

# Neutral Theory: A New, Unified Model for Ecology

BY SCOTT NORRIS



*The forest canopy of Panama's Barro Colorado Island in the dry season, viewed from above. Photographs: Stephen Hubbell.*

In evolutionary time, species come and go. In ecological time—anything from days to decades or even centuries—most species, in most places, persist. They do so in complex networks of local communities and extended metacommunities, within and between which even similar and closely related species may vary greatly in abundance. And while processes such as invasion and succession sometimes bring about a rapid reordering of the biological status quo for a particular site or region, species more typically maintain themselves in fairly constant numbers, neither taking over everything, like kudzu, nor dwindling to nothing, like the dodo.

**E**mpirical data reveal striking and often-repeated patterns in how species originate, persist, assemble in groups, and eventually go extinct. These regularities have always suggested, to some ecologists, the existence of general causal mechanisms that shape both the evolution of biodiversity and the structure of ecological communities. But what are these mechanisms, and how exactly do they work? Such questions are arguably among the most difficult problems receiving serious attention in any branch of science.

Much of the difficulty in formulating any general theories of biological diversity stems from the need to reconcile processes operating at very different spatial and temporal scales: from the evolution and biogeographic distribution of species to the births and deaths of individuals in local communities. Additional troubles arise from uncertainty in the interpretation of empirical patterns: How much is biologically meaningful, how much is the product of random chance, and how does the balance between the two depend on the scale of observation?

These issues lie at the heart of a recent book by ecologist Stephen Hubbell, of the University of Georgia. *The Unified Neutral Theory of Biodiversity and Biogeography*, published in 2001, is one of the most ambitious forays into grand theory that the field of ecology has seen for a long time. Hubbell's neutral theory builds on, and is intended to supplant, one of the field's

most influential and enduring theoretical edifices, *The Theory of Island Biogeography*, by Robert MacArthur and Edward Wilson. Hubbell's book has been widely and favorably reviewed in leading journals, but it has also sparked a sharp debate. The response of many theoretical ecologists to Hubbell's ideas is perhaps typified by a review in the journal *Evolution* by James H. Brown, an ecologist at the University of New Mexico, who calls the book a "milestone"—and then goes on to reject its fundamental premise.

That premise is neutrality, and it conflicts with what has long been a fundamental tenet of community ecology: that species populations are regulated by competition. According to this view, if different species are limited by the same resource, whichever is the best competitor will eventually exclude all others. Diversity is maintained by the separation of species into different ecological niches, allowing each species its own domain of competitive superiority. Neutral theory, in contrast, makes the admittedly unrealistic assumption that individuals of all ecologically similar species are competitively equal. And so the central question to greet Hubbell's book has been this: Why such obstinate denial of biological reality?

The answer lies, in part, in what Hubbell perceives to be the biological reality of the systems he studies: tropical forests. The answer also lies in what emerges as the solution to a complex mathematical problem. Although neutral theory can be discussed in conceptual terms using the general vocabulary of ecology, Hubbell's book is deeply and darkly mathematical. The pages swim with equations, some of them borrowed from the neutral model of evolutionary genetics, to which Hubbell's biodiversity theory is closely related. The friction the theory has generated originates at the point where mathematical abstraction meets real-world mechanism. Ultimately, understanding exactly what neutrality means in the context of Hubbell's model, and what this may presume or imply about ecological systems, requires a plunge beneath the surface into the theory itself.



Once a hill, now an island: Barro Colorado Island in Panama was formed by the damming of the Chagres River during the construction of the Panama Canal.

Under continuous study since 1923, the 600-acre island has been the site of classic studies on lowland moist tropical forest ecology and the effects of insularization on ecological communities. Research facilities on the island are maintained by the Smithsonian Tropical Research Institute.

Photograph: Marcos A. Guerra, Smithsonian.

### Laying the groundwork for a neutral theory

A tour of the neutral theory begins with an issue that has long tantalized ecologists: the relative abundances of different species coexisting in a biological community. Any thorough biological census reveals that species are not equally common. A graph of the number of species falling into sequentially doubling categories of abundance (one to two individuals, two to four, four to eight, and so on) is typically bell-shaped. The right and left tails of this so-called lognormal distribution indicate that few species are either extremely common or extremely rare; the hump in the middle indicates that most species are of moderate or relatively low abundance. Some ecologists (including Hubbell) argue that there are more species on the rare side, skewing the bell curve with a longer tail on the left than the right.

