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THE
DIVERSITY
of LIFE

New Edition

Edward O. Wilson

Two-Time Winner of the PULITZER PRIZE

The Creation of Ecosystems

THE BALD EAGLE, one species, flies above the Chippewa National Forest of Minnesota. A thousand species of plants compose the vegetation below. Why does this particular combination obtain rather than a thousand eagles and one plant? Or a thousand eagles and a thousand plants? It is natural to ask whether the numbers that do exist are governed by mathematical laws. If there are such laws, it follows that we can someday predict diversity in other places, in other groups of organisms. To master complexity by such an economical means would be the crowning achievement of ecology.

There are no laws unfortunately, at least none that biologists have hit upon yet, not in the sense ordained by physicists and chemists. But, as in any study of evolution, there are principles that can be written in the form of rules or statistical trends. The discipline formulating these weaker statements, community ecology, is still youthful and rapidly growing, which is a polite way of saying that it is a long way behind the physical sciences—but there is progress, and ambition.

Before us now is the overwhelmingly important problem of how biodiversity is assembled by the creation of ecosystems. We can address it by recognizing two extreme possibilities. One is that a community of organisms, like that occupying the Chippewa National Forest, is in total disorder. The species come and go as free spirits. Their colonization and extinction are not determined by the presence or absence of other species. Consequently, according to this extreme model, the amount of bio-

diversity is a random process, and the habitats in which the various species live fail to coincide except by accident. The second extreme possibility is perfect order. The species are so closely interdependent, the food webs so rigid, the symbioses so tightly bound that the community is virtually one great organism, a superorganism. This means that if only one of the species were named, say the Acadian flycatcher, marbled salamander, or goblin fern, the thousands of other species could be ticked off without further information about that particular community.

Ecologists dismiss the possibility of either extreme. They envision an intermediate form of community organization, something like this: whether a particular species occurs in a given suitable habitat is largely due to chance, but for most organisms the chance is strongly affected—the dice are loaded—by the identity of the species already present.

In such loosely organized communities there are little players and big players, and the biggest players of all are the keystone species. As the name implies, the removal of a keystone species causes a substantial part of the community to change drastically. Many other species decline to near or total extinction or else rise to unprecedented abundance. Sometimes other species previously excluded from the community by competition and lack of opportunity now invade it, altering its structure still more. Put the keystone species back in and the community typically, but not invariably, returns to something resembling its original state.

The most potent keystone species known in the world may be the sea otter (*Enhydra lutris*). This wonderful animal, large and supple in body, cousin to the weasels, whiskered like a cat, staring with a languorously deadpan expression, once thrived among the kelp beds close to shore from Alaska to southern California. It was hunted by European explorers and settlers for its fur, so that by the end of the nineteenth century it was close to extinction. In places where sea otters disappeared completely, an unexpected sequence of events unfolded. Sea urchins, normally among the major prey of the otters, exploded in numbers and proceeded to consume large portions of the kelp and other inshore seaweeds. In otter times, the heavy kelp growth, anchored on the sea bottom and reaching to the surface, was a veritable forest. Now it was mostly gone, literally eaten away. Large stretches of the shallow ocean floor were reduced to a desert-like terrain, called sea-urchin barrens.

With strong public support, conservationists were able to restore

the sea otter and with it the original habitat and biodiversity. A small number of the animals had managed to survive at far opposite ends of the range, in the outer Aleutian Islands to the north and a few localities along the southern California coast. Some of these were now transported to scattered intermediate sites in the United States and Canada, and strict measures were taken to protect the species throughout its range. The otters waxed and the sea urchins waned. The kelp forests grew back to their original luxuriance. A host of lesser algal species moved in, along with crustaceans, squid, fishes, and other organisms. Gray whales migrated **closer to shore** to park their young in breaks along the kelp edge while feeding on the dense concentrations of animal plankton.

Ecologists, like the organisms they study, cannot make nature conform to their perfect liking. They search for openings and seize opportunity, exploiting the occasional discovery of keystone species like sea otters to gain insight into the organization of communities in different environments. Other examples have been found. In the undisturbed forests of Central and South America—more precisely, in the dismayingly few such forests remaining—jaguars and pumas prey on a wide variety of small animals encountered on the ground. They are “searchers,” taking whatever animals they meet, as opposed to “pursuers” like cheetahs and wild dogs, which select only a few kinds of animals and then chase them down. The big cats are especially fond of coatis, members of the raccoon family with elongated bodies and tapered noses, and agoutis and pacas, outsized rodents variously resembling jackrabbits and small deer. When jaguars and pumas disappeared from Barro Colorado Island in Panama, because the forest was no longer extensive enough to support them, the prey species soon increased tenfold. Effects from this shift in balance now appear to be rippling downward through the food chain. Coatis, agoutis, and pacas feed on large seeds that fall from the rain-forest canopy. When they become superabundant, as on Barro Colorado Island, they reduce the reproductive ability of the particular tree species that produce these seeds. Other tree species whose seeds are too small to be of interest to the animals benefit by the lessened competition. Their seeds set and their seedlings flourish, and a larger

