On the Origin of Ecological Structure

CREDITS (TOP TO BOTTOM): KATHARINE SUTLIFF/*SCIENCE*; WIKIPEDIA/GEORGE RICHMOND, FROM ORIGINS, RICHARD LEAKEY AND ROBERT LEWIN

ON 23 JUNE 1802, PRUSSIAN NATURALIST Alexander von Humboldt attempted to reach the summit of Mount Chimborazo, the highest peak in the northern Andes. Bleeding, his beard caked with ice, the 33-year-old Humboldt worked his way along a 12-centimeter-wide ridge only to be blocked by a cliff some 400 meters from the top. Humboldt's barometer indicated 5878 meters—a climbing record unbeaten for decades and one that brought him international fame.

The lasting impact of the trip, however, came from his explorations of somewhat less lofty terrain. Having studied Mount Chimborazo and nearby peaks for months, Humboldt assembled the first comprehensive treatise—*Essay on the Geography of Plants*—on how vegetation varies with altitude, climate, soil, and other factors. The work was a groundbreaking exploration of the physical underpinnings of ecological structure: what determines the species that make up a community and their relative abundance.

More than a half-century later, Charles Darwin quietly conducted experiments in his garden at Down House that were even more seminal. Examining a patch of unkempt lawn as it went to seed, Darwin observed that the species changed through time: "more vigorous plants gradually kill the less vigorous, though fully grown plants," he wrote; nine of the original 20 species eventually disappeared. It was a compelling demonstration of competition, which became a cornerstone, albeit a controversial one, for community structure, and Darwin included the experiment in *On the Origin of Species*. "What a wondrous problem it is," Darwin wrote to the botanist Joseph Hooker in 1857, "what a play of forces, determining the kind and proportion of each plant in a square yard of turf!"

Ever since, ecologists have wrestled with understanding what dictates the kinds and proportions of organisms in communities ranging from meadows to montane forests. How these forces set up communities has "arguably been one of the most primary questions driving ecological science since its origins," says Brian Enquist of the University of Arizona, Tucson. Competition, predation, disturbance, and other factors have a heavy hand, and new research is showing the influential role of evolution as well. "You can't understand the assembly process if you don't think about evolution," says Jeannine Cavender-Bares of the University of Minnesota, Twin Cities.

Despite these achievements, there is still no consensus on the relative importance of the various forces. Darwin and many later ecologists emphasized competition among species, but proponents of a controversial theory of biodiversity that assumes competition has no impact argue that immigration and other random demographic events can account for much of the apparent makeup of communities. As a result, ecologists have a long way to go to come up with formulas that predict how communities might arise and change. Yet the ability to make predictions is important for the restoration and management of ecosystems impacted by invasive species or climate change.

Many forces

Species abundance and composition—i.e., structure—may be the salient feature of a biological community. A tropical rainforest, for example, is physically dominated by tall, broad-leafed trees with several layers of trees underneath adapted to lower light. Woody vines and epiphytes dangle from the branches, and shade-tolerant shrubs dot the forest floor. Even though the particular species vary from place to place, wet tropical forests still exist as recognizable entities on four continents. A combination of physical and biological forces organizes species into these predictable communities.

Following Humboldt's lead, scientists in the 19th century assembled evidence that the composition of communities depends on physical factors such as climate and soil chemistry. Today, ecologists call these factors "environmental filters" that broadly determine which species can live where. For example, forests in the eastern United States are rich in sugar maples in the north but gradually become dominated by oaks and hickories to the south as temperature rises. Hemlock and beech trees disappear to the west as conditions generally become drier.

On a global scale, the importance of physical factors varies with latitude, according to conventional thinking, popularized by Theodore Dobzhansky in 1950. Stress from cold and freezing limits diversity at high latitudes, according to this widely established view, whereas species diversity in the tropics is capped by another major driver, biological interactions.

But to what degree are local patterns driven by the direct influence of climate versus biological interactions such as competition? "Answering this question is critical for our ability to predict shifts in natural communities due to global climate change," says Nicholas Gotelli of the University of Vermont, Burlington.

