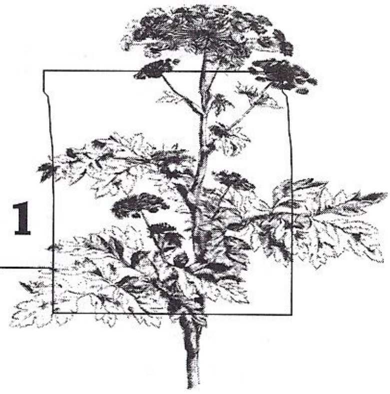
# CHAPTER 1



# Communities

> Ecology is the science of communities. A study of the relations of a single species to the environment conceived without reference to communities and, in the end, unrelated to the natural phenomena of its habitat and community associations is not properly included in the field of ecology.
>
> —Victor Shelford (1929)

## OVERVIEW

This chapter briefly describes how ecological communities are defined and classified and introduces some of the properties and interactions that community ecologists study. The major interspecific interactions, or elementary processes, between pairs of species include competition, predation, and mutualism. Complex indirect interactions can arise among chains of three or more interacting species. Important community properties include the number of species present, measures of diversity, which reflect both the number and relative abundances of species, and statistical distributions that describe how the species differ in abundance.

Observations of natural patterns and explorations of mathematical models have inspired generalizations about the underlying causes of community organization. One pattern important in the historical development of community ecology concerns an apparent limit to the similarity of coexisting species. The case of limiting similarity provides a cautionary example of the way in which community patterns are initially recognized, explained in terms of causal mechanisms, and eventually evaluated. Community patterns are the consequence of a hierarchy of processes that interact in complex ways to mold the diversity of life on earth.

## COMMUNITIES

Communities are collections of organisms.

Our best estimates suggest that somewhere between 1.5 million and 30 million different species of organisms live on earth today (Erwin 1982; May 1990). The small fraction of this enormous global collection of species that can be found at any particular place is an **ecological community**. One important goal of community ecology is to understand the origin, maintenance, and consequences of biological diversity within local communities. Different processes, operating on very different timescales, can influence the number and identity of species in communities. Long-term evolutionary processes operating over timescales spanning millions of years can produce different numbers of species in different locations. Short-term ecological interactions can either exclude or facilitate species over shorter timescales ranging from a few hours to many years. This book provides an overview of community patterns and the processes that create them.

Some basic questions.

Like many fields of modern biology, community ecology began as a descriptive science. Early community ecology was preoccupied with identifying and listing the species found in particular localities (Clements 1916; Elton 1966). These surveys revealed some of the basic community patterns that continue to fascinate ecologists. In many communities, a few dominant species are much more common than others. Dominant species often play an important role in schemes used to identify and categorize communities. But why should some species be so much more common than others? Communities also change over time, often in ways that are quite repeatable. But what processes drive temporal patterns of community change, and why are those patterns so regular within a given area? Different communities can also contain very different numbers of species. A hectare of temperate forest in New Jersey might contain up to 30 tree species (Robichaud and Buell 1973), while a similar-sized plot of rain forest in Panama might contain over 200 tree species

(Hubbell and Foster 1983). More than 10 hypotheses have been proposed to explain the striking latitudinal gradient in biodiversity that contributes to the differences between temperate and tropical communities (Pianka 1988). Although there are many reasonable competing explanations for the commonness and rarity of species and for latitudinal differences in biodiversity, the exact causes of these very basic patterns remain speculative. Related questions address the consequences of biodiversity for community processes. Do communities with many species function differently from those with fewer species? How do similar species manage to coexist in diverse communities?

The central questions in community ecology are disarmingly simple. Our ability to answer these questions says something important about our understanding of the sources of biological diversity and the processes that maintain biodiversity in increasingly stressed and fragmented natural ecosystems. Answering these questions allows us to wisely manage artificial communities, which include the major agricultural systems that we depend on for food and for biologically produced materials, and to restore the natural communities that we have damaged either through habitat destruction or overexploitation.

Ecologists use a variety of approaches to explore the sources of community patterns. Modern community ecology has progressed beyond basic description of patterns, and often experiments can identify which processes create particular patterns (Hairston 1989). However, some patterns and their underlying processes are experimentally intractable because the organisms driving those processes are so large, long lived, or wide ranging that experimental manipulations are impossible. Consequently, community ecologists must rely on information from many sources, including mathematical models, statistical comparisons, and experiments, to understand what maintains patterns in the diversity of life. The interplay among description, experiments, and mathematical models is a hallmark of modern community ecology.

Before describing how ecologists identify and classify communities, it is important to recognize that the term *community* means different things to different ecologists. Most definitions of ecological communities include the idea of a collection of species found in a particular place. The definitions part company over whether those species must interact in some significant way to be considered community members. For instance, Robert Whittaker's (1975) definition of a community as

Some definitions of ecological communities.

> an assemblage of populations of plants, animals, bacteria and fungi that live in an environment and interact with one another, forming together a distinctive living system with its own composition, structure, environmental relations, development, and function (pp. 1–2)

clearly emphasizes both physical proximity of community members and their various interactions. In contrast, Robert Ricklefs' (1990) definition does not stress interactions but does emphasize that communities are often identified by prominent features of the biota (dominant species) or physical habitat:

> [T]he term has often been tacked on to associations of plants and animals that are spatially delimited and that are dominated by one or more prominent species or by a physical characteristic. (p. 656)

Other succinct definitions include those by Peter Price (1984), "the organisms that interact in a given area[,]" and by John Emlen (1977), "A biological community is a collection of organisms in their environment[,] (p. 341)" which emphasize the somewhat arbitrary nature of communities as sets of organisms found in a particular place.

Charles Elton's (1927) definition, while focused on animals, differs from the previous ones in drawing an analogy between the roles that various individuals play in human communities and the functional roles of organisms in ecological communities:

> One of the first things with which an ecologist has to deal is the fact that each different kind of habitat contains a characteristic set of animals. We call these animal associations, or better, animal communities, for we shall see later on that they are not mere assemblages of species living together, but form closely-knit communities or societies comparable to our own. (p. 5)

Elton's emphasis on the functional roles of species remains crucial to our understanding of how functions and processes within communities change in response to natural or anthropogenic changes in community composition.

For our purposes, **community ecology** will include the study of patterns and processes involving at least two species at a particular location. This broad definition embraces topics such as predator-prey interactions and interspecific competition that are traditionally considered part of **population ecology**. Population ecology focuses primarily on patterns and processes involving single-species groups of individuals. Of course, any separation of the ecology of populations and communities must be highly artificial since natural populations always occur in association with other species in communities of varying complexity and often interact with many other species as competitors, consumers, prey, or mutually beneficial associates.

Community ecology vs. population ecology.

Most communities are extraordinarily complex. That complexity makes it difficult even to assemble a complete species list for a particular locale (e.g., Elton 1966; Martinez 1991). The problem is compounded by the fact that the taxonomy of smaller organisms, especially bacteria, protists, and many invertebrates, remains poorly known (Wilson 1992). Consequently, community ecologists often focus their attention on conspicuous, readily identified sets of species that are ecologically or taxonomically similar. One important subset of the community is the **guild**, a collection of species that use similar resources in similar ways (Root 1967). There are no taxonomic restrictions on guild membership, which depends only on the similarity of resource use. For example, the granivore guild in deserts of the southwestern United States consists of a taxonomically disparate group of birds, rodents, and insects that all consume seeds as their primary source of food (Brown and Davidson 1977). Another term, **taxocene** (Hutchinson 1978), refers to a set of taxonomically related species within a community. Ecologists often refer to lizard, bird, fish, and plant communities, but these assemblages are really various sorts of taxocenes. Unlike the guild, membership in a taxocene is restricted to taxonomically similar organisms. Although ecologists often study taxocenes rather than guilds, the use of the term taxocene to describe such associations has been slow to catch on.

Some useful subsets of communities.