Overleaf: A sea otter and the sea urchins on which it feeds in a California kelp forest.

number of the young trees reach full height and reproductive age. Over a period of years, the composition of the forest shifts in their favor. It seems inevitable that the animal species specialized to feed on them also prosper, the predators that attack these animals increase, the fungi and bacteria that parasitize the small-seed trees and associated animals spread, the microscopic animals feeding on the fungi and bacteria grow denser, the predators of these creatures increase, and so on outward across the food web and back again as the ecosystem reverberates from the removal of the keystone species.

In a very different way, elephants, rhinoceros, and other big herbivores rank as keystone species in the savannas and dry woodlands of Africa. When allowed to reach natural high densities, they control the entire physical structure of these habitats. "Modern African elephants," Norman Owen-Smith has written, "push over, break, or uproot trees,"

altering vegetation physiognomy and hence habitat conditions for other animal species. Trees killed by elephants are replaced by regenerating shrubs or grasses that offer more accessible foliage for consumption by smaller herbivores. The leaves of rapidly growing woody plants are less strongly defended chemically than those of the slower-growing trees they replace. Rates of nutrient cycling are also accelerated. Grazing pressure from white rhinoceroses and hippopotamuses transforms medium-tall grasslands into a mosaic of short and tall grass patches. Short, creeping grasses are generally less fibrous and more nutrient rich than taller grasses. As a result of such vegetation changes, food quality is improved for smaller, more selective grazers. Animal species dependent upon a dense cover of woody vegetation or tall grasses for predator evasion may persist in areas of low impact.

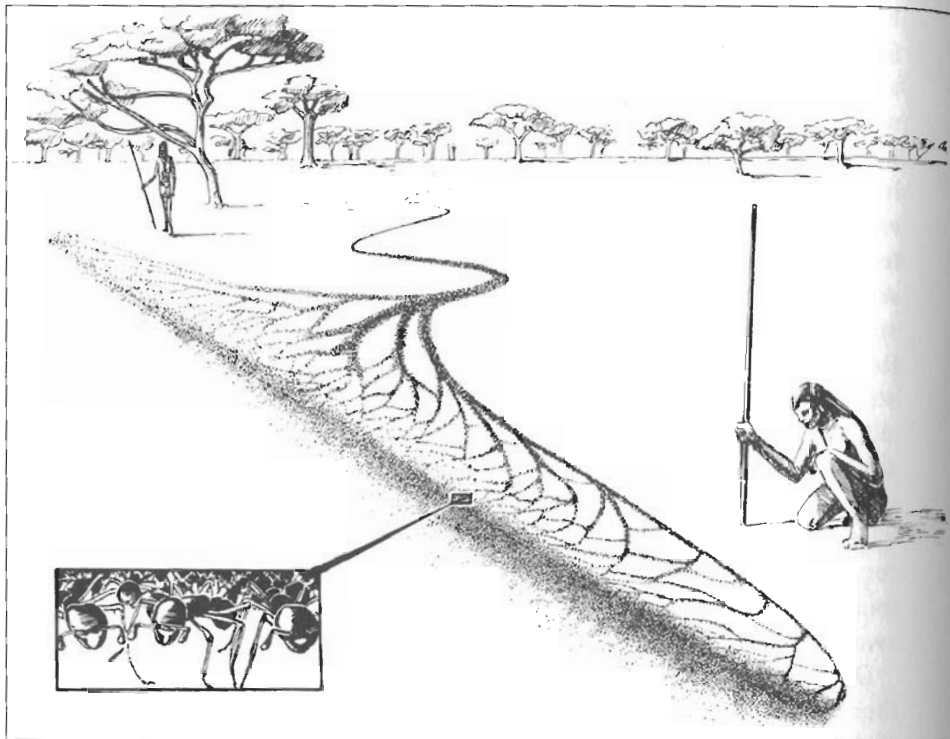
For millions of years the great herbivores of sub-Saharan Africa ranged freely across the vast parklands, creating a mosaic of habitats, a swath of short grassland here, an acacia copse or remnant of riverine forest there, reed-lined pools grown from mud wallows scattered widely about. The total effect was a huge enrichment of biological diversity.

