news feature

Neutrality versus the niche

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Graham Bell (left) and Stephen Hubbell's neutral models can describe rainforests and reefs (top).

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Testing time: tundra plants (above and right) are helping to reveal the limits of neutral models.

According to some ecologists, you don't need to invoke adaptation to explain biodiversity. They may sound like nihilists, but their ideas are proving remarkably resilient. John Whitfield reports.

Vive la différence? Forget it. *La différence est morte*. That is the message from the proponents of neutrality, a view of ecology that is anathema to many in the field. Rather than focusing on how differences between species allow them to coexist, neutrality assumes that trees in the rainforest, or corals on a tropical reef, are basically all the same.

Ecologists have strived to explain species' patterns of distribution, abundance and coexistence for more than half a century. The traditional explanation is that each species is adapted to exploit a unique niche — shady or sunny, wet or dry, and so on. But neutral theories assume that all organisms are equal, and consider only factors such as random dispersal, the birth and death of individuals and the total number of organisms in the community.

The troubling thing for most ecologists is that neutral simulations can produce ecosystems that look just like the real thing. "Neutrality starts with assumptions that are clearly wrong, but produces patterns that match what we see in nature," says Jonathan Levine of the UK Natural Environment Research Council's Centre for Population Biology at Silwood Park, west of London.

Sceptics say that recreating patterns isn't the same as understanding the mechanisms that cause them, and complain that the assumptions of neutrality are practically impossible to test. The debate isn't purely academic — our ideas of how biodiversity arises will influence how we attempt to conserve it. "We'd better figure these things out," says Stephen Hubbell of the University of Georgia, Athens, one of the gurus of neutrality.

Put it in neutral

Hubbell, a specialist in the ecology of tropical forest trees, last year published *The Unified Neutral Theory of Biodiversity and Biogeography*[1], which has become the bible of neutrality. Hubbell's neutral model considers only the birth and death of individuals, random dispersal, the overall population of individuals in the ecosystem, the total number of species and the origin of new species. The models favoured by neutral ecology's other leading proponent, Graham Bell of McGill University in Montreal, Canada, are even more austere, leaving out the birth of new species[2,3].

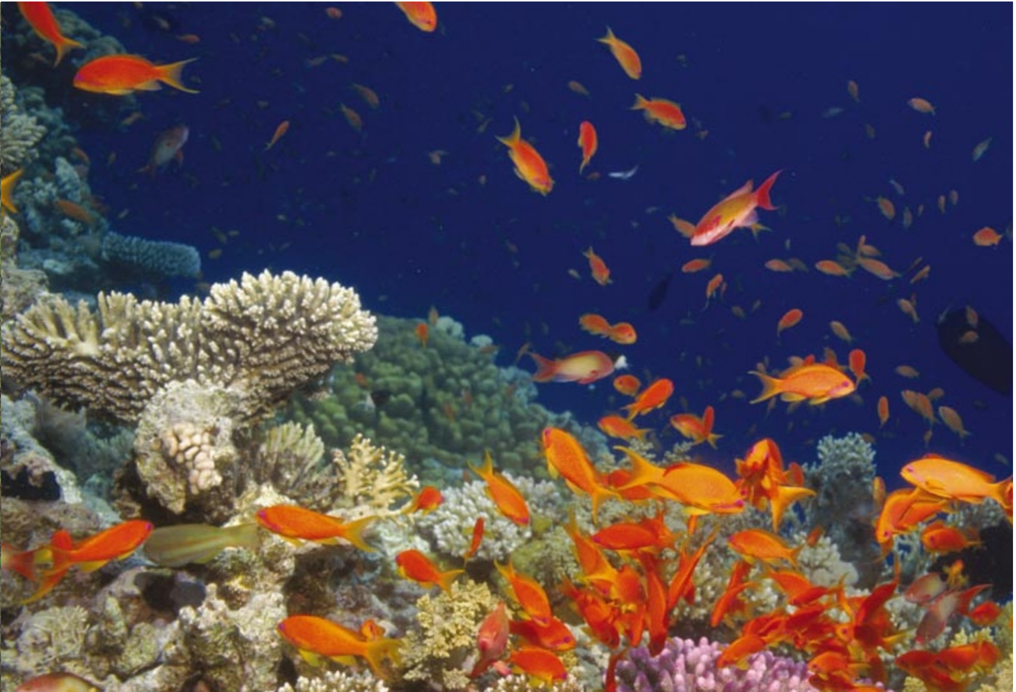
Neutral models consider the ecological properties of every individual in the population to be identical. Individuals compete for the same, fully exploited pot of resources, but the identity of the winner of any single contest — the tree that fills a gap in the canopy, for example — is left to chance.