Other useful abstractions refer to subsets of the community with similar feeding habits. **Trophic levels** provide a way to recognize subsets of species within communities that acquire energy in similar ways. Abstract examples of trophic levels include primary producers, herbivores, primary carnivores (which feed on herbivores), and decomposers (which consume dead organisms from all trophic levels). With the exception of most primary producers, many species acquire energy and matter from more than one adjacent trophic level, making it difficult to unambiguously assign many species to a particular trophic level. While trophic levels are a useful abstraction and have played a prominent role in the development of ecological theory (Lindeman 1942; Hairston et al. 1960), the problem of assigning real species to a particular trophic level can limit the concept's operational utility (Polis 1991).

Other descriptive devices help to summarize the feeding relations among organisms within communities. **Food chains** and **food webs** describe patterns of material and energy flow in communities, usually by diagramming the feeding links between consumers and the species that they consume. In practice, published examples of food webs usually describe feeding relations among a very small subset of the species in the complete community (Paine 1988). More complete descriptions of feeding connections in natural communities can be dauntingly complex and difficult to interpret (Winemiller 1990). Patterns in the organization of food webs are a topic considered in Chapter 6.

**Ecosystems** consist of one or more communities, together with their abiotic surroundings. Ecosystem ecologists often come closer than community ecologists to studying the workings of entire communities, although they often do so by lumping many species into large functional groups such as producers and decomposers. Ecosystem ecologists manage to study whole communities only by ignoring many of the details of population dynamics, focusing instead on fluxes and cycles of important substances like carbon, nitrogen, phosphorus, and water. There is an increasing awareness that distinctions between community and ecosystem ecology are just as artificial as distinctions between population and community ecology (Vitousek 1990). The processes of energy and material flow that interest ecosystem ecologists are certainly affected in no small way by interactions among species. Conversely, feedbacks between species and pools of abiotic nutrients may play an important role in affecting the dynamics of species in food chains (DeAngelis et al. 1989). Certain species that physically alter the environment through their presence or behavior effectively function as ecosystem engineers (Jones et al. 1994). Examples include modifications of stream courses by beavers, and changes in light, humidity, and physical structure created by dominant forest trees.

Communities vs. ecosystems.

## COMMUNITIES AND THEIR MEMBERS

Community ecologists recognize and classify communities in a variety of ways. Most of these approaches have something to do with the number and identity of species found in the community. Regardless of the criteria used, some communities are easier to delineate than others. Ecologists use several different approaches to delineate communities: 1) physically, by discrete habitat boundaries, 2) taxonomically, by the identity of a dominant indicator species, 3) interactively, by the existence of strong interactions among species, 4) or statistically, by patterns of association among species.

Different ways of identifying communities.

**Physically defined communities** include assemblages of species found in a particular place or habitat. To the extent that the boundaries of the habitat are easily recognized, so are the boundaries of the community. Some spatially discrete habitats, such as lakes, ponds, rotting fruits, and decaying carcasses, contain equally discrete communities of resident organisms. Less discrete communities may grade gradually into other communities, defying a simple spatial delimitation. For example, forests grade relatively imperceptibly into savannas and then into grasslands, without any clear boundaries. Whittaker and

Some communities are defined by habitat.

Niering's (1965) study of plant communities along an elevational gradient in southeastern Arizona illustrates the gradual transition between different kinds of terrestrial communities (Figure 1.1). The Sonoran desert scrub and subalpine forest communities at the base and summit of the Santa Catalina Mountains are quite distinct, with giant cactus present in the desert scrub and evergreen fir trees abundant at the summit; however, the transitions between these endpoints are gradual and contain intervening communities.

**Biomes** are basic categories of communities that differ in their physical environments and in the lifestyles of their dominant organisms. A list of the major biomes of the world recognized by Whittaker (1975) is shown in Table 1-1. The composition of the list betrays Whittaker's keen interest in terrestrial plants, since most of the biomes describe differences among assemblages of terrestrial plants and their associated biota. Had the list been drawn up by a limnologist or a marine ecologist, more kinds of aquatic biomes certainly would have been recognized. Biomes are a useful shorthand for describing certain kinds of communities and, as such, help to facilitate communication among ecologists. The global distribution of terrestrial biomes is strongly influenced by annual precipitation and average temperature (Holdridge 1947), as summarized in Figure 1.2.

**TABLE 1-1. Major biomes of the world.**

1. Tropical rain forests
2. Tropical seasonal forests
3. Temperate rain forests
4. Temperate deciduous forests
5. Temperate evergreen forests
6. Taiga forests
7. Elfinwoods
8. Tropical broadleaf woodlands
9. Thornwoods
10. Temperate woodlands
11. Temperate shrublands
12. Savannas
13. Temperate grasslands
14. Alpine shrublands
15. Alpine grasslands
16. Tundras
17. Warm semidesert scrubs
18. Cool semideserts
19. Arctic-alpine semideserts
20. True deserts
21. Arctic-alpine deserts
22. Cool temperate bogs
23. Tropical freshwater swamp forests
24. Temperate freshwater swamp forests
25. Mangrove swamps
26. Salt marshes
27. Freshwater lentic communities (lakes and ponds)
28. Freshwater lotic communities (rivers and streams)
29. Marine rocky shores
30. Marine sandy beaches
31. Marine mudflats
32. Coral reefs
33. Marine surface pelagic
34. Marine deep pelagic
35. Continental shelf benthos
36. Deep-ocean benthos

Source: Whittaker (1975).