Focusing now from the kilometer reach of elephants down to grass-root level, we find a wholly different class of keystone species. Where big mammals control the vegetation structure, a colony of driver ants at their feet captures millions of victims each day and alters the nature of the community of small animals. Viewed a few meters away, a driver-ant raiding column seems a living thing, a giant pseudopodium reaching out to engulf its prey. The victims are snared with

hook-shaped jaws, stung to death, and carried to the bivouac, a labyrinth of underground tunnels and chambers housing the queen and immature forms. Each expeditionary force comprises several million workers who flow out of this retreat. The hungry legions emerging from the bivouac are like an expanding sheet that lengthens into a treelike formation. The trunk grows from the nest, the crown expands as an advancing front, and numerous branches pour back and forth between the two. The swarm is shaped but leaderless. Excited workers rush back and forth throughout its length at an average speed of a centimeter per second. Those in the van press forward for a short distance and then fall back to yield their front position to other runners. The feeder columns resemble thick black ropes laid along the ground, slowly writhing from side to side. The front, advancing at 20 meters an hour, blankets all the ground and low vegetation in its path. The columns expand into it like a river entering a delta, where the workers race back and forth in a feeding frenzy, consuming most of the insects, spiders, and other invertebrates in their path, attacking snakes and other large animals unable to move away.

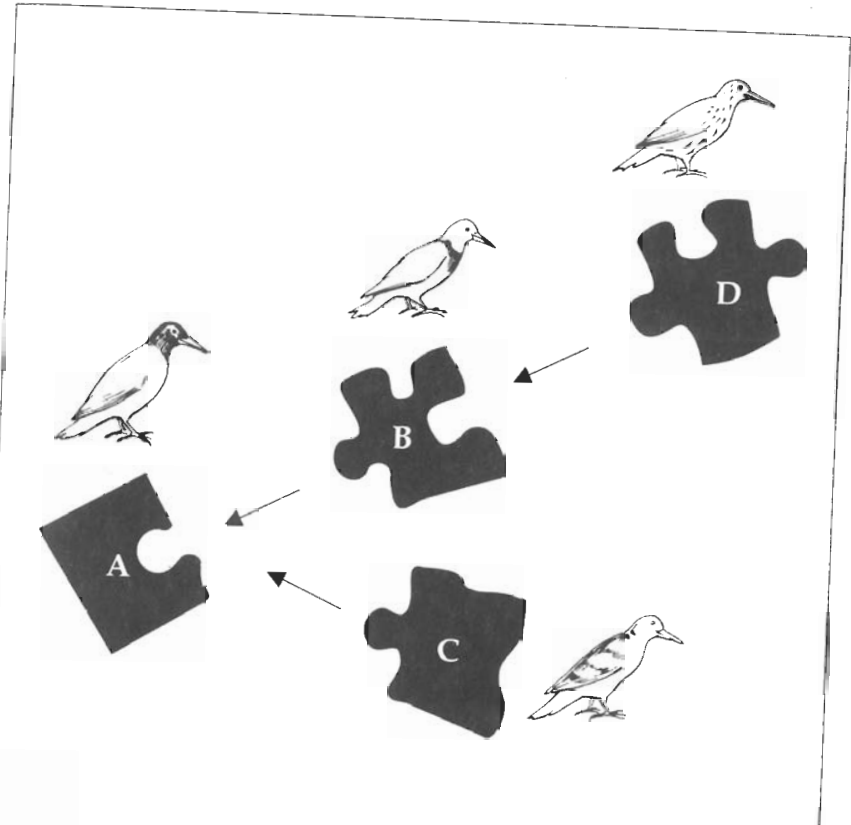
Day after day the driver ants scythe through the animal life around their bivouac. They reduce its biomass and change the proportions of species. The most active flying insects escape. So do invertebrate animals too small to be noticed by the ants, particularly roundworms, mites, and springtails. Other insects and invertebrates are hit hard. One driver-ant colony, comprising as many as 20 million workers—all daughters of a single mother queen—is a heavy burden for the ecosystem to bear. Even the insectivorous birds must fly to a different spot to find enough food.

It has become clear that an elite group of species exercises an influence on biological diversity out of all proportion to its numbers. Scientists are drawn to such strong cases, not just in ecology but in other fields as disparate as astrophysics and neurobiology, because they yield quick information and an entry into systems that are otherwise intractable. But they can be misleading if overgeneralized. There comes a time, in all science, when it is profitable to move away from the bold and obvious and circle around a bit, inventing more subtle approaches to search for concealed phenomena. In the study of communities, **this strategy** requires greater attention to context, history, and chance.



A keystone species at the grassroots level: a swarm of driver ants marches across a savanna in Kenya. The ant armies drastically alter the abundance of insects and other small animals in the habitats through which they pass.

