaffected (Figure 10.16, bottom).
- (iii) Species distributions were pushed up the shoreline as exposure increased. Figure 10.17 shows how aquatics such as *Lobelia dortmanna* moved up the shoreline as exposure to waves increased. This pattern also showed up in the joint distribution of species as a landward shift in distributional limits (Figure 10.18).
- (iv) Mean niche width did not significantly increase as the number of species in a transect increased.

That is to say, more species were not packed in by increased specialization of each species in the community. However, while the mean may be the same, exposed shores have significantly greater variation in niche widths. That is, some species have very narrow distributions, and others have much broader distributions, than in sheltered bays.

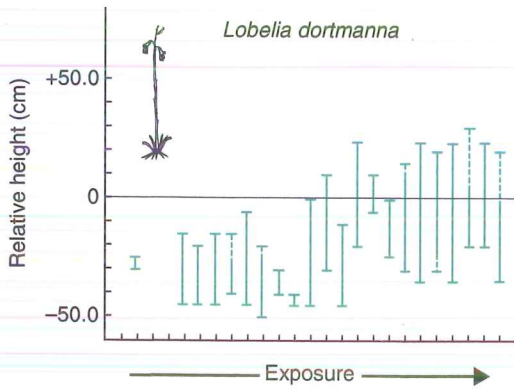


FIGURE 10.17 The relative height occupied by a shoreline plant as a function of exposure to waves; zero marks the August water line. (After Keddy 1983.)

The above patterns occurred in a lake in Ontario. How general are they? As a first test for biogeographic generality, the same questions were posed for a lake in Nova Scotia, a lake in a different biographic region, with a substantially different flora and a different type of bedrock (Keddy 1984). Similar patterns were found (Table 10.3), except that the intensity of clustering did not increase with exposure. These patterns, and their relative consistency across eastern North America, suggest that it may be possible to group zoned wetlands into categories having specified patterns. Further, some of these properties may be related to broader debates over the kinds of communities that occur in nature, and the manner in which species are packed into them. Several more recent studies have added to both the empirical data base and its conceptual interpretation, so let us continue with the theme of statistical investigations of zonation patterns.

We have just seen that it is possible to measure different properties of zonation, and to test whether these measured values are different from those which would arise by chance. Measurement is an important

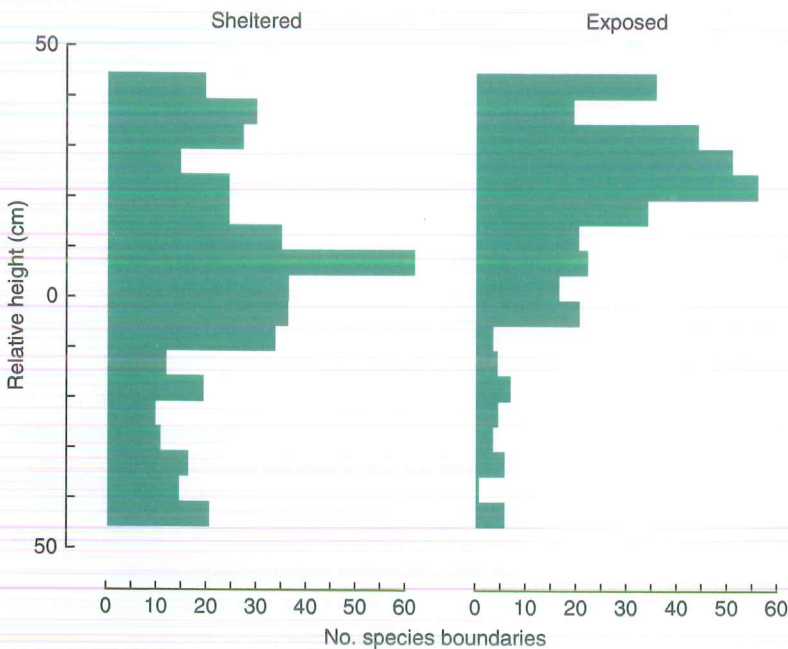


FIGURE 10.18 The relative height (see Figure 10.17) of species distributional limits (upper and lower boundaries combined) for ten sheltered transects (left) and ten exposed transects (right) at Axe Lake. (From Keddy 1983.)

Table 10.3 Clustering of species boundaries on a lakeshore in eastern North America. Data consisted of 30 transects with 117 species on the shoreline of Gillfillan Lake (Lat. 43° 57', Long. 65° 48') in the Tusket River valley of Nova Scotia.