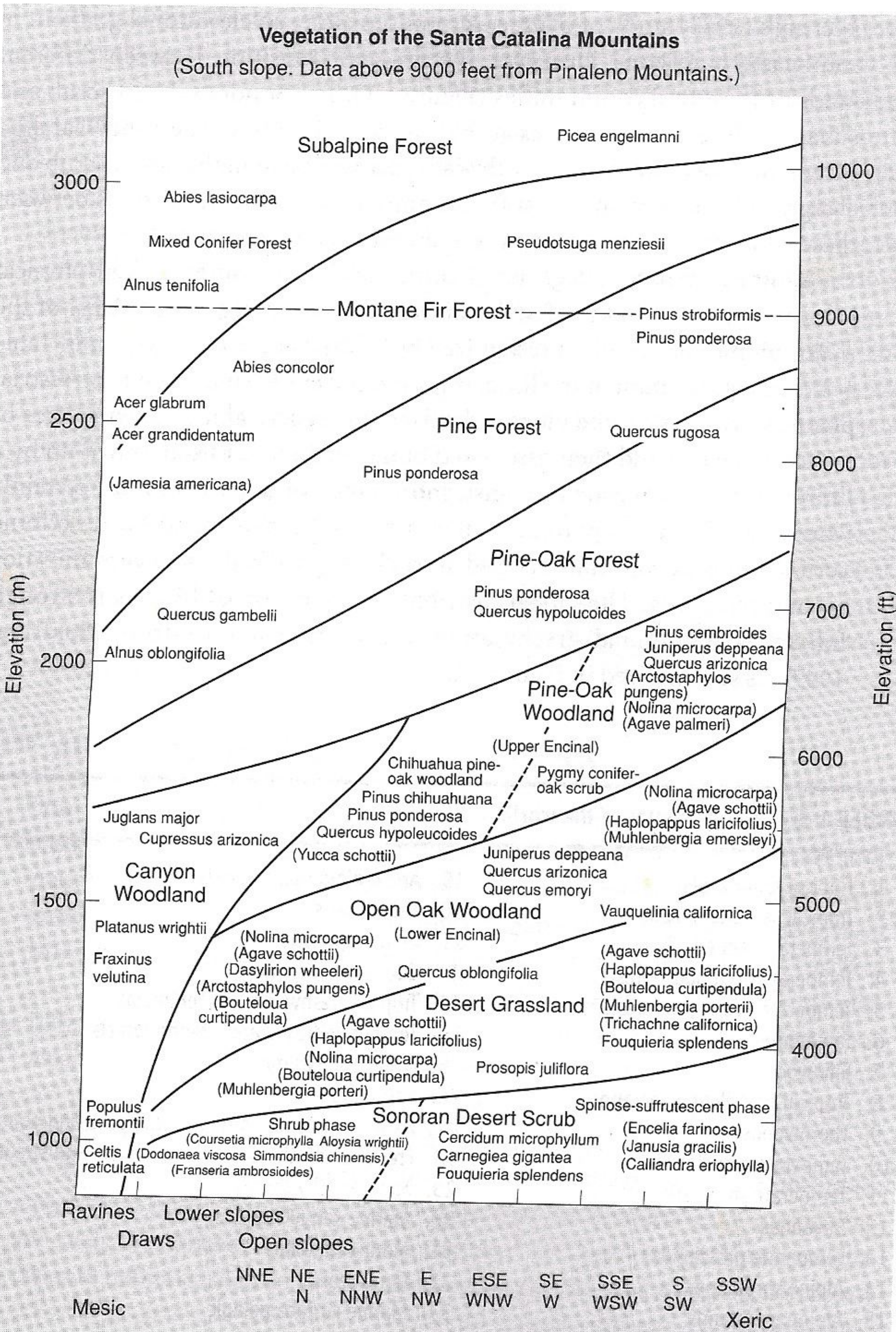


**FIGURE 1.1.** *Changes in plant species composition along an elevational gradient in the Santa Catalina Mountains of southeastern Arizona. Changes in elevation result in changes in both temperature and rainfall that lead to differences in the identity of predominant plant species. (Adapted from Whittaker and Niering, 1965, with permission of the Ecological Society of America.)*

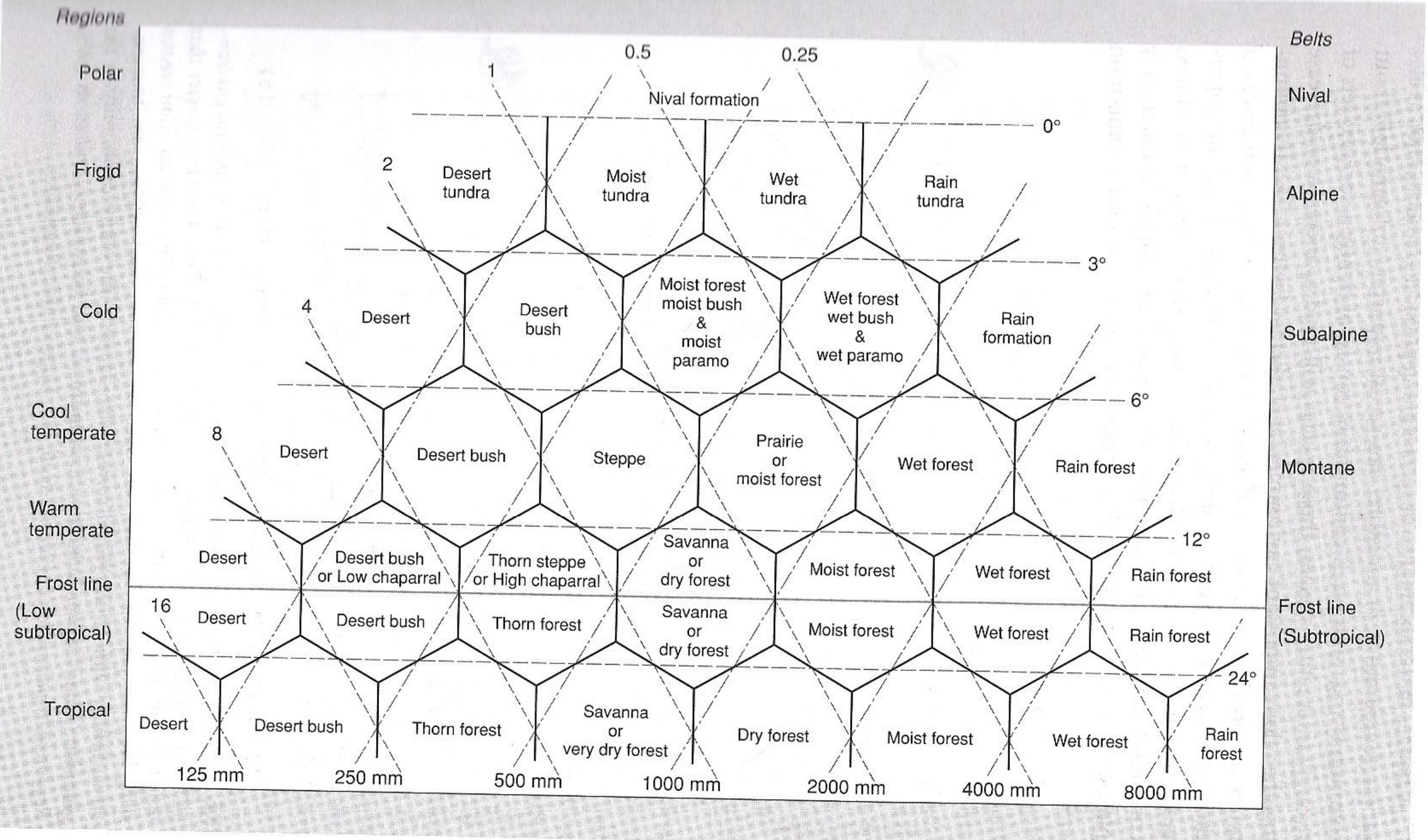


**FIGURE 1.2.** *Relation between average annual temperature, rainfall, and the presence of particular terrestrial biomes characterized by different kinds of vegetation. Annual rainfall (in mm) is indicated along the base of the chart. Increasing elevation or latitude is indicated by increasing height along both sides of the graph. (Adapted with permission from Holdridge, 1947. © 1947 American Association for the Advancement of Science).*

Changes in the abundance of species along physical gradients, such as elevation, temperature, or moisture, can reveal important information about community organization. If communities consist of tightly associated sets of strongly interacting species, those species will tend to increase or decrease together along important environmental gradients (Figure 1.3A). If communities are loosely associated sets of weakly interacting species, abundances of those species will tend to vary independently, or individually, along important gradients (Figure 1.3B). Most of the information gathered to address community patterns along gradients describes single trophic levels, usually plants, and seems consistent with a loose model of community organization

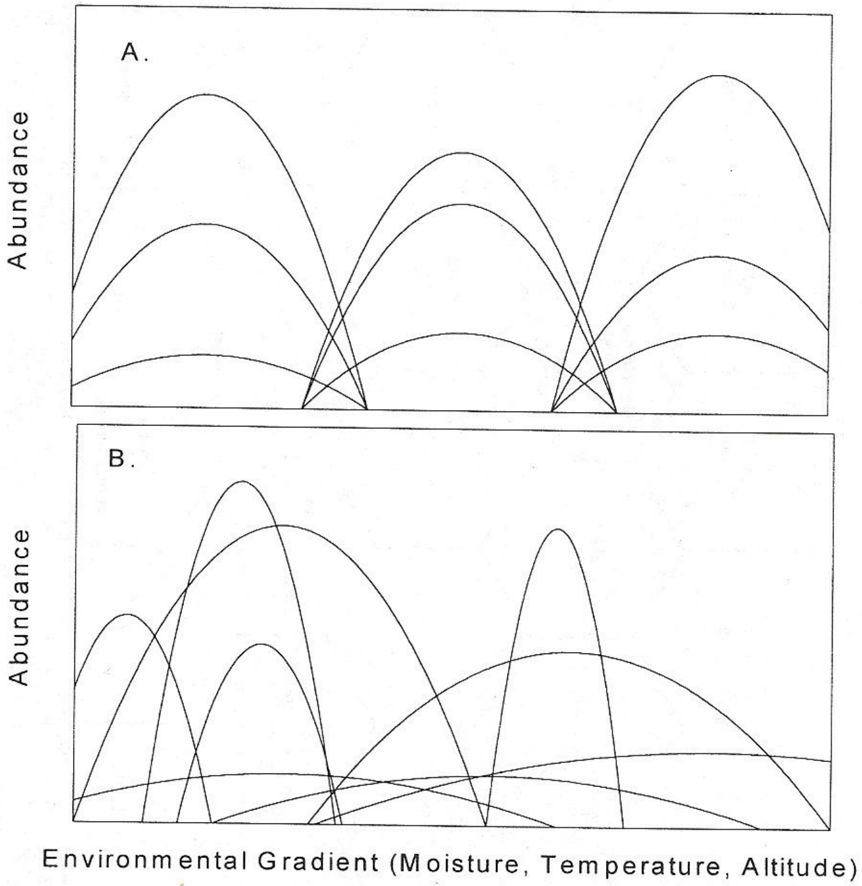


**FIGURE 1.3.** *Two hypothetical patterns of abundance for sets of species along an environmental gradient. (A) Groups of tightly integrated and strongly competing species that respond as an entire community to environmental variation. Strong competition creates sharp breaks in species composition. (B) Species responding individually to environmental variation, with no integrated correlated response of the entire community to the gradient. (Modified from Whittaker,* Communities and Ecosystems, *2nd ed. © 1975. Reprinted by permission of Prentice-Hall, Inc., Upper Saddle River, NJ.)*