Classic approaches to the distribution of abundance problem have focused on community-wide rules for dividing resources. The concept of the ecological niche has evolved to describe the unique slice of the resource pie carved out by each species. However, the use of niche theory to explain the regularity of species abundance patterns has never been completely successful. By what means are re-

sources divided up in such a way as to produce the commonly observed patterns of numerical dominance and rarity? And when does the division process stop, resulting in a fixed or equilibrium number of species?

For Hubbell, part of the answer lies in another empirical pattern, exhibited not by species but by individuals. One of the neutral theory's key assumptions is that, within groups of ecologically similar species, individuals tend to fill landscapes to a point of saturation. This is true regardless of how many species are represented: A tropical forest may contain hundreds more tree species than a northern coniferous forest, but the number of mature individual trees present in equal-area samples of each forest type is roughly the same. An important consequence of this kind of biological saturation is that a population increase in one species must necessarily be offset by a decrease in another. This is especially apparent when considering trees occupying a two-dimensional area, where space itself is limiting, but Hubbell argues that the same principle applies for any finite resource distributed across a broad area. His theory grows out of an attempt to model the dynamics of ecological communities subject to this general limitation, which he calls the "zero-sum constraint."





*The great biological diversity of tropical forests is exemplified on Stephen Hubbell's study site on Barro Colorado Island. Since 1980, Hubbell and other researchers here have conducted long-term studies of forest dynamics, censusing and re-censusing hundreds of thousands of individual trees to document species growth, mortality, productivity, and distribution. The data produced by this mammoth effort have shown that tropical tree communities undergo constant changes in composition and have helped point the way to the unified neutral theory of biodiversity and biogeography. Photograph provided by Stephen Hubbell.*

Specifically, Hubbell set out to create a model in which all of the factors influencing community composition—births, deaths, immigration, and (on longer time scales) speciation—interact to produce the commonly observed empirical patterns of diversity and distribution of abundance. Such a model requires a method for choosing, every generation, the species identity of those individuals that die and those that come to occupy, by birth or immigration, the vacancies created. In a niche-based theory, this method would be based on competitive interactions between species. But the sim-

plest of all methods might be simply to draw the replacing species at random from the existing community.

Hubbell calls this random replacement process “zero-sum ecological drift,” and it is precisely what makes the neutral theory neutral. Under ecological drift, all individuals in the community, regardless of species, have equal probabilities of giving birth, dying, immigrating to another location, and (in one version of the model) acquiring a mutation that will eventually result in speciation. But that does not mean that all species have an equal chance of filling a vacancy.

Abundant species have a greater likelihood of being drawn, but only by virtue of their abundance. Individuals are equal, but species, as collective entities, are not.

The neutral theory emerges from a mathematical description of zero-sum ecological drift operating over many generations. The assumption of individual equivalence in model parameters is built in, but Hubbell did not choose neutrality simply because it is simple. His computer modeling shows that ecological drift alone, with no other mechanism, produces patterns of diversity and abundance that closely mirror those observed in nature. Indeed, he argues, the neutral model is a better predictor of empirical patterns than models that incorporate species-specific population regulation.