THE YEAR OF
DARWIN

This essay is the 10th in a monthly series. For more on evolutionary topics online, see the Origins blog at **blogs.sciencemag.org/origins**. For more on ecological structure, listen to a podcast by author Erik Stokstad at **www.sciencemag.org/multimedia/podcast**.

It's long been clear that biological interactions—competition, predation, and so on—can be big players. In the 1930s, Soviet microbiologist Georgii Gause conducted influential research into how competition sets up communities. Gause studied mixtures of three species of the protist *Paramecium* that were provided with one or two kinds of food: yeast, bacteria, or both. The experiments revealed that one species of *Paramecium* would always drive the others extinct if they had to compete for the same resource. This led to the principle of competitive exclusion and eventually to the idea that species that are ecologically too similar cannot coexist. Although ecologists now know that the natural world is more complicated—there are ways for similar species to coexist—the principle had a major impact on thinking about the structuring of communities.

Over subsequent decades, ecologists recognized that predators, too, can strongly shape

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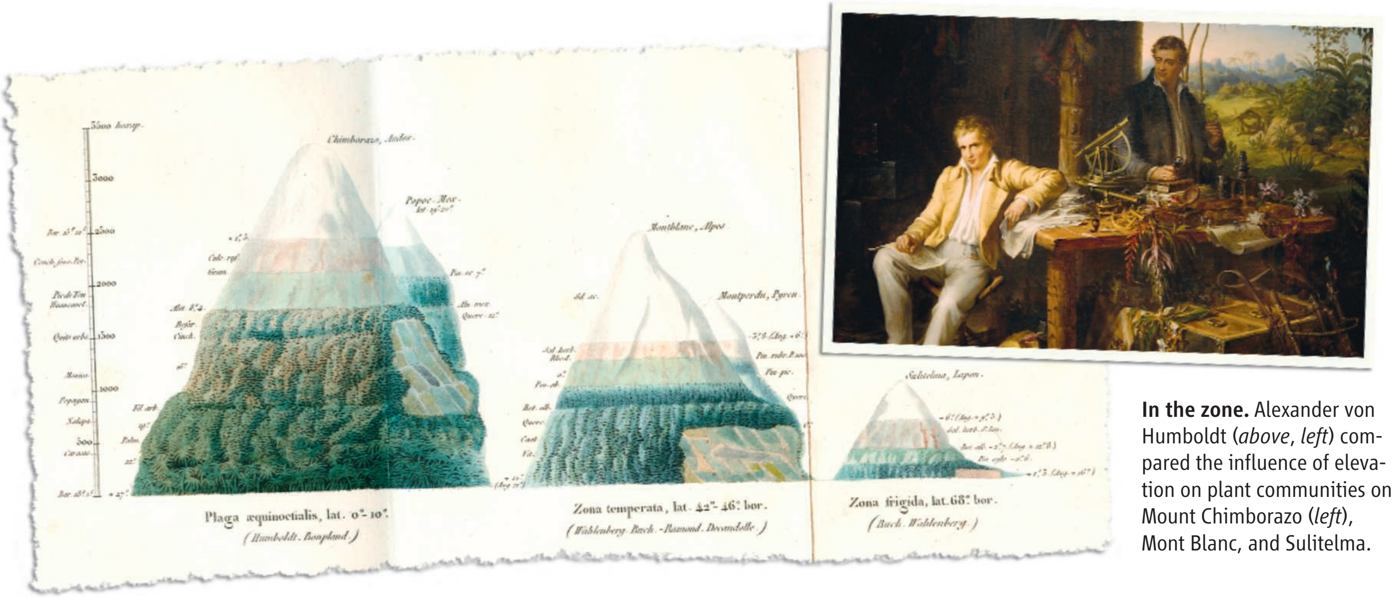

In the zone. Alexander von Humboldt (*above, left*) compared the influence of elevation on plant communities on Mount Chimborazo (*left*), Mont Blanc, and Sulitelma.

communities. Working in rocky tide pools of the Pacific Northwest, for example, Robert Paine of the University of Washington, Seattle, proposed in 1966 that species diversity is controlled by keystone predators. By eating species that are strong competitors within the food web, keystone predators help weaker competitors persist. Sea stars, for example, feed on mussels and keep them from crowding out barnacles and algae.