One successful recent approach has been to deduce the assembly rules of faunas and floras. Although the attempt to identify keystone species takes a community pretty much as it is and figures out what happens when the candidate species is removed, the assembly rules reconstruct the sequence in which species were added when the community came into being. It does more: it postulates the sequences that are possible and those that are not. Let me express the idea with an imaginary example chosen for clarity. A certain plant species establishes itself, say on a mountainous island. Its presence allows the colonization of the habitat by a beetle species that feeds only on it. A wasp species that parasitizes the beetle is added next. In another dimension, entailing competition, a second assembly rule is manifested. A woodpecker species arrives; call it A. It multiplies to such



Assembly rules determine which species can coexist in a community of organisms (such as the bird species occupying a forest patch). The rules also determine the sequence in which species are able to colonize the habitat. A set of imaginary rules is represented here as pieces of a jigsaw puzzle that can be fitted together in one of two combinations, ABD or AC.

abundance and dominates so much of the food supply that when two more woodpecker species arrive, B and C, either one of them but not both can squeeze into the community. Now we have a woodpecker fauna consisting of either AB or AC, depending on which of the latecomers arrived first. Finally, woodpecker species D appears. Occupying a distinctive niche of its own—say foraging on large conifers—it can squeeze in with the other species if the preexisting combination is AB but not if the combination is AC. So the first stable woodpecker fauna in the community is either ABD or AC.

Ecologists deduce assembly rules by observing which species actually live together in nature. One approach, used by Jared Diamond in pioneering work on the birds of New Guinea, compares communities in many different localities to see which combinations of species occur and which ones rarely or never occur. The preliminary conclusions reached in this way can then be tested further by detailed studies of habitat preferences of the individual species. Suppose, in the woodpecker case just cited, B and C almost never coexist in the same localities because they compete until one or the other is extinguished. Suppose further that additional studies refine the pattern: B and C occur on some mountains together but almost always at different elevations, so in fact they are seldom members of the same community. On mountains where both occur, B ranges from 200 to 1,000 meters and C from 1,000 to 2,000 meters. Where only one of the species occurs on a mountain, it spreads all the way from 200 to 2,000 meters. This expansion in the absence of a competitor is the same phenomenon we have already met, ecological release. The constriction in the presence of the competitor is called *ecological displacement*. The existence of ecological release and displacement is considered strong presumptive evidence that even when B and C occupy the same geographical range they cannot live closely together in the same habitat and community. They withdraw to elevations where each in turn is the superior competitor, in this case B in the lowlands and C higher up.

It will be interesting now to return to Krakatau and to recall the example it offers of the assembly of species. A community does not arrive on the shores of such an island as a finished product. Instead, it is stacked like a house of cards, one species on another, loosely obedient to assembly rules. Most propagules, whether plant seeds or wandering bird flocks, are doomed to failure. For them the soil is wrong, the forest glades are still too small, the prey species have not yet arrived, or formidable competitors wait at the shore. Even many of the species established earlier cannot hold on as conditions inevitably change: grassy swales are closed out by forest growth, disease strikes, a stronger competitor invades, chance fluctuations in members bounce the population to zero. The community shifts continuously, and by an unconscious trial and error, through innumerable fits and starts, its biodiversity slowly rises. Species excluded earlier at last find room, symbiotic pairs and trios are **fitted together**, the

forest grows deeper and richer, new niches are prepared. The community thus approaches a mature state, actually a dynamic equilibrium with species forever arriving and disappearing and the total species numbers bobbing up and down inside narrow limits.

Throughout the process of colonization, accommodations are made. Species in collision sometimes compromise through ecological displacement. They yield part of the environment to their competitors and survive. Fire ants, for example, are among the most aggressive territorial animals known, and it is unusual to find more than two or three species coexisting in the same community. Their colonies, made up of a mother queen and thousands of stinging, biting workers, engage each other in organized combat. They seek out and destroy smaller colonies and settle territorial boundaries with larger ones by continuous *combat d'usure*, pushing at one another until a balance of power is attained. Sometime during the 1930s a South American species, the imported fire ant *Solenopsis invicta*, was accidentally introduced into the port of Mobile, Alabama. It was successful from the start, needing just forty years to spread across the southern United States from the Carolinas to Texas. Throughout most of that range it confronted a native fire ant, *Solenopsis gemirata*, which up to that time had been a dominant ant in both woodland and open habitats. The native fire ant is still abundant, but it has been largely forced back into scattered woodland sites. The habitats most favored by fire ants generally, pastureland, lawns, and roadsides, are now owned by the newcomers. If the imported fire ant could somehow be removed (an event fervently but hopelessly desired by southerners), the native fire ant would almost certainly reoccupy its old haunts.