### **Drift in ecological communities**

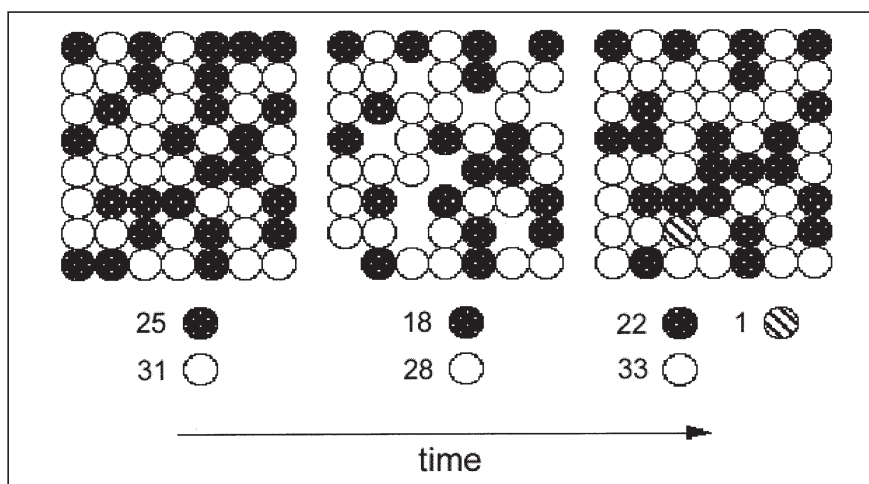
At the scale of local communities, the easiest way to think about ecological drift is to imagine a vast checkerboard of “resource space.” Every square is occupied by an individual of some species, and the total number of squares occupied by each species can be counted and grouped to produce an abundance distribution. A few species will occupy many squares; most will occupy only a few. As time passes, some squares become vacant (by an individual death) and are reoccupied by an individual of the same or another species. Each species has some chance of filling the vacancy, in direct proportion to its current share of the checkerboard. An observer might record and graph the steady, small changes in abundance of each species through time. Imagine a spool of paper on which 26 differently colored pens record the ups and downs of species A through Z over many generations. The line at the top of the sheet is the species with the highest abundance, and so on down. As the spool rolls and the lines fluctuate, some follow long-term upward or downward trajectories, crossing other lines in the process. Sometimes a line at the bottom of the page will fluctuate to zero and disappear: an extinction. Sometimes a new line will rise up off the bottom and become part of the pattern: a successful immigration of a new species from outside the community, or perhaps a speciation event.

Generation to generation, all of this change is randomly driven. The rank (in abundance) of any species can change through time, but the abundance of whatever species is currently number 1, or 2, or 26, stays fairly constant, as does the total number of species present. If one were to unroll the graph, point to a particular moment in time, and ask what produced *that* particular community configuration, one would—according to Hubbell—be asking exactly the wrong question. Nothing about the biology of species D can explain why it was 20 times more common than species R. Communities are not like puzzles whose assembly is tightly constrained by the attributes of the individual pieces. Their structure—as observed by ecologists in the present moment—is simply a snapshot of the simultaneous neutral drift of species through evolutionary time.

The theoretical unity alluded to in the title of Hubbell's book is the result of mapping out the implications of zero-sum ecological drift beyond the scale of local communities and short time frames. At the local level, the model requires a source of new species—immigrants from the surrounding metacommunity—to maintain diversity patterns and prevent an eventual takeover of all resource space by the most abundant species. The metacommunity is a group of trophically similar species spread over a broad geographic area encompassing many local communities, and over a time period long enough that speciation events figure in the dynamics of species distribution and abundance. Like local communities, the metacommunity is governed by zero-sum drift and sometimes experiences extinctions. Thus it too requires a source of new species, which can only be provided by an evolutionary process of speciation.

### A unified theory

Incorporating speciation into a theory of local biological diversity was one of Hubbell's goals from the outset. It is in this regard that the neutral theory follows directly from the famous MacArthur and Wilson model of island biogeography. That model predicts an equilibrium number of species that will be present in isolated or "island" habitats, based on



*One generational or disturbance cycle in a community undergoing zero-sum ecological drift. On the left, all available resource space is occupied by individuals of two different species. In the center, individual mortality in both species produces vacant sites or unutilized resources. On the right, vacancies are filled by recruits from the local community, and by the arrival of a third species from the surrounding metacommunity. The identity of each new arrival is a matter of probability, based on the local abundance of each species and on the frequency with which outside species may wander into the local community.*

