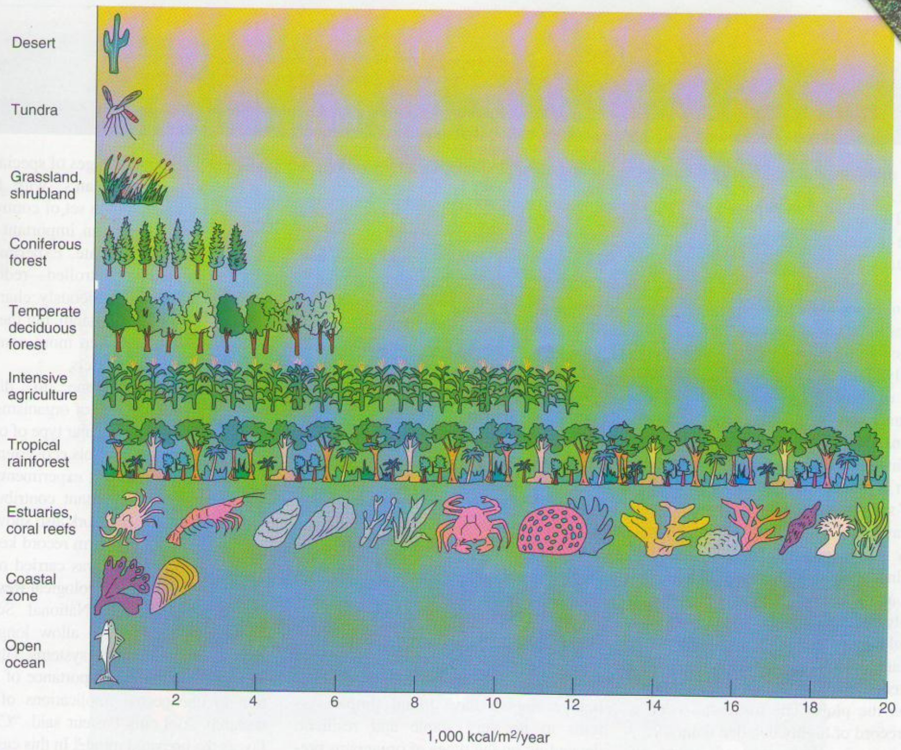

FIGURE 3.21 *Relative biomass accumulation of major world ecosystems. Only plants and some bacteria capture solar energy. Animals consume biomass to build their own bodies.*

in respiration and cooling. A large oak tree can transpire (evaporate) several thousand liters of water on a warm, dry, sunny day, while making only a few kilograms of sugars and other energy-rich organic compounds.

Abundance and Diversity

Abundance is an expression of the number of individuals of a species in an area. **Diversity** is the number of different species in an area. Diversity is also a useful measure of the variety of ecological niches or genetic variation in a community. Communities with high diversity often have low abundance of most species. As a general rule, diversity decreases as we go from the equator toward the poles, but abundance of a smaller number of species increases. The Arctic has a vast abundance of mosquitoes, for example, but relatively few other insect species. The tropics, on the other hand, have vast numbers of insect species—some of which have incredibly bizarre forms and habits—but often only a few individuals of any particular species in a given area.

Bird populations also vary dramatically with latitude. Greenland is home to 56 species of breeding birds, while Colombia, which is only one-fifth the size of Greenland, has 1,395. Why so many species in Colombia and so few in Greenland?

Climate and history are important factors. Greenland has such a harsh climate that the need to survive through the winter or escape to milder climates becomes the single most important critical factor that overwhelms all other considerations and severely limits the ability of species to specialize or differentiate into new forms. Furthermore, because glaciers covered Greenland until about 10,000 years ago, new species have had little time to develop.

Many areas in the tropics, by contrast, have relatively abundant rainfall and warm temperatures year-round so that ecosystems there are highly productive. The year-round availability of

CASE STUDY

BIODIVERSITY AND STABILITY

Is a more diverse community more stable and resilient in the face of environmental stress? This has been an ongoing debate among ecologists. One of the important contributors to the debate has been experimental ecologist David Tilman. Since 1982, Tilman and his colleagues have been studying the effects of nitrogen fertilization on grassland plots. Initially, Tilman's goal was to study the effect of fertilizer on regenerating grass on abandoned farm fields and natural oak savannas in central Minnesota. The experimental design was to randomly assign different fertilizer treatments to a set of sample plots on old fields and natural savannas. Study plots varied considerably in species diversity: some contained only one species, some had as many as 26. Using the same set of sample plots for nearly two decades, Tilman and his colleagues—and platoons of student assistants—have carefully gathered, counted, and weighed all the plants growing on the plots. The result has been a long record of highly detailed data.