The case of the fire ants illustrates the well-documented principle that closely similar species can fit together when their requirements are elastic. Elasticity is the hallmark of Darwin's finches of the Galápagos, for the simple reason that their long-term survival depends on it. They live on volcanic desert islands with harsh, variable environments, changing in the quality of life they offer from month to month and year to year. During the wet season, when most plant growth occurs and food is relatively abundant, the birds enjoy a broad diet. Species that live on the same island and are anatomically similar to one another feed to substantial degree on the same items. In the dry season, food grows scarce and the species come to differ in the items they select. Some become specialists, while others broaden their diets.

The tiny island of Daphne Major is home to two resident species, the medium ground finch *Geospiza fortis* and the cactus finch *Geospiza scandens*. Both live in dense stands of opuntia cactus. In the wet season, when the cactus is in full bloom, the two species consume much the same food. They take the nectar and pollen of the flowers, and they also feast on various kinds of seeds and insects. In the dry season, as the food supply drops, *scandens* narrows its diet to concentrate on edible parts of the opuntia plant. *Fortis* broadens its diet to include an even broader range of items than before, wherever it can find them.

Imagine a case in which two such species have been squeezed together in the same communities long enough for evolution to occur. When they first came into contact, they were elastic and could diverge in their habits enough to lessen competition. The differences were phenotypic, the result of environment and not genes. The compression occurred in traits that were relatively easy to change, most likely by a retreat from parts of the habitat and diet by one or both of the species. As the generations passed, genetic differences arose and hardened the distinction between the two species. Individual birds found it advantageous to excel in those portions of the niche to which they had been driven. The success of those genetically predisposed to do so caused the population as a whole to specialize—to consume a certain food or to build nests in one or another habitat. The differences between the two species next extended to anatomy and physiology. Then the two species competed less with one another, most likely at the price of some of their original elasticity. They experienced the evolutionary change called *character displacement*.

The classic example of character displacement is the change in bill size and food habits of Darwin's finches. Adaptive radiation among the thirteen Galápagos species was based to a large degree on variations in thickness of the bill, and this trait has been engineered in part by character displacement. The selection pressure behind the evolution is improved efficiency during specialization. The deeper the bill at the plane of its attachment to the head, the more power it can exert along the cutting edges and at the tip. Finches with thick bills are well equipped to rip open tougher fruits and to crush bigger and more brittle seeds. Finches with thin bills are limited to softer fare, but they are compensated by an ability to probe narrow crevices and manipulate small objects. A rough analogy from human technology is the adaptive radiation of pliers. To turn a bolt or twist a thick wire with dispatch calls for either linesman's pliers or parrot-

head gripping pliers. To manipulate fine bolts and wires you need nose pliers, which are thinner and proportionately longer.

The shape of the bill is not the whole story of displacement and radiation in Darwin's finches. The size of the jaw muscles, the stereotyped movement of the birds during feeding, and perhaps even the chemistry of the digestive traits have been altered as part of dietary specialization among the species. But bill depth remains the most obvious and easily measured among all the traits. It is a convenient proxy by which the larger syndrome of specialized changes can be studied.

The surest test of character displacement as an engine of adaptive radiation is the demonstration of a certain two-part geographic pattern: species have evolved away from each other in places where they are in contact, but they have failed to do so, or have even converged, where they live alone. In the special case of Darwin's finches, we look for enhanced differences among the species on islands where they live together, and particularly in those traits such as bill shape that allow them to specialize and reduce competition. And we need a control: on other islands harboring only a single species, the competitors should more closely resemble each other, again in those traits believed to be most subject to competition. If this dual pattern is strong and convincing, we may reasonably conclude that where the species has been forced to compete, it evolved away from its opponent to fill a special niche, and where it lacked competition it stayed put—or else evolved in the direction of the opponent to fill both niches.

In testing for character displacement in Darwin's finches, Peter Grant put to use the fact that some of the species occur on many islands in the Galápagos. He looked at thirteen cases where pairs of closely related species occur together on various islands. In eleven such instances he found them to differ more in beak depth than when they occur alone, on islands of their own. The evidence was nevertheless short of decisive. Grant recognized that there is another way in which such a pattern can arise in the absence of competition. Character displacement could also occur by reproductive reinforcement of the differences that isolate species as distinct gene pools. If two species hybridize to some extent when they meet, and the hybrids are inferior or sterile, it is to the advantage of both species to avoid interbreeding altogether. One device might be to evolve traits such as distinctive bill shapes that allow individuals to select members of their own species with greater accuracy. Using stuffed female

birds, which in spite of their immobility are courted by unsuspecting males, Grant discovered that the males prefer females with the right bill shape on islands where similar species live together. They are much less selective, however, where the same species lives alone. In other words, bill shape is used as a cue by male finches to choose females of their own species, and reproductive reinforcement does occur as an evolutionary process. By closely weighing the factors, however, Grant showed that character displacement occurs primarily through competition, and reproductive reinforcement is hooked onto it as a secondary effect. This means that once bills evolve apart as a consequence of competition, related species of Darwin's finches also use the differences to avoid hybridization.