(Whittaker 1967). However, the kinds of tight associations between species that would yield the pattern seen in Figure 1.3A are far more likely to occur between trophic levels, such as for species-specific predator-prey, parasite-host, or mutualistic relations. Descriptions of associations between plants and their specialized herbivores (see Futuyma and Gould 1979) or between herbivores and their specialized predators or parasites might yield a pattern more like that seen in Figure 1.3A. Strangely, such studies are rare, perhaps because the taxonomic biases of ecologists restrict their attention to particular groups of organisms that tend to fall within single trophic levels.

**Taxonomically defined communities** usually are recognized by the presence of one or more conspicuous species that either dominate the community through sheer biomass or otherwise contribute importantly to the physical attributes of the community. Examples would include the beech (*Fagus*) and maple (*Acer*) forests of the northeastern United States and the longleaf pine (*Pinus palustris*) and wiregrass (*Aristida*) savannas of the southeastern United States. In both cases, the predominance of one or two plant species defines the community. In some cases, the dominant, or most abundant, species that identifies a particular community type also plays an important role in defining the physical structure of the community (Jones et al. 1994).

Other communities are recognized by dominant species.

**Statistically defined communities** consist of sets of species whose abundances are significantly correlated, positively or negatively, over space or time. The approach makes use of overall patterns in the identity and abundance of species to quantify similarities and differences among communities. One way to describe the species composition of a community is to simply list the identity and abundance of each species. But how do you compare these lists? For long lists containing many species, such comparisons are difficult to make by just reading down the list and making species-by-species comparisons. Imagine instead a geometric space defined by $S$ independent axes, each of which represents the abundance of a different species (Figure 1.4). The species composition of a particular community is represented by a point whose coordinates correspond to the abundance of each species, $(n_1, n_2, \ldots, n_s)$, where $n_i$ is some measure of the abundance of species $i$. While it is difficult to visualize species composition in more than three dimensions (more than three species), in principle the mathematical and geometric interpretations of this approach generalize for any number of species, $S$. Species composition then has a geometric interpretation as a directional vector, or arrow, in $S$-dimensional space, as shown in Figure 1.4.

Statistical associations can also identify communities.

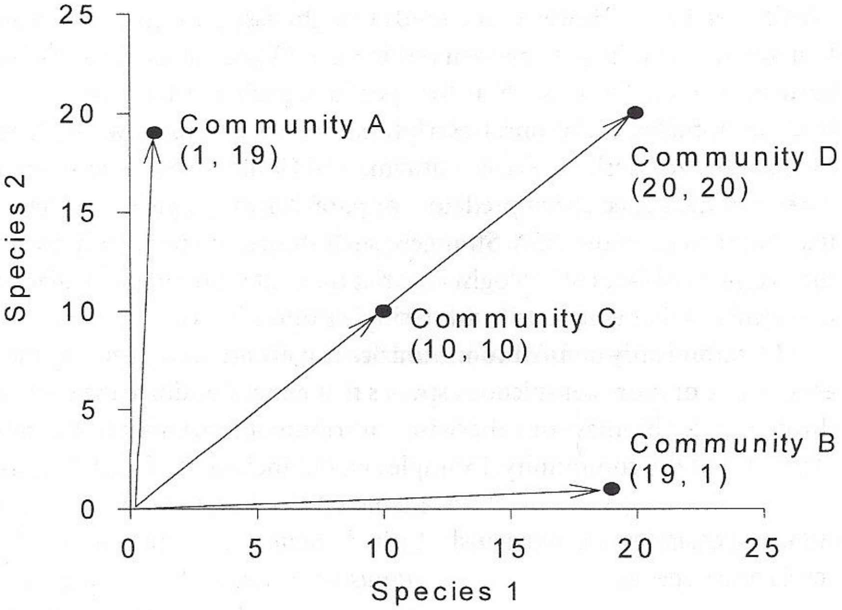


**FIGURE 1.4.** *A geometric representation of species composition as a vector in a space defined by axes that describe the abundances of different species measured in a comparable sample area. This simple example focuses only on communities of two hypothetical species. Note that both communities A and B have identical values of species richness, S = 2, and species diversity, H′ = 0.199, but they clearly differ in species composition, as shown by the different directions of the arrows. Communities C and D have identical relative abundances of the two species, but one community contains twice the number of individuals as the other. This approach generalizes to patterns for any value of species richness, although it is difficult to visualize for S > 3.*

One advantage of the geometric approach is that it clearly distinguishes among communities with similar numbers of species that differ in the identity of common and rare species. In such cases, community composition vectors point in different directions in the space defined by the abundances of different species in the communities being compared. Comparisons involving more than three species rely on various statistical techniques, mostly involving ways of classifying or ordering communities based on the identity and abundance of species. The development of effective statistical techniques for the description of species composition has been a major goal of mathematical ecology. Many of the techniques employ multivariate statistics to derive concise descriptors of community composition that can be interpreted in terms of differences among communities in the abundance of particular sets of species. The computational details of these techniques, which are collectively termed **ordination**, fall outside the scope of this book, but Gauch (1982) and Pielou (1984) provide excellent summaries geared toward the interests of ecologists.

Two examples of ordinated sets of communities are shown in Figure 1.5. In each case, overall species composition is represented by an index, or score, for a community along a set of coordinate axes. The score for a community along one axis is a linear function of the species composition in each community, with the general form $a_{11}n_{11} + a_{12}n_{12} + \ldots + a_{ij}n_{ij} + \ldots a_{1S}n_{1S}$, where the $a_{ij}$'s are constants selected to maximize the variation among communities represented in this new space, and the $n_{ij}$'s represent the abundance of the *j*th species in the *i*th community. For different axes the coefficients $a_{ij}$ will also differ, so that the axes, and the patterns of species occurrence that they describe, are statistically independent. Often two or three ordination axes, with different sets of coefficients, are sufficient to describe the majority of the variation in species composition among communities. Figure 1.5A shows patterns of similarity in a large number of sampled stands of vegetation, based on abundances of 101 plant species. Stands of similar composition fall near each other in this two-dimensional space, whereas increasingly different stands are separated by larger distances. Figure 1.5B shows the results of a similar approach applied to the zooplankton species found in a large number of Canadian lakes. Lakes with similar species composition have similar locations in the set of coordinates used to describe species composition. In both cases, the position of a community with respect to the coordinate axes says something about the abundance of a few key species that vary in abundance among communities, that is, the species that make these communities recognizably different. The advantage of these approaches is that information about a large number of species can be distilled into measures of position along one to several coordinate axes. The resulting classification usually does not identify the proximal factors leading to the predominance of one species versus another in a particular community. Such information usually comes from direct experimental studies of interspecific interactions.

**Interactively defined communities** consist of those subsets of species in a particular place or habitat whose interactions significantly influence their abundances. Only some, and perhaps none, of the species in a physically defined community may constitute an interactively defined community. Hairston (1981) used this approach to point out that only a small subset of the species of salamanders found in the mountains of North Carolina could be shown to interact and affect each other's abundance. Of the seven common species of plethodontid salamanders in his study plots, only the two most common species, *Plethodon jordani* and *Plethodon glutinosus*, significantly affected each other's abundance. The remaining five species, while taxonomically and ecologically similar to the others, remained unaffected by the

Interactions can also be used to define communities.