*Graphic provided by Stephen Hubbell.*

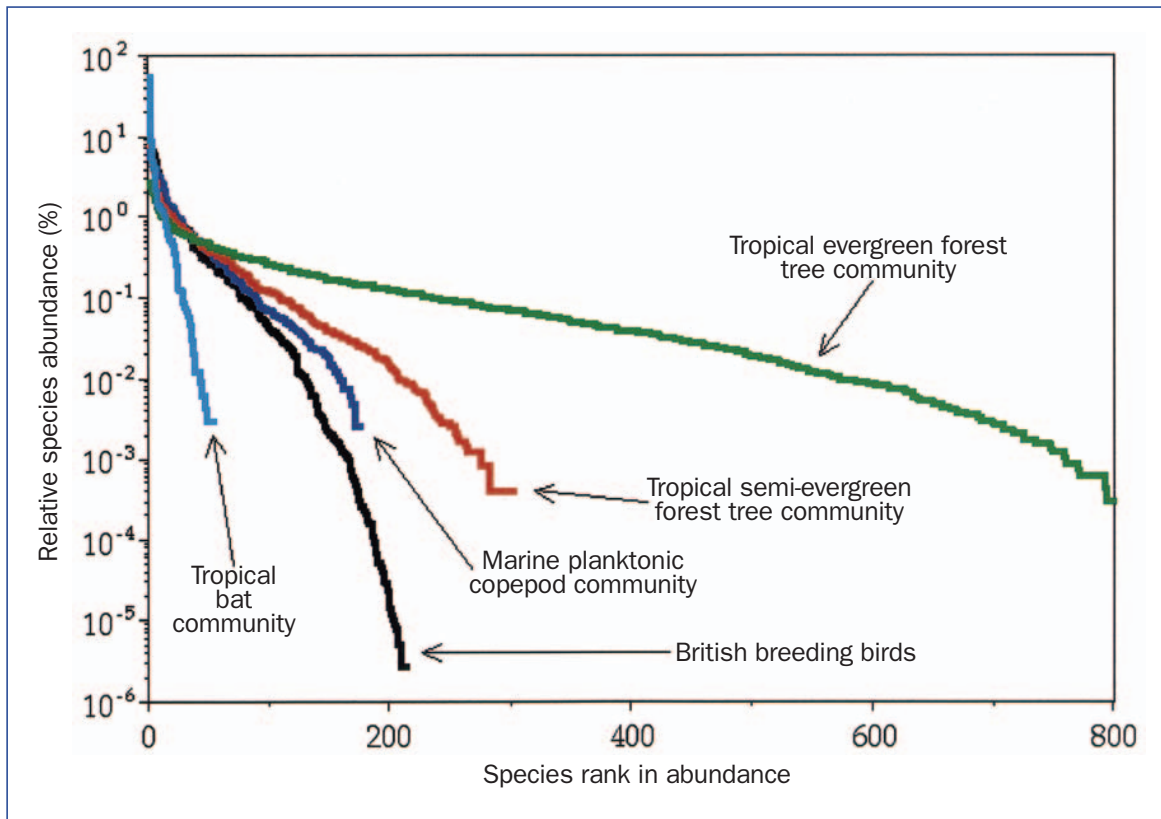
rates of immigration and local extinction that are themselves dependent on island size and degree of isolation. But it does not include speciation as a source of new species, and it says little about the dynamics of "mainland" or source communities, other than to view them as the pool of potential immigrants from which island communities are assembled. And because it does not address population dynamics, the MacArthur and Wilson model can predict only species diversity; it says nothing about relative abundance.

Hubbell's neutral theory represents an attempt to fill in these theoretical gaps in the classic model of island biogeography. Originally, Hubbell says, his work was directed toward adding a mechanism of speciation to island biogeography, in order to calculate a predicted equilibrium number of species not only for islands but for continental metacommunities undergoing zero-sum ecological drift. But speciation and drift together produced something that was, he says, "totally unexpected." The mathematics that led to a prediction of species diversity also produced a predicted distribution of relative species abundance. And with the added element of dispersal,

both factors could be modeled continuously, from the slow and spatially expansive dynamics of metacommunities to the faster dynamics of present-day ecological communities, where species may arrive as immigrants from adjoining areas or go locally extinct.

Both diversity and abundance are described in the neutral model in terms of a single mathematical parameter, which Hubbell calls "the fundamental biodiversity number." Whether or not one accepts the assumption of competitive neutrality, this formulation emerges as one of the triumphs of Hubbell's theory. The parameter itself is a function of just two variables: the total number of individuals in the metacommunity and the rate or probability of speciation. With these two pieces of information alone, the neutral model makes predictions that are closely in line with relative abundance data for a variety of species groups, from tropical trees to marine copepods.

This unified mathematical approach seems likely to exert a lasting influence on the field of community ecology. But it also raises a new series of questions, particularly concerning the model's treatment of speciation. How, for the purposes of the



The distribution of species abundance within a biological community can be plotted as a “dominance–diversity curve.” On the vertical axis is the number of individuals of a particular species, as a percentage of the total individuals in the community. On the horizontal axis is the rank of each species in abundance, descending from one. Typically, a large percentage of the individuals present belong to one of a small number of dominant species. Hubbell believes his model provides the best explanation to date of the characteristically different slopes and shapes of dominance–diversity curves in different kinds of communities.