Character displacement has been persuasively documented in a few other groups of organisms, including frogs, fruit flies, ants, and snails, but it is far from a universal biological process. It allows a bit of compression here and there, and enables a few more species to squeeze into local communities. It represents one process by which communities can be organized to some degree, mediating a rise in general biological diversity.

To the forces that increase biodiversity, add predators. In a celebrated experiment on the seacoast of Washington state, Robert Paine discovered that carnivores, far from destroying their prey species, can protect them from extinction and thereby salvage diversity. The starfish *Pisaster ochraceus* is a keystone predator of mollusks living in rock-bound tidal waters, including mussels, limpets, and chitons. It also attacks barnacles, which look like mollusks but are actually shell-encased crustaceans that remain rooted to one spot. Where the *Pisaster* starfish occurred in Paine's study area, fifteen species of the mollusk and barnacle species coexisted. When Paine removed the starfish by hand, the number of species declined to eight. What occurred was unexpected but in hindsight logical. Free of the deprivations of *Pisaster*, mussels and barnacles increased to abnormally high densities and crowded out seven of the other species. In other words, the predator in this case was less dangerous than the competitors. The assembly rule is this: insert a certain predator, and more species of sedentary animals can invade the community later.

Still another dimension of complexity is added by symbiosis, defined broadly as the intimate association of two or more species. Biologists recognize three classes of symbiosis. In parasitism, the first, the symbiont is dependent on the host and harms but does not kill it. Put another way, parasitism is predation in which the predator

eats the prey in units of less than one. Being eaten one small piece at a time and surviving, often well, a host organism is able to support an entire population of another species. It can also sustain many species simultaneously. A single unfortunate and unmedicated human being might, theoretically at least, support head lice (*Pediculus humanus capitis*), body lice (*Pediculus humanus humanus*), crab lice (*Phthirus pubis*), human fleas (*Pulex irritans*), human bot flies (*Dermatobia hominis*), and a multitude of roundworms, tapeworms, flukes, protozoans, fungi, and bacteria, all metabolically adapted for life on the human body. Each species of organism, especially each kind of larger plant or animal, is host to such a customized fauna and flora of parasites. The gorilla, for example, has its own crab louse, *Phthirus gorillae*, which closely resembles the one on *Homo sapiens*. A mite has been found that lives entirely on the blood it sucks from the hind feet of the soldier caste of one kind of South American army ant. Tiny wasps are known whose larvae parasitize the larvae of still other kinds of wasps that live inside the bodies of the caterpillars of certain species of moths that feed on certain kinds of plants that live on other plants.

Raising diversity still more are the commensals, symbiotic organisms that live on the bodies of other species or in their nests but neither harm nor help them. Without any awareness of the fact, most human beings carry around on their foreheads two kinds of mites, slender creatures with wormlike bodies and spidery heads so small as to be almost invisible to the naked eye. One (*Demodex folliculorum*) dwells in the hair follicles, the other (*Demodex brevis*) in the sebaceous glands. You can get to know your own forehead mites the following way: stretch the skin tight with one hand, carefully scrape a spatula or butter knife over the skin in the opposite direction, squeezing out traces of oily material from the sebum glands. (Avoid using too sharp an object, such as a glass edge or sharpened knife.) Next scrape the extracted material off the spatula with a cover slip and lower the slip face down onto a drop of immersion oil previously placed on a glass microscope slide. Then examine the material with an ordinary compound microscope. You will see the creatures that literally make your skin crawl.

People would never notice their forehead mites in any other way. These acarines and other commensals slip the thin wedge in, sip small amounts of nutrients and energy virtually useless to their hosts, and live secure lives of flawless modesty. Their biomass is small to microscopic, their diversity immense. They are everywhere, but it

takes a special eye to find them. On the leaves of trees in the tropical rain forests grow flat, centimeter-wide gardens of lichens, mosses, and liverworts. Among the epiphylls—plants that live on the leaves—thrive a host of tiny mites, springtails, and barklice. Some of the animals browse on the epiphylls, others prey on the epiphyll browsers. Thus a single leaf of a tree, often composing less than one part in 10,000 of that single large organism, is home to an entire miniaturized fauna and flora.