A species doesn't have to be a predator or a competitor to have a profound effect. By altering the physical environment, some species influence which organisms live where. When beavers build dams they flood land, providing new aquatic habitat for fish and amphibians. Corals create a three-dimensional space full of places to hide, eat, and live for a wide variety of marine life. Thus one organism can facilitate the settlement or success of another.

Debating competition

Although certain ecosystems present clear examples of how biological interactions shape communities, coming up with general principles has been much more difficult. Arguments have raged for decades about the relative importance of factors such as competition, predation, and chance events: colonization, for example. A major debate about competition and how to spot it kicked off in 1975, when Jared Diamond of the University of California, Los Angeles, proposed seven broad patterns of species distributions, which he dubbed "assembly rules," for communities. The first rule was that only some of all the possible combinations of species actually coexist in nature. Diamond identified several instances of "forbidden species combinations," based on literature and fieldwork on fruit-eating birds living in the Bismarck Archipelago and Solomon Islands near New Guinea. For example, the black honeyeater (*Myzomela pammelaena*) lives on 23 of the 41 surveyed islands in the Bismarck Archipelago, but not on any of the 14 islands inhabited by the black sunbird (*Nectarinia sericea*). Both birds are about the same size and use curved bills to sip nectar, and Diamond noted that competition affects their distribution.

But without any experimental evidence or strong statistical tests, it was a bold leap to conclude that competition was a major force structuring island communities. Another interpretation came from Daniel Simberloff and Edward Connor, then at Florida State University, Tallahassee. Starting in 1979, they argued that patterns of species distribution on these islands appeared to be random. "The pattern was eyeballed," Simberloff says of Diamond's results.

The disagreement continues to this day. Working with James Sanderson of the Wildlife Conservation Network in Los Altos, California, and Stuart Pimm of Duke University in Durham, North Carolina, Diamond published a new analysis of the bird species of the Bismarck and Solomon Islands in *Evolutionary Ecology Research* in July. By using what they say are more sophisticated statistical tests, the team verified that the patterns of species combinations identified by Diamond in 1975 were indeed highly unlikely to be due to chance. Although chance may determine which species end up colonizing an island, interspecific competition then tends to keep out ecologically similar species, Pimm says. Simberloff, meanwhile, has a paper in press in which he finds that the patterns in the same data are better explained by the historical and chance factors that control how birds disperse than by competition.

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> —Evan Weiher, University of Wisconsin, Eau Claire

A handful of so-called assembly rules have been proposed since Diamond's early work popularized the search for these patterns. But local communities are so varied that it seems difficult to extrapolate from one to another. "I think what we're going to find out is that assembly rules are vague, gentle constraints," says Evan Weiher of the University of Wisconsin, Eau Claire.

In 1997, Stephen Hubbell, now at the University of Georgia, Athens, proposed an alternative to assembly driven by competition or other biological interactions. Instead, Hubbell suggested, the abundance and diversity of species in a community is determined mainly by random dispersal, speciation, and extinction. The idea, which he dubbed the "unified neutral theory of biodiversity," makes a radical assumption: It considers all organisms of the same trophic level (plants, say, or herbivores) as demographically identical; that is, each organism in a particular level has about the same chance of reproducing, dying, migrating, or giving rise to a new species. Testing the idea on a 50-hectare plot of tropical forest in Panama, Hubbell showed that the model predicted the species richness and relative abundance in the area. Hubbell doesn't dispute that some species differ in their ability to compete, but competition wasn't really an important factor in determining what plants grew where, he noted.