Boundary	Are boundaries clustered?	Does intensity of clustering change with exposure?	Does location shift with exposure?
Upper	yes ($t = -9.12$, $p < 0.001$)	no ($t = 0.0$, $p = 1.00$)	landward 40 cm
Lower	yes ($t = -3.16$, $p < 0.01$)	no ($t = 0.06$, $p = 0.64$)	landward 20 cm

Source: Data collection and analysis as in Keddy (1983.)

first step in science. Measurement discloses that there are non-random patterns in zonation. Further, we have seen that the degree of non-randomness (or, if you prefer, the intensity of the patterns) sometimes changes along environmental gradients. These empirical relationships provide tools for the quantitative exploration of zonation patterns.

Such measurements and relationships are of far greater significance if they can be related to broader theoretical issues, or to general models for how ecological communities are assembled. One of the most persistent themes of enquiry in community ecology over the last century has revolved around the existence of communities. The first question has been rather general: (i) do ecological communities exist? The second has been more empirical: (ii) what non-random patterns occur in assemblages of species? In practice, these two questions are often mixed together, the assumption being that non-random patterns prove the existence of communities. The general question has therefore been: are living organisms organized into discrete communities as opposed to random assemblages (e.g. Whittaker 1967; Connor and Simberloff 1979; McIntosh 1985)?

There have been two basic approaches to search for evidence of communities. The first has used rigorously defined null models for species composition and compared observed composition to that which would occur randomly (e.g. Connor and Simberloff 1979). In

some cases, non-random composition of communities has indeed been detected (Harvey *et al.* 1983; Weiher and Keddy 1995). The second approach, and this is the one more relevant to zonation, has created null models for species distributions along gradients and compared real communities against these null models (Pielou 1975). A vast majority of the published studies on the existence of communities examines island data (Harvey *et al.* 1983), and very few have followed Pielou's suggestion to exploit the power of null models for zonation patterns, although, conveniently for us, most of the latter have been done in wetlands. Let us therefore consider the use of zonation patterns in more depth.

The debate concerning the nature of community organization has continued sporadically for more than 70 years. Colinvaux (1978) provides an entertaining introduction to this controversy, and Whittaker (1962) a more technical view. A convenient starting point is Clements (1916), who proposed that there are relatively discrete ecological units, called communities, that tend to repeat across landscapes. His view, also called the "community unit concept" (Whittaker 1975) was accepted by the majority of ecologists during the first part of the last century. Gleason (1926, 1939) argued, instead, that each organism is distributed individually, and that communities are not discrete, but rather intergrade. His view came to predominate, in part, because the description of zonation patterns

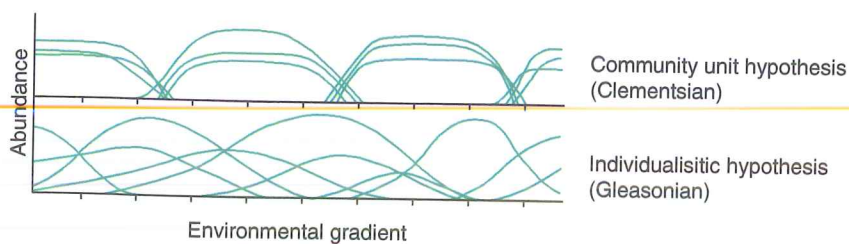


FIGURE 10.19 The individualistic and community unit hypotheses recast into a testable form. (After Shipley and Keddy 1987.)

		Boundaries	
		Clustered	Random
Upper and lower boundaries	Coincide	Community unit hypothesis	?
	Independent	?	Individualistic hypothesis

appeared to show patterns of species replacement that were inconsistent with the patterns predicted by Clements (McIntosh 1967; Whittaker 1967). However, all such studies suffered from the problem of using subjective methods of analysing the observed patterns; they failed to employ inferential statistics to compare empirical data to the proposed models. The relative merits of the individualistic as opposed to community unit views therefore remained to be statistically evaluated.

It is possible to test between these alternatives by casting them into testable form using species distributions patterns (Shipley and Keddy 1987). The “community unit” concept proposes that, when species distributions are plotted along some gradient or gradient-complex whose rate of change is constant, there exist groups of species, “communities,” which replace themselves along the chosen gradient (Whittaker 1975). Within each grouping, most species have similar distributions, and the end of

one group coincides with the beginning of another. The individualistic concept, in contrast, proposes that “centres and boundaries of species distributions are scattered along the environmental gradient” (Whittaker 1975). No distinct groups of species are predicted to exist. These alternatives are illustrated in the top part of Figure 10.19.