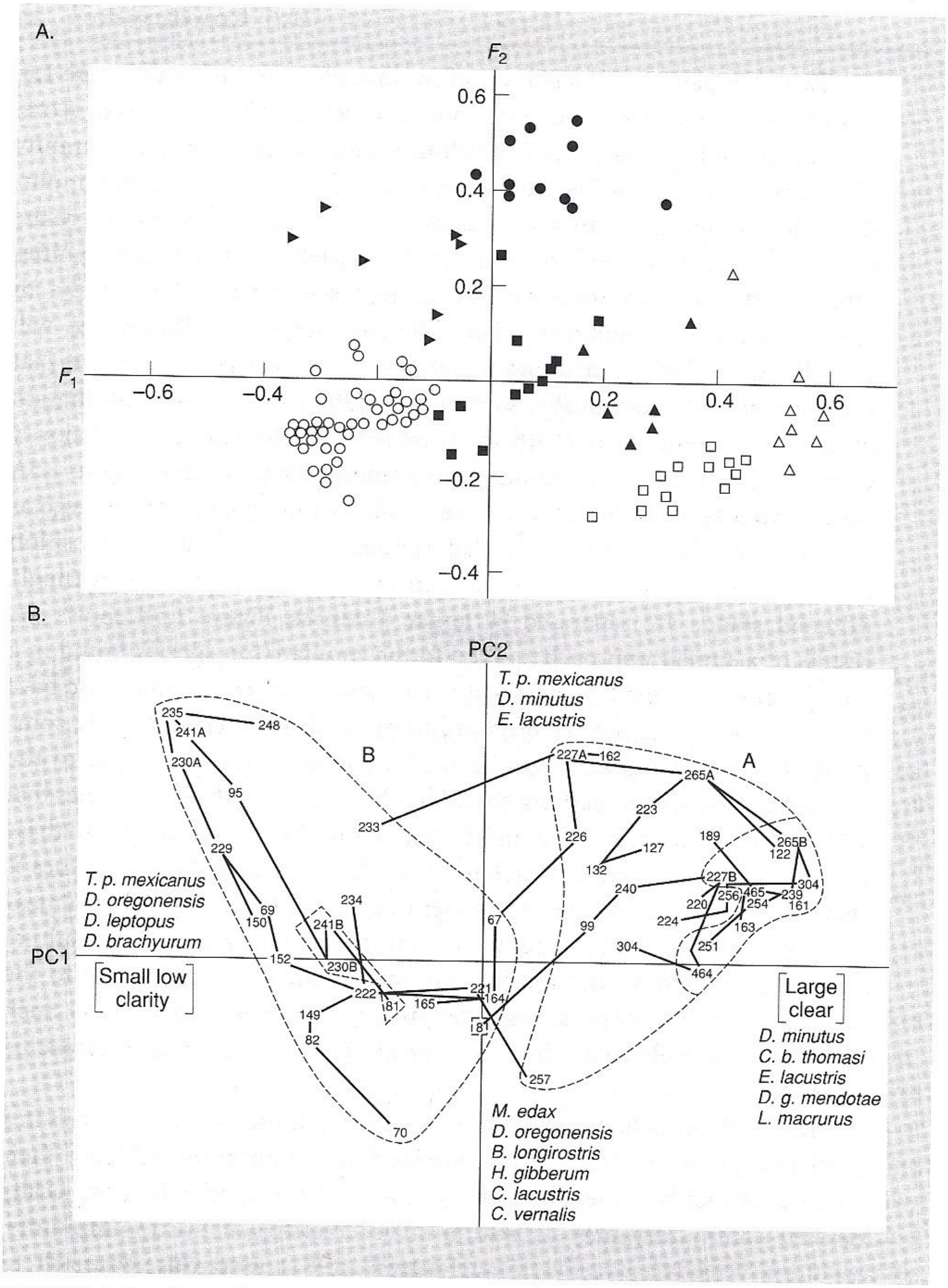


**FIGURE 1.5.** *Examples of statistically classified or ordinated communities. (A) Plant assemblages growing on sand dunes. Different symbols correspond to different habitat types. Positions of each community represent the frequency (abundance) of 101 plant species. (Reprinted from Orloci, 1966, with permission of Blackwell Science Ltd.) (B) Zooplankton assemblages from a large number of Canadian lakes. Each number corresponds to a particular lake. Similarity in species composition is represented by proximity in a complex space defined by weighted functions of the original abundances of various species in field samples. The axes can be interpreted as indicating a predominance of some species as opposed to others, or as gradients in physical factors that are correlated with the abundance of particular species. (Adapted from Sprules, 1977, with permission of the NRC Research Press.)*

abundance of the two most common species. The key point is that the assignment of membership in a guild or taxocene based on similarity of resource use or taxonomy is no guarantee that species will really interact.

## COMMUNITY PROPERTIES

Given that you can identify communities using some repeatable criteria, what is the best way to compare complex systems composed of many species that can interact in many ways? The potentially bewildering complexity of communities encourages ecologists to use various descriptors to condense and summarize information about the number, identity, and relative abundance of species. No single number, index, or graph can provide a complete description of a community, but some of these measures provide a useful way of comparing different communities.

### Species Richness

Robert May (1975) observed that "one single number that goes a long way toward characterizing a biological community is simply the total number of species present, $S_T$" (p. 82). This number, often called **species richness**, is synonymous with our most basic notions of biodiversity. It is, in practice, a difficult number to obtain, partly because we simply do not have complete taxonomic information about many of the groups of organisms found in even the most-studied communities. Even if we did have the ability to unambiguously identify all the species found in a particular place, there would still be the practical problem of deciding whether we had searched long and hard enough to say that all the species in that place had been found. Therefore, in practice, species richness is evaluated for groups that are taxonomically well known and readily sampled according to some repeatable unit of effort. One way to decide whether enough sampling effort has been made is to plot the cumulative number of species found against the amount of sampling effort. Beyond a certain amount of effort, the species versus effort curve should reach an asymptote. That asymptote provides a reasonable estimate of the number of species present. Comparisons among communities that have been sampled with different amounts of effort can be made by using rarefaction curves (Sanders 1968; Hurlbert 1971). These are essentially catch per unit effort curves that permit comparisons among communities scaled to the same amount of effort.

Species richness is an important community attribute.

Species richness is more than a convenient descriptive device. There is increasing evidence that it is related to important functional attributes of communities. Recent experimental work indicates that primary production, resistance to natural disturbances, and resistance to invasion all increase as species richness increases (Tilman and Downing 1994; Naeem et al. 1994; Tilman et al. 1996; Tilman 1997; McGrady-Steed et al. 1997).

## Diversity

Although species richness provides an important basis for comparisons among communities, it says nothing about the relative commonness and rarity of species. Various diversity indices have been proposed to account for variation in both the number of species in a community and the way that individuals within the community are distributed among species (Magurran 1988). One measure is the Shannon-Weaver index of diversity,

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

where $S$ is the total number of species present in a sample and $p_i$ is the fraction of the total number of individuals in the sample that belong to species $i$. For instance, imagine that two communities have the same species richness, but individuals are evenly distributed among species in the first community and unevenly distributed among species in the second. A satisfying measure of species diversity would give the first community a higher measure of diversity.

Species diversity measures species richness and relative abundance.

The comparisons get complicated when comparing communities that vary in both species richness and the evenness of distribution of individuals among species. For this reason, it is often preferable to break species diversity down into its two components, species richness and evenness. Evenness is usually defined as

$$J = H'/H_{\max}$$

where $H'$ is the observed value of species diversity and $H_{\max}$ is the value that would be obtained if individuals were evenly distributed among the number of species found in the community (if the values of $p_i$ were identical for each species). Species diversity indices are seductive in that they offer a simple way to describe the complexity present in a community. Their main drawback is that they gloss over potentially important information about the actual identities of the species.

The amount of diversity found within a single type of habitat is sometimes called **alpha diversity** (Whittaker 1975). Within a region, the turnover in species composition among different habitats will contribute additional diversity to a region. This interhabitat component of diversity is called **beta diversity**.