In a fortuitous turn of events, an extreme case of environmental stress occurred several years into the experiment. The summer of 1988 was the hottest, driest summer in 50 years. When researchers tallied up the total plant productivity on the study plots that year, they found that the plots with the most species suffered much less than those with few species. On species-rich plots, drought-tolerant plants still grew, while more sensitive species languished. By contrast, the most species-poor plots had only about one-eighth their pre-drought productivity.

In subsequent years, the species-poor plots also took longer to recover from the drought. Ability to recover from stress—or resilience—is an important factor in ecosystem stability.

The idea that biodiversity increases ecosystem stability is one that ecologists have long believed was true, but that they have had difficulty proving. Many field researchers have concluded that complex communities are more stable, but their evidence has been ambiguous because natural environments have so many simultaneously changing variables. Other field ecologists have found simple systems to be very stable and resilient, depending on the types of organisms present. Mathematical models have suggested that simple communities of a few generalist species can be more stable than more complex assemblages of specialists. Experiments like Tilman's, with long-term data gathering on a set of controlled sample plots, provide an important type of evidence to the debate. Experimental data are relatively controlled—reducing the number of simultaneously changing variables of a natural system, but they are more realistic (and often more convincing) than computer models.

Ecologists continue to dispute whether it is the variety of organisms in a community, or the particular type of organisms (or both) that controls ecosystem stability and resilience, but experiments like Tilman's provide important contributions to the discussion. This work also shows the value of careful, long-term record keeping in science. This work was carried out on one of 18 Long-Term Ecological Research sites, funded by the National Science Foundation precisely to allow long-term monitoring of ecological systems. Tilman's work also shows the importance of attention to unexpected implications of your research. As Louis Pasteur said, "Chance favors the prepared mind." In this case, the 1988 drought provided an unexpected opportunity to explore critical questions about stability and resilience.

food, moisture, and warmth supports a great exuberance of life and allows a high degree of specialization in physical shape and behavior. Coral reefs are similarly stable, productive, and conducive to proliferation of diverse and exotic life-forms. The enormous abundance of brightly colored and fantastically shaped fish, corals, sponges, and arthropods in the reef community is one of the best examples we have of community diversity.

Productivity is related to abundance and diversity (both of which depend on total resource availability in an ecosystem), as well as the reliability of resources, the adaptations of the member species, and the interactions between species. You shouldn't assume that all communities are perfectly suited to their environment. A relatively new community that hasn't had time for niche specialization, or a disturbed one where roles such as top predators are missing, may not achieve maximum efficiency of resource use or reach its maximum level of either abundance or diversity.

We will discuss the importance of biodiversity and abundance further in chapter 5.

Complexity, Resilience, and Stability

Community complexity involves diversity and community functions. **Complexity** in ecological terms refers to the number of species at each trophic level and the number of trophic levels in a community. A diverse community may not be very complex if all of its species are clustered in only a few trophic levels and form a relatively simple food chain.

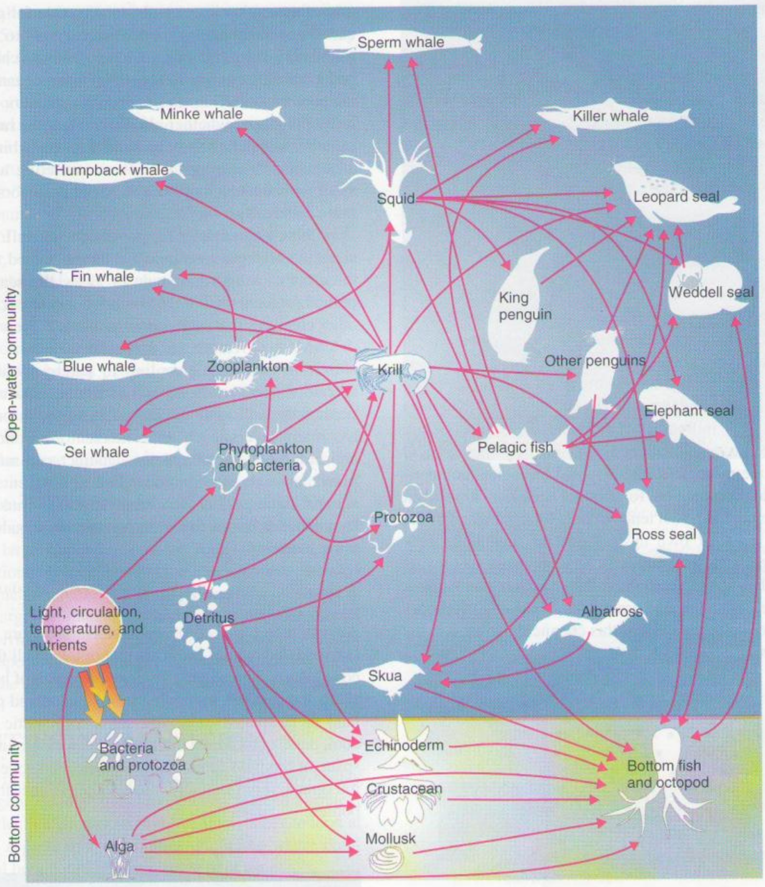

FIGURE 3.22 *A complex and highly interconnected community can have many species at each trophic level and many relationships, as this Antarctic marine food web illustrates.*