Following Pielou (1975, 1977), explicit hypotheses of these two concepts can be formulated using upper and lower boundaries of species along gradients.

The *community unit hypothesis* states that:

- (i) there should be significantly more boundaries (both upper and lower) in some intervals of the gradient than in others, i.e. boundaries are clustered;
- (ii) the number of upper and lower boundaries per interval should increase and decrease together along the gradient.

The *individualistic hypothesis* states that:

- (i) the average number of boundaries (both upper and lower) in each interval of the gradient should be equal except for random variation about the mean;
- (ii) the number of upper boundaries per interval of the gradient should be independent of the number of lower boundaries.

The patterns generated by these hypotheses are shown in Figure 10.19. Note that the 2×2 table suggests at least two other possibilities for patterns along a gradient, as pointed out by Whittaker (1975). Shipley and Keddy (1987) collected data on species boundaries from 13 transects located in a freshwater riverine marsh. As with the example from Axe Lake, the distribution of species boundaries was tabulated for 5-cm increments of elevation. Along this gradient the dominant species changed from *Carex crinita* to *Acorus calamus* to *Typha angustifolia*. These data were analyzed using analysis of deviance, which is analogous to analysis of variance, but does not assume normality in the error structure of the model. They found that both upper and lower boundaries (Figure 10.20) were clustered. This was clearly contrary to the individualistic concept, but they also found that the pattern of clustering was different between upper and lower boundaries, a result inconsistent with their formulation of the community unit concept. They therefore concluded that, rather than a simple dichotomy between two models, the data suggested the need to erect multiple models for the kinds of communities that exist in nature. In other words, more than 50 years of debate about pattern had dragged on, in part, because the patterns were not expressed in clear testable form. This example illustrates the power of zonation patterns as a research tool in ecology.

This study, however, also had two significant weaknesses. First, it tested a broad general model with data from a single wetland. Second, it used only data on the distributional limits of species. Hoagland and Collins (1997a) have tried to rectify these deficiencies. First, they collected data from 42

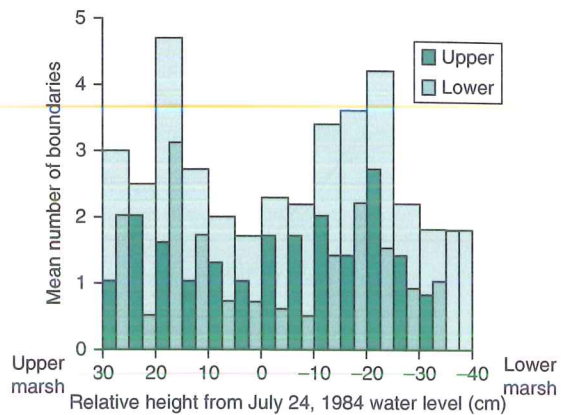


FIGURE 10.20 Zonation in a riverine marsh. The mean number of species boundaries in each 5-cm height interval is plotted against relative height. Within each height interval the mean number of upper boundaries (dark), lower boundaries (medium), and total boundaries (light) are shown. (From Shipley and Keddy 1987.)

wetland sites. Second, they measured three attributes of zonation patterns: (i) boundaries of species distributions, (ii) modes of species response curves, and (iii) nested structure. The use of the three properties not only provides a more powerful way to test among competing models, but it also allows the creation of new kinds of community models. Hoagland and Collins trace the origins of four contrasting models of zoned communities:

- (i) The highly deterministic community unit model of Clements (1936) could be interpreted to imply that plant communities are comprised of distinguishable associations of species with little overlap in species distributions among associations. This model can be portrayed as a series of species response curves in which the starting and ending points of species distributions are clustered (Figure 10.21a).
- (ii) Other interpretations of this community unit model are possible. Clements (1936) described the occurrence of “predominants,” species that were dominant and spanned one or more associations. Figure 10.21b shows a model in which boundaries and modes of response