## Species Abundance Relations

Graphical ways of summarizing the relative abundances of species in a sample have a long tradition of use in community ecology. Many communities display well-defined patterns, which may or may not have important ecological significance. Examples of some of the more historically important species-abundance distributions are shown in Figure 1.6. Each distribution has an underlying statistical distribution, which can be derived by making some assumptions about the way in which species interact in communities. In each case, the importance value of each species, usually a measure of the fraction of total number of individuals or biomass in the sample accounted for by each species, is plotted against the importance rank of each species, where a rank of 1 corresponds to the most important species and a rank of $s$ corresponds to the least important (least abundant) species in a sample of $s$ species.

Species abundance relations graphically summarize community patterns.

Three of the more important species-abundance relations that have attracted the attention of ecologists are the broken stick distribution, the geometric series, and the lognormal distribution (Whittaker 1975; May 1975). Each distribution can be derived by making particular assumptions about the way that species divide up resources within a community. For example, the geometric series can be obtained by assuming that a dominant species accounts for some fraction, $k$, of the total number of individuals in a sample, and each successively less abundant species accounts for a fraction $k$ of the remaining number of individuals. This leads to the following formula for the abundance of the $i$th species:

$$n_i = Nk(1-k)^{i-1},$$

where $N$ is the total number of individuals in the sample and $i$ runs from 1 for the most abundant species to $s$ for the least. The fraction $k$ is usually approximated by $n_1/N$.

The problem with using these statistical distributions to infer the existence of underlying processes is that even if collections of species are found to fit a particular distribution, there is no guarantee that the species in fact interact in the fashion assumed by the underlying model (Cohen 1968). Largely for this reason, the study of species abundance patterns no longer figures prominently in community ecology, although there are occasional efforts to revive interest in particular patterns (e.g., Sugihara 1980). These distributions are described here primarily because they played an important role in the historical development of community ecology and because they continue to provide a useful alternate way of describing patterns of abundance within communities.

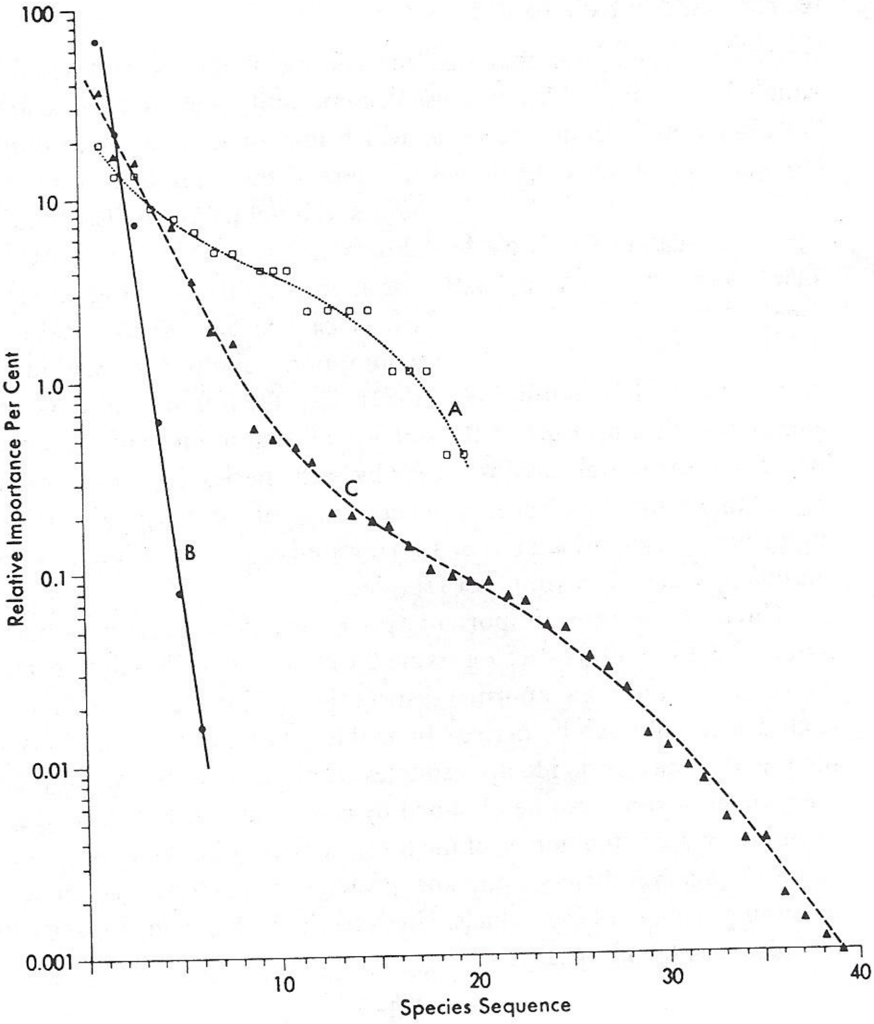


**FIGURE 1.6.** *Examples of three common species-abundance relations that fit different collections of species. (A) Nesting birds in a West Virginia forest, following a broken stick distribution. (B) Vascular plants in a subalpine fir forest in Tennessee, following a geometric series. (C) Vascular plants in a deciduous cove forest in Tennessee, following the lognormal distribution. (Reprinted from Whittaker,* Communities and Ecosystems, *2nd ed. © 1975. Reprinted by permission of Prentice-Hall, Inc., Upper Saddle River, NJ.)*

## Species Composition

We have already seen how the species composition of a particular community can be represented by a point whose coordinates correspond to the abundance of each species (see Figures 1.4 and 1.5). This geometric representation conveys more information than either species richness or species diversity measures, but that information comes with a somewhat greater difficulty of interpretation. It differs from measures of richness or diversity in that both the identity and abundance of particular species are considered to be important attributes.

## INTERSPECIFIC INTERACTIONS

Rather than attempting to infer the influence of interspecific interactions on community patterns from indirect means, such as the species abundance relations described above, community ecologists often directly study how various interactions affect patterns of abundance. Interspecific interactions are the basic elementary processes that can influence species abundances and the community composition. Figure 1.7 shows how interactions between a pair of species can be categorized by assigning positive or negative signs to the net effect that a population of each species has on the population size of the other (Burkholder 1952; Price 1984). More complex interactions involving chains of three or more species can be represented similarly (Holt 1977). Abrams (1987) has

Species interact in a limited number of ways.

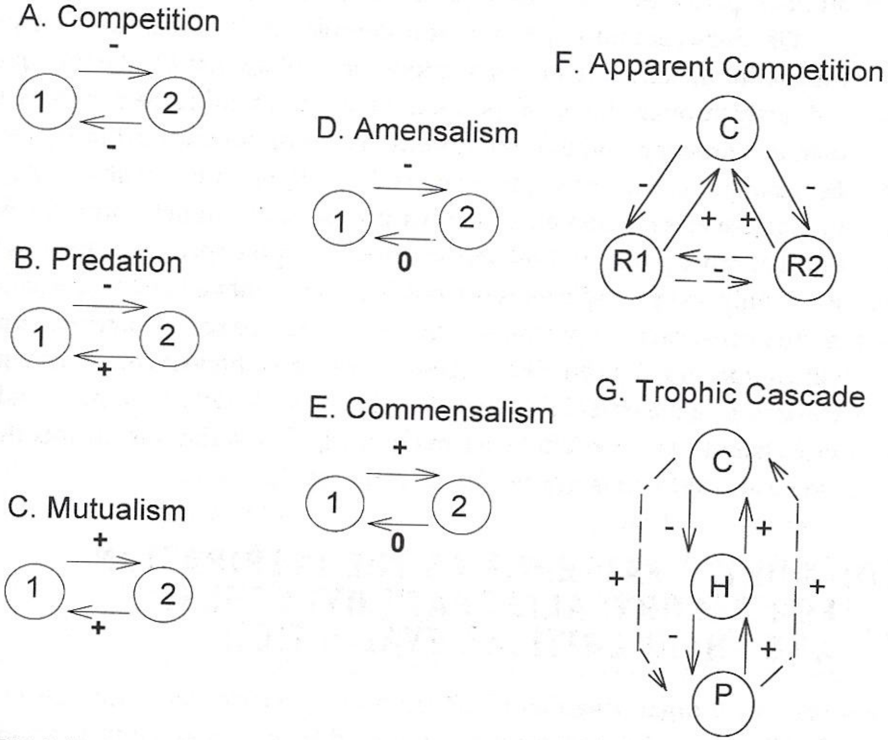


**FIGURE 1.7.** *Examples of direct and indirect interactions among species in communities. Direct effects are indicated by solid lines, with signs corresponding to the signs of interactions between the species. Net indirect effects are indicated by broken lines. C, consumer; R1, resource 1; R2, resource 2; P, primary producer, H, herbivore.*

criticized the approach of classifying interspecific interactions by the signs of net effects because the sign of the interactions can depend on the responses used to classify interactions, such as population growth rates, population size, or relative fitness. However, as long as the criteria used to describe how one species affects another are explicit, the approach often has heuristic value.