The tightest bond of all among species, the one that gives the word *community* more than metaphorical meaning, is mutualism. This third kind of relationship, often considered the true symbiosis and employed that way in less formal prose, is an intimate coexistence of two species benefiting both. A large part of dead wood is decomposed by termites—not by the termites really, but by protozoans and bacteria that live in the hind guts of the termites. And not entirely by these microorganisms either, since they need the termites to provide them a home and a steady stream of wood chewed into digestible pulp. So the right way to put the original phrase is: a large part of wood is decomposed by the termite-microorganism symbiosis. The termites harvest the wood but cannot digest it; the microorganisms digest the wood but cannot harvest it. It might be said that over millions of years the termites domesticated the microorganisms to serve their special needs. That, however, would be big-organism chauvinism. It is equally correct to say that termites have been harnessed to the needs of the microorganisms. Such is the nature of mutualistic symbiosis: to attain the highest level of intimacy, the partners are melded into a single organism.

Mutualistic symbioses are more than simply curiosities for the delectation of biologists. Most life on land depends ultimately on one such relationship: the mycorrhiza (literally from the Greek for fungus-root), the intimate and mutually dependent coexistence of fungi and the root systems of plants. Most kinds of plants, from ferns to conifers and flowering plants, harbor fungi that are specialized to absorb phosphorus and other chemically simple nutrients from the soil. The mycorrhizal fungi give up part of these vital materials to their plant hosts, and the plants repay them with shelter and a supply of carbohydrates. Plants deprived of their fungi grow slowly; many die.

According to species, the fungi either enter the outer root cells of their plant hosts or envelop the entire roots to form dense webs. A plant pulled up almost anywhere in the world reveals a tangle of

delicate fibers clutching masses of soil particles. Some of the extensions are likely to be rootlets of the plant, but others are the moldlike hyphae of the symbiotic fungi. In many kinds of plants, fungal hyphae have completely replaced the rootlets during evolution.

Without the plant-fungus partnership, the very colonization of the land by higher plants and animals, 450 to 400 million years ago, probably could not have been accomplished. The barren, rain-lashed soil of that time was not hospitable to organisms more complex than bacteria, simple algae, and mosses. The earliest vascular plants were leafless, seedless forms that superficially resembled modern-day horsetails and quillworts. By allying themselves with fungi, they took hold of the land. Some of the pioneers evolved into the lycoplyte trees and seed ferns of the great Paleozoic coal forests. They also gave rise to the ancestors of modern conifers and flowering plants, whose vegetation came in the fullness of time to harbor the largest array of animal life that has ever existed. Today the tropical rain forests, which may contain more than half the species of plants and animals on earth, grow on a mat of mycorrhizal fungi.

Coral reefs, the marine equivalents of rain forests, are also built on a platform of mutualistic symbiosis. The living coral organisms, which cover the carbonaceous bulk of the reef, are the polyps, close relatives of the jellyfish. Like the jellyfish and other coelenterates, they use feathery tentacles to capture crustaceans and other small animals. They also depend on the energy provided by single-celled algae, which they shelter within their tissues and to which they donate some of the nutrients extracted from their prey. In most coral species, each individual polyp lays down a skeletal container of calcium carbonate that surrounds and protects its soft body. Coral colonies grow by the budding of individual polyps, with the skeletal cups being added one on another in a set geometric pattern particular to each species. The result is a lovely, bewildering array of skeletal forms that mass together to make the whole reef—a tangled field of horn corals, brain corals, staghorn corals, organ pipes, sea fans, and sea whips. As the colony grows, the older polyps die, leaving their calcareous shells intact beneath; and in time the living members form a layer on top of a growing reef of skeletal remains. These massive remains, many of which are thousands of years old, play a major role in the formation of tropical islands, in particular the fringing reefs of volcanic islands and the atolls left behind when the volcanoes erode away. They create the physical basis and photosynthetic energy

for tightly packed communities of thousands of species, from sea hornets and mantis shrimps to carpet sharks.

What, in summarizing to this point, do we understand of the assembly of communities? Obviously we know that there is a large amount of organization in the connections among species. But how much? The answer is unknown for any kind of community—all the organisms in a patch of hardwood forest, for example, or in a coral reef or desert spring. We know some keystone species, some assembly rules, some processes of competition and symbiosis that serve as a weak gravitational force.