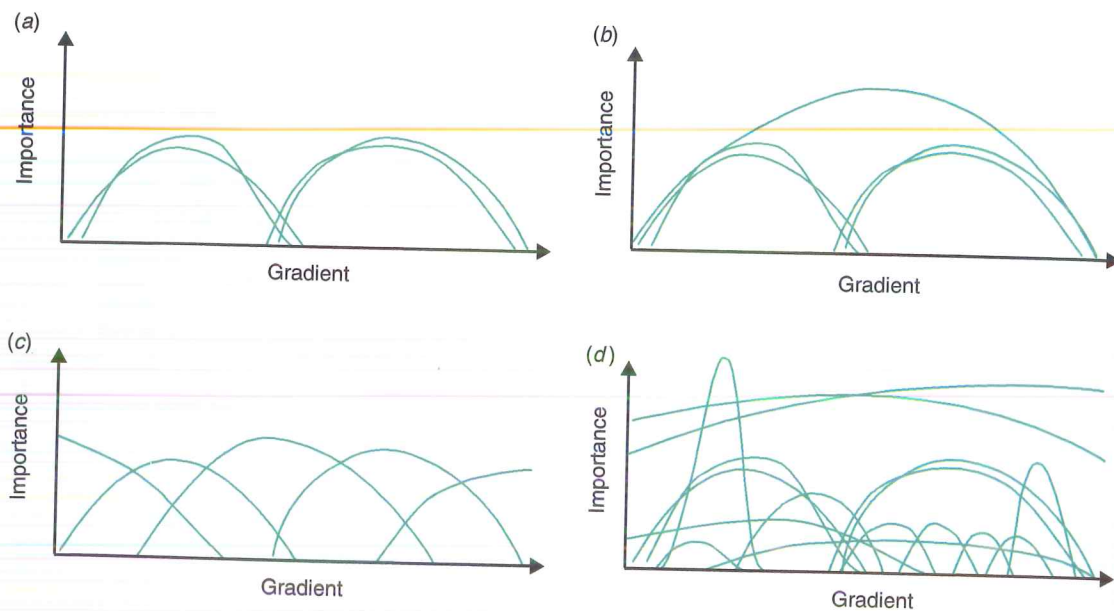


FIGURE 10.21 Four possible zonation patterns. The top pair (a, b) represent the community model, whereas the lower two (c, d) represent the continuum model. The right-hand pair (b, d) possess the additional feature of being nested. (From Hoagland and Collins 1997a).

curves are clustered yet some species response curves are nested within the curves of other, more dominant species.

- (iii) The individualistic distribution of species (Gleason 1926) and the continuum concept of vegetation (Whittaker 1967) are represented in Figure 10.21c as a series of broadly overlapping species response curves with randomly distributed starting and stopping boundaries, and modes, along an environmental gradient.
- (iv) Dominant species may be regularly spaced and encompass several curves of subordinate species; the hierarchical continuum model predicts that modes and boundaries of species response curves are random, but because distributions are hierarchical, this model predicts that species distributions are nested (Figure 10.21d).

Three test statistics were used to discriminate among these models in the 42 wetland sites. The three test statistics were as follows: Morisita's index

(Hurlbert 1990) was used to determine whether or not species boundaries were clustered:

$$I = Q \sum_{i=1}^Q \left(\frac{n_i}{N} \right) \left(\frac{n_i - 1}{N - 1} \right)$$

where Q is the number of quadrats, n_i is the number of starting and stopping boundaries in the i th quadrat, and N is the total number of boundaries.

The degree of aggregation (P) of species modes was determined using the sample variance of distance between modes (Poole and Rathcke 1979):

$$P = \frac{1}{k+1} \times \sum_{i=0}^k \{y_{i+1} - y_i - [1/(k+1)]\}^2$$

where k is the number of species, $y_{i+1} - y_i$ is the distance between modes, and $1/(k+1)$ is the mean of $y_{i+1} - y_i$. If $P = 1$, modes are randomly distributed, if $P < 1$, modes are regularly distributed, and if $P > 1$, modes are aggregated.

Table 10.4 Summary of models of distribution along gradients (based on distribution of boundaries of species response curves, modes of species response curves, and degree of nestedness of species distributions) and the prevalences of these models in a set of 42 transects from Minnesota and Oklahoma wetlands

	Boundaries clustered	Modes clustered	Distributions nested	Examples found
Community unit	yes	yes	no	0
Nested community unit	yes	yes	yes	3
Alternative model a	yes	no	yes	7
Alternative model b	no	yes	yes	16
Continuum	no	no	no	0
Nested continuum	no	no	yes	16

Source: After Hoagland and Collins (1997a).

Nestedness was determined by using the index of Wright and Reeves (1992):

$$N_C = \sum_{i=1}^{K-1} \sum_{m=i-1}^K \sum_{j=1}^S X_{ij} X_{mj}$$

where S is the total number of species, K is the number of quadrats, and $X_{ij} = 1$ if species j is present at quadrat i and 0 if it is absent. This index counts the number of times that a species' presence in a quadrat correctly predicts that species' presence in quadrats that are more species rich.