Graph provided by Stephen Hubbell.

model, should new species be recognized? Which of several possible mechanisms of speciation should be used, and how should these be represented mathematically? Can the model be used to generate and test hypotheses about speciation and phylogenetic evolution?

It is perhaps in its treatment of speciation that the integrative potential of Hubbell’s model emerges most clearly. For example, the theory suggests ways in which the makeup of present-day ecological communities may carry revealing signatures of distant evolutionary dynamics. Hubbell models speciation in two different ways and discusses the possible consequences of each model on metacommunity structure. In one, species originate through rare mutations that, at some very low frequency, occur and eventually spread throughout populations. In the other, speciation occurs with the division of a preexisting population

into separate groups. Each speciation model is a greatly simplified rendering of a complex biological process. At present, Hubbell notes, “this is a top-down, mechanism-free theory that describes the patterns we see in nature. There’s lots of room to enrich the theory, for example, by incorporating more definitive models of speciation.”

### Questioning the theory

It’s easy to argue that the neutrality assumption is simply wrong. Ecologists have plenty of data indicating that different species play different ecological roles, have different tolerances and requirements, and accordingly are non-randomly distributed in the environment. Such points are well taken but may not entirely counter the neutralist argument. Species do differ, but it may be equally self-evident that in real communities some process resembling ecological drift must

be operating alongside these differences. The appearance of particular species in particular places is never entirely predictable. The question, Brown says, is really about the relative strengths of random and deterministic processes in shaping communities.

Brown believes that Hubbell has the mathematics of diversity and abundance essentially correct but gives too much weight to randomness as the driving force. “I think the differences between species really do matter,” he says. “So much of what we see in evolution is the diversification of form and function.” The neutralist response is that the model applies only in cases where such diversification is limited. “Neutral models refer only to ecologically similar species and not, emphatically not, to trophically complex communities,” cautions Graham Bell, of McGill University, a strong advocate of the neutral approach.

Hubbell justifies the neutral assumption in two contrasting ways. On the one hand, neutrality can be seen as a kind of analytical filter through which phenomena attributable to chance can be accounted for, in order to reveal other patterns that must stem from biological differences. "You have to understand the role of chance, so you can factor it out and figure out what's left over," Hubbell says. "Deviations from predictions of the neutral theory will tell us where to look." For example, if a dominant species is more abundant in a local community than the neutral theory predicts, this may be evidence of the kind of competitive advantage in fitness that ecologists have long assumed must underlie community structure.

On the other hand, Hubbell also maintains that the assumption of individual equivalence may be far closer to the truth than many ecologists believe. Here the exact meaning of neutrality becomes particularly important. The theory has been characterized as assuming equivalence in demographic parameters across species, but this is not necessarily the case. Species may differ in birthrates, for

example, as long as they share an equal per capita probability of occupying vacancies in the community. Within this constraint, ecological variation and trade-offs in life history characteristics remain possible. Competition and niche partitioning are still possible as well: There are simply no predictable winners and losers, and so these processes do not determine the composition of the community.

Apart from the validity of its assumptions, the neutral theory faces many experimental and empirical challenges, which will determine how closely its predictions square with biological reality. In the real world, for example, communities frequently must respond to environmental change, which may favor some species while reducing opportunities for others. Species turnover as depicted in the neutral model, Brown says, fails to capture the kind of rapid ecological change sometimes seen in nature. "The dynamics of the model are way too slow," he says.

Robert Ricklefs, of the University of Missouri–St. Louis, makes a similar point about the evolutionary longevity of

species. Because the number of individuals in the metacommunity is so large, extinctions due to drift are infrequent. With no mechanism for differential species response to environmental change, Ricklefs argues, diversity in the neutral model would build up to unrealistic levels, and species would persist longer than is indicated by the fossil record.

What seems indisputable is that Hubbell's book will continue to spark both philosophical debate and original research. The unified neutral theory is sufficiently ambitious, Brown says, that it would be unreasonable to expect it to succeed at every level. "Often we learn as much when models fail as when they succeed," he says. "The challenge is to take the good stuff from this model and look at how it might be reinterpreted in a less obligatorily neutral way. Every ecology program in the country should have a graduate seminar that really grapples with this book."

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