We know how some species fit together in twos and threes, but not how the whole community fits together. There are a few hints of what is to come as research grows more sophisticated. Think of the community as a food web, a connection of species that prey on other species. Consider what might happen when a species is extinguished, simply plucked out of the food web as were the sea otters. What is the effect? With field studies and mathematical models, ecologists have pieced together a few of the most general properties of food webs that bear on the result of such an experiment. They have learned that the food chains making up the web are very short. If you track who eats whom in different parts of the web, you will usually find the number of links in the chain to be five or fewer. For example: in a marshy glade of the north central states, reedgrass is eaten by short-horned grasshoppers, the grasshoppers are eaten by orb-weaver spiders, the spiders are eaten by palm warblers, and the warblers are eaten by marsh hawks. Because the grass eats no one and the hawks are eaten by no one (except by bacteria and other decomposers when they die), these two species form the ends of the chain. A second rule is that the number of links in the food web does not increase as the size of the community increases. No matter how many species manage to persist in the community, the average number of links from a given plant species to a given top predator does not increase.

I cite these two generalizations to illustrate the more solid principles of community ecology. But I cite them also to show how incomplete and tenuous those principles are. Imagine that you excise the palm warblers from the marsh food web. That food chain is broken, but the ecosystem remains intact, more or less. The reason is that each species in the chain is linked to additional chains. Other species

of birds still present in the marsh will eat more spiders, and the marsh hawks will turn, almost imperceptibly, to a larger number of birds, rodents, snakes, and other creatures. Feather mites, bird lice, and other symbionts found only on palm warblers, part of yet other chains, disappear with their host, but their loss has a negligible effect on the community at large.

Expand the thought experiment to extirpate two warbler species, then all warbler species, and finally all the songbirds in the community. As the knife cuts deeper, its effects will spread with increasing severity through a large but indeterminate part of the community. Take out the ants, the principal predators and scavengers of insects and other small animals, and the effects will intensify—yet the details are even less predictable. Most species of birds, ants, and other plants and animals are linked to multiple chains in the food web. It is very difficult to assess which survivors will fill in for the extinguished species and how competently they will perform in that role. Physicists can chart the behavior of a single particle; they can predict with confidence the interaction of two particles; they begin to lose it at three and above. Keep in mind that ecology is a far more complex subject than physics.

The reverse of the extinction process is species packing. Ecologists are unable for the most part to predict which species can still invade the community and add to its diversity. Select a habitat at random. How tightly packed are the species? What is the upper limit of stable diversity, the highest number of species that can be maintained without human intervention? It is easy to enhance local diversity by the artificial introduction of more and more species—orchids affixed to tree trunks, zoo-bred tigers released into the jungle—but most would eventually perish. Without constant and intrusive manipulation, most overloaded communities will revert to a lower state of diversity, perhaps resembling the original, perhaps not.

The indeterminacy of community structure is increased by the existence of connections between species lying beyond the conventional food webs, and for which few reliable laws or rules exist. Competition—especially that resulting in the exclusion of one species by another—is especially difficult to call. So are the effects of removing scavengers and symbionts. Most difficult of all to assess is the impact of species that alter the physical environment over many years. Dominant tree species overgrow and change the temperature and humidity regimes in which other plants and animals must live. Mound-building termites turn and enrich the soil; they alter the

composition of chemical elements and determine the species of plants that can grow near their underground tunnels. Populations of mites and springtails bloom, and fungus spores and humus correspondingly decline—all to indeterminate degree.

The unpredictability of ecosystems is a consequence of the particularity of the species that compose them. Each species is an entity with a unique evolutionary history and set of genes, and so each species responds to the rest of the community in a special way. I will finish with my own favorite example of law-destroying idiosyncrasy. Tree holes often fill with rainwater, creating small aquatic habitats for animals and microorganisms. On the west coast of the United States live larvae of a tree-hole mosquito species, *Aedes sierrensis*. They feed on microscopic ciliated protozoans, *Lambornella clarki*, which resemble the familiar paramecia used in biology courses. The protozoans in turn feed on bacteria and other microorganisms breeding in the tree-hole water. After the protozoans have been exposed to the odor of the mosquito larvae for one to three days, they turn the tables on their tormentors. Some of them metamorphose into parasitic forms that invade the bodies of the larvae and start to feed on their tissues and blood. Thus a segment of the food chain is flipped upside down, creating a food cycle where each species is simultaneously predator and prey of the other.

The mosquito-protozoan cycle of predation and counterpredation is emblematic of the direction that community ecology must take: analyze ecosystems in detail, from the bottom up. Biologists are returning to natural history with a new sense of mission. They cannot expect to learn much more from the top down, from the properties of whole ecosystems (energy flow, nutrient cycles, biomass) interpolated to the properties of communities and species. Only with a detailed knowledge of the life cycles and biology of large numbers of constituent species will it be possible to create principles and methods that can precisely chart the future of ecosystems in the face of the human onslaught.

Then there might be an answer to the question I am asked most frequently about the diversity of life: if enough species are extinguished, will the ecosystems collapse, and will the extinction of most other species follow soon afterward? The only answer anyone can give is: possibly. By the time we find out, however, it might be too late. One planet, one experiment.