Get the balance between birth, death and dispersal right, and you get a near-perfect recreation of natural communities. "It predicts the individual species abundances of more the 800 tree species in a Malaysian rainforest with just three numbers," says Hubbell of his model[1]. Neutral theories also make predictions about evolutionary history, for example that rare species will have arisen recently — although Hubbell acknowledges that these will be difficult to test. "By the time a species is detectable it's already really old and really abundant," he argues.

Hubbell admits to being taken aback by neutrality's success in mimicking the natural world. "I'm very puzzled by how well it's worked, and I was really unprepared for how theoretically rich in questions it was," he says.

If correct, neutral theory means that the species in a habitat have been thrown together — and will come and go — at random. This insight, Hubbell believes, might be useful in designing nature reserves. If species are closely adapted to fit an ecological niche, communities will be relatively stable, and hard to invade. Reserves can therefore be small. But if species are more equal, and come and go at random, communities will be more fluid, and bigger reserves will be needed to protect rare species from the buffetings of chance. "My view is that most communities are open and easily invaded," he says.

But if species are essentially all the same, does it matter if we lose one of them? That is a dangerous line of argument, says Bell. If just



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1% of species perform a vital and specific ecological function, he explains, this will make little difference to the statistical predictions of neutral ecological models. But take those species away, and a previously healthy ecosystem will be in serious trouble.

Even the staunchest supporters of neutral ecology accept that the theory has limitations. It only applies within one level of the food web — it might explain the diversity of trees, for example, or the diversity of herbivorous insects, but not how the number of tree species might affect the number of herbivorous insect species. Hubbell says that the theory is more likely to hold for plants or microbes — where different species overlap more in the way that they exploit resources — than animals. Moreover, it breaks down on large spatial scales. To give an extreme example, alpine plants are clearly adapted to different conditions from those in which lianas and mahogany trees thrive, so would struggle to survive in the rainforest.

The big question is whether biodiversity really results from neutral ecological processes — indicating that ecologists have overestimated the importance of the niche — or whether the models' accuracy is a coincidence. Some ecologists, such as Levine, believe that neutral models are most useful as an ecological 'null hypothesis' for revealing the differences between their predictions and real ecosystems. Others point out that niche-based models can also produce a good description of the natural world. This year, for instance, a team led by Jérôme Chave, now at the Laboratory of Terrestrial Ecology in Toulouse, part of the CNRS, France's national research agency, showed that both niche and neutral models can reproduce natural patterns of species abundance[4].

A simple life

Hubbell counters that theories that stress the importance of the niche generally have to be much more complex than neutral models to achieve superior results. "To say that 100 or more parameters gives a better fit is not very satisfying as a critique," he says.

The niche may still be a valid concept, Hubbell suspects, albeit not as important as ecologists have long supposed. But Bell goes further, arguing that there is little experimental evidence to support the idea of niches. If plants are closely matched to their local environments, they should perform poorly if transplanted. But that isn't what Bell found when his team tried moving plants within Canadian forests[5]. "The results puzzled us — they clearly didn't point to any powerful degree of local adaptation, and sometimes the rarest species was the most successful in a new location," he says.

Bell is now looking at tundra plant communities to try and work out the scales on which the predictions of neutral theory hold. The key test, he says, is how likely species are to be present together. If particular species tend to occur together, it would suggest that some environmental factor determines community composition, says Bell. But more haphazard patterns of cohabitation would support the neutral theory.

Scale bars

Other studies have produced mixed results. One, published earlier this year by a team including Chave and Hubbell, found that, in Panamanian and Amazonian forests, random dispersal could explain patterns of tree diversity between different areas at scales of between 0.2 and 50 square kilometres. However, the neutral theory broke down at smaller and larger scales[6]. A study of sawflies feeding on birch trees in Finland, which showed that species are specialized to feeding on leaves of a particular age[7], has also been cited[8] as evidence against the strongest interpretations of neutrality.

Some sceptics, meanwhile, still find it impossible to accept that neutral theories can yield real insight into ecological processes. They also point to the difficulty of validating Hubbell's model, given that it includes parameters such as the rate at which new species arise, which cannot readily be measured. Neutral models are intriguing, concludes Peter Petraitis of the University of Pennsylvania in Philadephia, who studies rocky-shore communities. "But they don't offer much insight into what's operating underneath. It doesn't push us forward."

Bell senses the tide turning his way, however. "At first people thought neutral theory was nonsense. Now they think there's something in it," he says. Bell compares the debate to one that began more than 20 years ago among population geneticists about whether changes in gene frequencies are driven primarily by natural selection or by random 'genetic drift'. After initial resistance, most researchers now accept that genetic drift can be a significant factor. Bell suspects that it may take two decades for ecologists to reach a similar consensus.

While the debate goes on, even those who are unconvinced about neutral theory's validity value its stimulating effect on community ecology. "It's forcing us to address fundamental questions and work out what we really think," concludes Sean Nee, an evolutionary biologist and ecological geneticist at the University of Edinburgh, UK. ■

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