A complex, highly interconnected community might have many trophic levels, some of which can be compartmentalized into subdivisions (fig. 3.22). In tropical rainforests, for instance, herbivores can be grouped into "guilds," based on the specialized ways they feed on plants. There may be fruit-eaters, leaf-nibblers, root-borers, seed-gnawers, and sap-suckers—each composed of species of very different size, shape, and even biological kingdom, but that feed in related ways. A highly interconnected community such as this can form a very elaborate food web.

How is complexity related to stability in an ecosystem and to resilience (the ability to recover from disturbance)? Ecologists have debated this question for many years. We can identify three kinds of stability or resiliency in ecosystems: (1) constancy (lack of fluctuations in composition or functions), (2) inertia (resistance to perturbations), and (3) renewal (ability to repair damage after disturbance).

In 1955, Robert MacArthur, who was then a graduate student at Yale, proposed that the more complex and interconnected a community is, the more stable and resilient it will be in the face of disturbance. If many different species occupy each trophic level, some can fill in if others are stressed or eliminated by external forces, making the whole community resistant to perturbations and able to recover relatively easily from disruptions. On the other hand, in a diverse and highly specialized ecosystem, removal of a few keystone members can eliminate many other associated species. Eliminating a major tree species from a tropical forest, for example, may destroy pollinators and fruit distributors as well. We might replant the trees, but could we replace the whole web of relationships on which they depend? In this case, diversity makes the forest less resilient, rather than more. This relationship between diversity and stability remains controversial (see Case Study, p. 66).

Community Structure

Ecological structure refers to patterns of spatial distribution of individuals and populations within a community, as well as the relation of a particular community to its surroundings. At the local level, even in a relatively homogeneous environment, individuals in a single population can be distributed randomly, clumped together, or in highly regular patterns (fig. 3.23). In randomly arranged populations, individuals live wherever resources are available. Ordered patterns may be determined by the physical environment but are more often the result of biological competition. For example, competition for nesting space in a penguin colony is often fierce. Each nest tends to be just out of reach of the neighbors sitting on their own nests. Constant squabbling produces a highly regular pattern. Similarly, sagebrush releases toxins from roots and fallen leaves that inhibit the growth of competitors and create a circle of bare ground around each bush. As neighbors fill in empty spaces up to the limit of this chemical barrier, a regular spacing results.

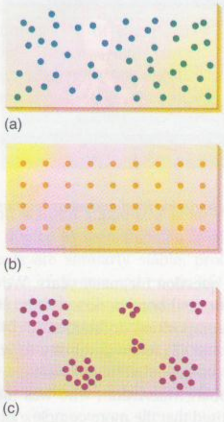

FIGURE 3.23 *Distribution of members of a population in a given space can be* (a) *random,* (b) *ordered, or* (c) *clustered. The physical environment and biological interactions determine these patterns. The patterns may produce a graininess or patchiness in community structure.*

Some other species cluster together for protection, mutu assistance, reproduction, or to gain access to a particular env ronmental resource (fig. 3.23c). Dense schools of fish, f instance, cluster closely together in the ocean, increasing th chances of detecting and escaping predators (fig. 3.24). Sin larly, predators, whether sharks, wolves, or humans, often hu in packs to catch their prey. A flock of blackbirds descending a cornfield or a troop of baboons traveling across the Afric savanna band together both to avoid predators and to find fo more efficiently.

Plants can cluster for protection, as well. A grove of win sheared evergreen trees is often found packed tightly together the crest of a high mountain or along the seashore. They off mutual protection from the wind not only to each other but also other creatures that find shelter in or under their branches.

Most environments are patchy at some scale. Organisr cluster or disperse according to patchy availability of wate nutrients, or other resources. Distribution in a community can vertical as well as horizontal. The tropical forest, for instanc has many layers, each with different environmental conditio and combinations of species. Distinct communities of small plants, animals, and microbes live at different levels. Similarl aquatic communities are often stratified into layers based light penetration in the water, temperature, salinity, pressure, other factors.

Edges and Boundaries

An important aspect of community structure is the bounda between one habitat and its neighbors. We call these relationshi edge effects. Sometimes, the edge of a patch of habitat is relative sharp and distinct. In moving from a woodland patch into a gras land or cultivated field, you sense a dramatic change from t cool, dark, quiet forest interior to the windy, sunny, warmer, op space of the field or pasture. In other cases, one habitat type m intergrade very gradually into another so that there is no distin border.

FIGURE 3.24 *Fish and birds often flock in dense bands for protection or mutual feeding.*