**Predation**, **parasitism**, and **herbivory** all involve a –/+ interaction between a pair of species, in which the net effect of an individual consumer on an individual prey is negative, and the effect of the consumed prey on the predator is positive. These interactions share the common features of consumer-resource interactions, where all or part of the resource species is consumed by the other. Predation and other –/+ interactions drive processes of energy and material flow through food webs. **Competition** involves a mutually negative (–/–) interaction between a pair of species. **Amensalism** is a one-sided competitive interaction (0/–), in which one species has a negative effect on another, but the other has no detectable effect on the first. **Mutualism** involves a mutually positive (+/+) interaction between a pair of species, in which each has a positive effect on the other. **Commensalism** is a one-sided mutualistic (0/+) interaction, in which one species has a positive effect on another species, but the second species has no net effect on the first.

Of course, communities are more complex entities than simple pairs of interacting species. Interactions among pairs of species can be transmitted indirectly through chains of species to others. Such indirect effects have their own terminology; some of the simpler scenarios are outlined in Figure 1.7. For example, consider two prey species, A and B, that are consumed by a third predator species. Assume that neither prey species competes with the other, but that more predators will persist when both prey species are present than when only one prey species is present. The net result will be that predation is more intense on both prey when they co-occur. This scenario, termed **apparent competition** by Holt (1977), results when each prey has an indirect negative effect on the other by virtue of its direct positive effect on the abundance of a shared predator. There are many intriguing variations on this theme, which are explored in greater detail in Chapter 8.

## COMMUNITY PATTERNS AS THE INSPIRATION FOR THEORY: ALTERNATE HYPOTHESES AND THEIR CRITICAL EVALUATION

The major organizing themes in community ecology have been inspired by the discovery of particular patterns, and different ideas about the causes of those patterns play an important role in the development of theories of community organization. Progress toward the development of predictive theories of community ecology has sometimes been sidetracked by focusing on

Examples of community patterns and their causes.

patterns that were not clearly related to particular processes. Also, some patterns may arise from multiple processes, and important processes may be difficult to identify by observation alone. In some cases, what initially appeared to be an important community pattern eventually proved to be indistinguishable from a random pattern!

One community-level pattern that has yielded important insights into the roles of interspecific interactions in community organization is the striking vertical zonation of marine organisms in the rocky intertidal zone. One particularly well-studied example of this zonation concerns two species of barnacles found on the rocky coast of Scotland. The smaller of the two species, *Chthamalus stellatus*, is consistently found higher in the intertidal zone than the larger species, *Balanus balanoides.* Such differences in zonation were historically attributed entirely to physiological differences between the barnacles, presumably reflecting differences in the ability of the two species to withstand desiccation at low tide and immersion at high tide. However, observations and a careful series of experimental transplants and removals showed that several factors, including interspecific competition, predation, and physiological constraints, produce the pattern (Connell 1961). Both species initially settle within a broadly overlapping area of the intertidal zone, but overgrowth by the larger barnacle, *Balanus*, smothers and crushes the smaller *Chthamalus*, excluding it from the lower reaches of the intertidal zone. Other experiments show that predation by the snail *Thais* influences the lower limit of the *Balanus* distribution, whereas different tolerances to desiccation during low tide set the upper limits of both barnacle distributions. Consequently, a rather simple pattern of vertical zonation ultimately proves to depend on a complex interaction among competition, predation, and physiological tolerances. This example illustrates the important role of natural community patterns as a source for ideas about the processes that organize communities. It also emphasizes that inductive reasoning alone may not provide an accurate explanation for a given pattern, especially when there are several competing hypotheses that could account for that pattern.

Not all community patterns are as readily recognized and understood as the intertidal zonation of barnacles. Some of the patterns that preoccupied ecologists for decades have eventually been recognized as artifacts that offer little insight into community-level processes. Differences in the body sizes of ecologically similar coexisting species provide a telling case in point. The story begins with observations about the body sizes of aquatic insects in the family Corixidae, called water boatmen (Figure 1.8). Hutchinson (1959) noted that three European species, *Corixa affinis*, *Corixa macrocephala*, and *Corixa punctata*, have segregated distributions, such that the largest species, *C. punctata,*

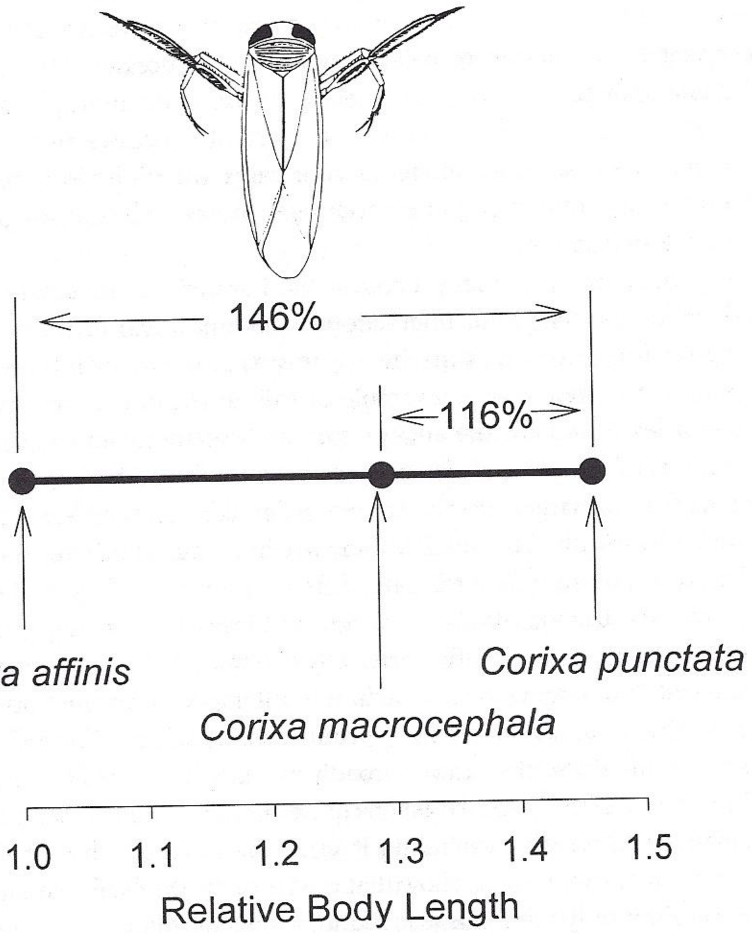


**FIGURE 1.8.** *Corixids, a kind of common aquatic hemipteran insect, inspired Hutchinson's (1959) concept of limiting morphological similarity of coexisting species. Relative sizes of the three species considered by Hutchinson are indicated by their positions along a scale that corresponds to relative body size.*

occurs with either *C. affinis* or *C. macrocephala*, whereas the two smaller species do not coexist in the same pond. *C. punctata* is larger than either of the species with which it coexists by about 116% to 146%. Hutchinson suggested that species that differ sufficiently in size or other life history features may also differ sufficiently in resource use to avoid competitive exclusion. Examination of other taxa indicated that coexisting species tended to differ in some aspect of size by a factor of about 1.3, or 130%. Hutchinson did not mention that the two species that fail to coexist also differ in size by a factor of 1.46/1.16, or 1.259, which is clearly within the range observed for the two pairs of species that do coexist! Also, many sets of inanimate objects, including cooking utensils and musical instruments (Horn and May 1977), also fit the 1.3 rule to a good approximation, which casts considerable doubt on the pattern holding deep ecological significance.