CREDITS (TOP TO BOTTOM): A. VON HUMBOLDT, 1817, *DE DISTRIBUTIONE GEOGRAPHICA PLANTARUM*; AKADEMIE DER WISSENSCHAFTEN, BERLIN/AKG IMAGES

Neutral theory has generated a lot of interest, especially among theorists, and controversy. On the one hand, researchers find it appealing because of its simplicity and the fact that it provides predictions for many kinds of communities. But many ecologists remain skeptical of the assumption that species are essentially equivalent in how they function in the community. A recent paper by Nathan Kraft of the University of California, Berkeley, and others even challenges the adequacy of neutral theory in tropical forests, where it was first proposed, and instead makes a case for functional differences among species, and perhaps competition, as contributing factors (*Science*, 24 October 2008, p. 580).

Researchers also point out that biological interactions and "neutral" factors, such as the stochastic effects of dispersal, aren't mutually exclusive. Both can sometimes happen in different ways simultaneously. For example, in a 2005 paper in *Ecology Letters*, Tadashi Fukami, now of Stanford University in Palo Alto, California, and Wim Van der Putten of Wageningen University in the Netherlands described a 9-year experiment with plants on abandoned farmland. They found that small communities of plants ended up with the same array of functional traits, such as whether a seed is dispersed by an animal or whether the plant is a perennial, indicating that biological interactions were determining what kinds of plant species could successfully establish. But the particular species that showed up were essentially random selections from the regional species pool, a result consistent with neutral theory.

Diversity. Structure results from many sources, including predators such as star fish and habitat-building organisms such as coral; physical factors such as temperature also influence where species, like these trees in Quebec, Canada, can thrive.

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Predicting the future

Ecologists would also like to know how the structure of communities will shift through time. Moreover, with all the changes humans have made to the environment, restoration ecologists and conservation biologists want to predict the future of these altered communities.

Communities are typically in flux, with some species disappearing and new ones taking hold after relatively minor disturbances. In forests, for example, when a storm knocks down a stand of trees, more light reaches the forest floor. Small, short-lived flowering plants move in, then shrubs, and tree seedlings that within a decade or so begin to shade out the herbaceous plants.

A pioneer in the study of this process, called succession, was Frederic Clements of the University of Nebraska, Lincoln. He thought succession would inevitably lead to a particular climax community, and the system would remain in equilibrium until a disturbance started the cycle over again. Although this seems to be largely true for some plant communities, such as temperate forests, other types of communities appear to behave differently.

In rocky intertidal communities in the Gulf of Maine, for example, the community can shift between two alternate states, dominated by either algae or mussels. Peter Petraitis of the University of Pennsylvania and Steve Dudgeon of California State University, Northridge, scraped all the life off coastal rocks in the Gulf of Maine to create patches of open habitat. As they and colleagues reported in *Oecologia* in April, the identity of the new community depended on which organism got there first. If mussel larvae landed, they grew faster than the algae. But if the algae had enough time to get started, they sheltered mussel predators like starfish that keep the mollusks in check.

Although it's not known how common alternate stable states might be, the concept has important implications for restoration ecologists, who want to know whether degraded habitat will repair itself or whether it needs intervention to prevent it from falling into an undesirable new state. But there are so many variables that predicting what will happen is difficult.

That same limitation applies to assembly rules. In a study of salt marshes published in March in *Ecological Applications*, a group of ecologists found that although physical stress chiefly determines the distribution of plants in a California marsh, competition is the main force in similar salt-marsh communities in Chile. The finding suggests that general rules won't provide conservation biologists with easy shortcuts when they're trying to save or restore unstudied communities.

But Brian Silliman of the University of Florida, Gainesville, a study author, says that ecology still provides valuable insights, such as the potential impact of removing keystone predators. "We can generalize in large ways," he says. Pimm agrees that some broad principles do exist. Although general community rules may not always provide fine-scale predictions about how a community will assemble, he says, they are "hugely useful and critical for conservation."

–ERIK STOKSTAD

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