The value of N_C was then used to calculate a relative nestedness index:

$$C = \frac{N_C - E\{N_C\}}{\max\{N_C\} - E\{N_C\}}$$

where $E\{N_C\}$ is the expected value and $\max\{N_C\}$ is the value of N_C for a perfectly nested matrix. C ranges from 0 (complete independence) to 1 (perfect nestedness). Cochran's Q was used to test for significance of nested species distributions.

All 42 transects were nested (Table 10.4). This is an important generalization; Hoagland and Collins

interpret this as evidence for "hierarchical" community structure. Given the many uses of the word hierarchy, it may be more useful to simply use the descriptive result: nested patterns are the rule in zoned vegetation.

Clustering of boundaries occurred in only 10/42 transects; thus the continuum model is more prevalent than indicated by Pielou and Routledge (1976), Keddy (1981), or Shipley and Keddy (1987). Unfortunately, the use of Morisita's index rather than previously used indices raises the possibility that the prevalence of the continuum model in Hoagland and Collins (1997a) data may be an artefact of the test used. Such problems emphasize the need for methodological consistency.

More than half of the transects did not fit into any of the four main models (Table 10.4). Seven had clustered boundaries but unclustered modes, whereas 16 had clustered modes but unclustered boundaries. This work shows the merit of applying a battery of tests to zonation patterns. The differences among the transects, and among published studies, suggest that ecologists need to use a number of different models to describe the kinds of zonation patterns in nature.

10.6 General lessons from analysis of zonation

Here is a situation where wetland ecology can contribute to an understanding of all ecological communities. Do communities exist? There is perhaps a general lesson emerging from the above statistical studies. The continuum hypothesis of Gleason is now generally regarded as correct; Colinvaux's entertaining review (1978) states that Clements was wrong because Whittaker's data show that "zone boundaries could not be found. Instead the data showed clearly that individual species of plants came and went with gentle gradualness as one ascended a mountain, that there was that endless blending of species that should result if each kind of plant did its own free thing, without benefit of social organization" (p. 71). Remarkably, this important conclusion was reached based on two sources of evidence. The first was ordination of plant communities (e.g. McIntosh 1967; Whittaker 1967) (sometimes called "indirect gradient analysis"), a technique that by its very nature assumes the continuum hypothesis. The second source was the visual inspection of species distributions along real environmental gradients (e.g. Whittaker 1956, 1967), an approach that was carried out without creating null models, and without using techniques developed by Pielou (1975, 1977). An important unifying theme in ecology was therefore evaluated with inadequate (or even inappropriate) techniques, leading to a conclusion that now appears to be just wrong.

For whatever the general zonation patterns in forests may be, the few herbaceous zonation patterns that have been carefully analyzed and tested against null models (e.g. Pielou and Routledge 1976; Keddy 1983; Shipley and Keddy 1987; Hoagland and Collins 1997a) do seem to show that species boundaries occur in clusters. The interpretation of these clustered boundaries is still unclear. It may be that there is some discontinuity in the underlying gradient, such as a sudden transition from aerobic to anaerobic conditions, or the upper limit of ice scour on a shoreline.

It may also be that a competitive dominant sets the distributional limits for a group of weaker competitors. Or perhaps a few dominant species are distributed as Gleason postulated, each dominant having a group of subordinates and commensals associated with it. The cluster of upper boundaries observed at Axe Lake (Figure 10.17) occurred where shrubs began to occur, suggesting that one of the latter two explanations may account for the patterns there. But, even if the last explanation – a dominant with subordinates and commensals – were the mechanistic explanation for clustered boundaries, is this not more in accord with Clements than Gleason (Figure 10.21, top)? Zoned wetland communities indeed may have important lessons for the entire discipline of community ecology.

CONCLUSION

A first step in any scientific discipline, or in a single study, is to find pattern. Zonation makes pattern obvious, and therefore provides a powerful tool for the investigation of wetland communities. While many explanations for the pattern have been offered, it is only recently that experiments have begun to unravel the many factors that cause them. Competition and mutualism are two biological forces involved. Fertility and disturbance also are important. Hence, the causes of zonation require that we combine our understanding of physical factors like flooding with biological factors like competition. It is no longer acceptable to assume that zonation is simply a physical phenomenon.

Of course, one does not always need to understand every detail of cause and effect to uncover broad generalizations in science. A toolbox of statistical methods for examining the patterns in zonation has yielded significant new evidence on the nature of communities. Here is a case where wetlands provide some general insight into many other types of plant communities. If we are looking for a general lesson from this chapter, it might come from Pielou (1975), who was of the opinion that instead of seeking mythical uniform habitats, we would be better off to look for and study gradients.