Competitive exclusion of species that are too similar in size, and therefore too similar in resource use, is one possible explanation for the differences in body size that Hutchinson observed, but alternative explanations exist. One possibility is that differences in the sizes of coexisting species might be no greater than expected for any randomly selected sets of species (Strong et al. 1979), that is, no greater than expected by chance. Clearly, some differences in the sizes of any set of species would be expected to occur regardless of the intensity of their interactions, since by definition species must differ in some way for taxonomists to recognize them as separate entities. The crucial question is whether those differences are any greater than would be expected to occur by chance (Simberloff and Boecklin 1981). Determinations of the randomness or nonrandomness of the sizes of coexisting species are by no means straightforward (Colwell and Winkler 1984), but some studies suggest that observed size differences among coexisting species may be no greater than those expected in randomly selected sets of noninteracting species.

Another way to assess the ecological significance of size differences among coexisting species would be to experimentally measure whether species that differ greatly in body size compete less intensely than species of similar size. Experimental studies of competition among corixids in other aquatic systems suggest that substantial morphological differences among species do not prevent competition. Both Istock (1973) and Pajunen (1982) have shown that even when coexisting corixid species differ substantially in size, they still compete strongly. Pajunen (1982) suggested that his corixid species only manage to coexist by virtue of their ability to disperse among pools as adults and to rapidly recolonize pools after competitive extinctions. Co-occurrence of similarly sized species may be fleeting and illusory, rather than a persistent consequence of differences in resource use. Strangely, no one has directly tested whether the intensity of competition among corixid species depends on similarity in size or some other aspect of morphology.

Studies of another group of aquatic insects also offer little support for the idea that morphological similarity is a good predictor of competition's intensity. Juliano and Lawton (1990a,b) examined patterns of co-occurrence for several species of larval dytiscid beetles, which prey on other aquatic organisms. Size differences among coexisting species were no greater than expected by chance. Experimental manipulations of these species failed to identify a clear relation between body size and competition. In fact, competition among these species was generally quite weak, despite their similar requirements as small aquatic predators.

Hutchinson's corixids and the concept of limiting morphological similarity provide a cautionary tale about the kinds of patterns that intrigue community ecologists and the need to critically evaluate the explanations proposed for those patterns. The search for general mechanisms that might explain such patterns is one of the main goals of community ecology. Examples of other kinds of patterns in multispecies assemblages include geographic patterns of diversity and species richness, repeatable patterns in the structure of guilds, and recurring patterns observed in the architecture of food webs. Discovery of these patterns depends on careful observational studies of natural systems, but it is important to remember that each pattern may result from multiple processes that can only be disentangled by experiments.

## Community Patterns Are a Consequence of a Hierarchy of Interacting Processes

Community ecologists recognize that many factors affect the species composition of a given community, with no single factor providing a complete explanation for observed patterns (Schoener 1986). The factors can interact in a complex hierarchical fashion, as sketched in Figure 1.9. For example, the composition of a regional species pool of potential community members sets an upper limit on the species composition of a new community developing in a given place, as might happen after the creation of a new lake or after removal of an established natural community by a catastrophic disturbance. Membership in the regional species pool is constrained by physiological tolerances, historical factors, and the evolutionary processes responsible for the generation of different numbers of species in different taxonomic groups or habitats. Species generally do not occur in areas that tax their physiological limits. Successful introductions of species into areas far from their normal ranges show that accidents of biogeography can exclude whole groups of species from some geographic regions (Elton 1958). For example, salamanders are absent from Australia and sub-Saharan Africa, although many species possess physiological adaptations that allow them to inhabit climatically similar regions on other continents.

Community patterns arise from a hierarchy of processes.

Dispersal and habitat selection sift and filter species from the regional species pool to set the identity of those species available to colonize a given community. The idea of community assembly as a filtering process has been developed for plant assemblages by Paul Keddy (1992), and it applies equally well to other kinds of organisms. These factors act to make communities nonrandom subsets of the regional species pool. Habitat selection can be influenced by the species already present in the community. Finally, interspecific interactions, or the lack thereof, influence the subsequent success or failure of species that actually arrive at a community. The following chapters will consider how various patterns arise in communities by first considering

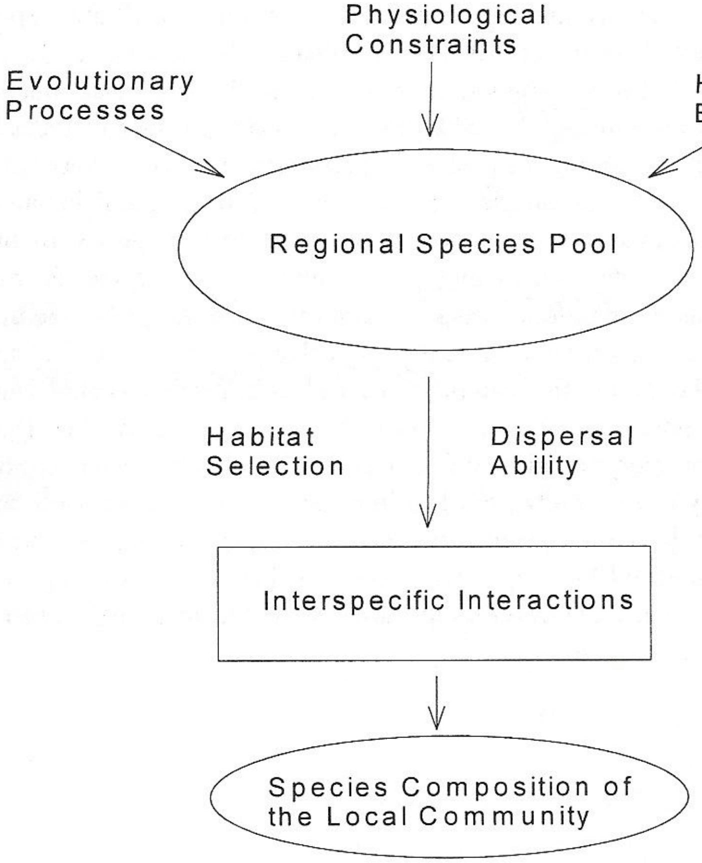


**FIGURE 1.9.** *The species composition of a local community at any time is a consequence of many factors interacting in a hierarchical fashion. The composition of the species pool of potential community members depends on past evolutionary and historical events, as well as physiological constraints. Dispersal ability and habitat selection influence which members of the species pool arrive in a particular location. Interspecific interactions among those species that manage to arrive in a particular place further inhibit or facilitate the inclusion of species in the community.*

how interspecific interactions affect the success or failure of species as community members. Subsequent chapters explore some of the processes that influence which species interact and how those interactions vary over space and time.

## CONCLUSIONS

The many definitions of ecological communities all identify collections of species found in particular locations. Useful commonly studied subsets of communities include guilds, taxocenes, and trophic levels. Species richness and species diversity are two important community attributes. Species-abundance relations, sometimes called dominance-diversity curves, provide a graphical way of describing species richness and the relative abundance of species in communities. The concept of species composition includes these ideas, as well as coupling the identity of particular species to patterns of relative abundance. Communities can be identified by physical habitats, by dominant organisms, by statistical associations among species, or by the identification of sets of interacting species. Fundamental interspecific interactions, such as competition, predation, and mutualism, contribute to important community patterns. Some patterns, such as vertical zonation of species in intertidal communities, can be shown to result from interactions among species and physiological constraints. Other patterns, such as the suggested regularity of morphological differences among closely related coexisting species, may not be easily linked to interspecific interactions. Community patterns can have multiple alternate explanations, which may not be completely understood by simple inspection and inductive reasoning. It does seem likely, though, that community patterns result from a complex hierarchy of interacting processes.