Research Focus

Emergent neutrality

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Community ecology is in a current state of creative ferment, stimulated by the development of neutral models of community organization. Here, I reflect on recent papers by Scheffer and van Nes, and by Gravel *et al.*, which illuminate how neutrality can emerge from ecological and evolutionary processes, thus suggesting ways to unify neutral and niche perspectives.

Unifying niche and neutral theories

All naturalists know that species differ, and in many exquisite ways. But do such differences matter for determining broad patterns of distribution and abundance in communities? The ongoing debate about neutrality in community ecology [1,2] has focused the attention of ecologists on this fundamental issue. The basic assumption of neutrality is that to understand issues such as the relative abundances of species, species–area relationships, and spatial and temporal turnover in species community composition, one can assume that all species are the same. In neutral theories, relative abundances change by chance, rather than because one species is superior to another.

The provocative core assumption of neutral theory (see Glossary) is that individuals are equivalent with respect to key processes: the stochastic demographic rates of birth, death and dispersal, and the introduction of evolutionary novelty via mutation and speciation. There is an undoubted elegance to minimalist models [2], and neutral models have enjoyed success at explaining patterns such as species abundance and species–area relationships [2,3]. Yet many ecologists [4,5] are uncomfortable with the assumption of ecological equivalence, and close analyses of some systems do reveal non-neutral patterns [5]. Ecologists are now engaged in unifying niche and neutral theories [6]. As I discuss here, recent papers by Scheffer and van Nes [7] and by Gravel *et al.* [8] provide significant insights as to key elements of such a unified theory.

Sources of neutrality in community ecology

There are three reasons why species dynamics might match a neutral perspective.

Speciation creates ecologically equivalent species

First, from the moment that they arise by speciation, species could be equivalent with respect to probabilities of birth, death and dispersal. This justifies a 'hard' form of neutrality [9] in which species identity really does not matter in determining patterns such as relative abundances. Allopatric speciation, for instance, can occur

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without ecological differences arising between sister species. When species created without ecological differentiation come into contact, their relative numbers should drift by chance [10,11]. Many extant communities are relatively recent products of large-scale Earth processes, such as glaciation cycles. These could generate sets of competitively equivalent species via speciation, and then bring these together in novel assemblages [12] where relative abundances would be governed by ecological drift. One would expect species to be eventually lost by extinction, but the timescale over which such extinctions occur could be quite long.

The world is very noisy

Second, even if species show niche differentiation and tradeoffs in functional traits, the dynamical consequences of such differences might be obscured because of stochastic processes such as climatic variability. In its 'weak' form, neutral theory at the very least provides the appropriate null model for evaluating patterns in comparative data sets [9]. There is increasing appreciation of the importance of dispersal limitation in metacommunities over large spatial scales [13]; such limitation tends to increase the role of stochastic and historical processes such as the placement of dispersal barriers in determining local community composition, and so null models might suffice reasonably well in describing community patterns, even if closer scrutiny of species shows that they do differ in niche properties. This is a 'weak' version of neutrality.

Ecological and evolutionary processes generate nearly neutral species

Finally, community and evolutionary processes themselves might act on species that are not initially ecologically equivalent but which, for dynamical reasons, converge on states that are, to a reasonable approximation, neutral, at least when examined over certain spatial and temporal scales. In other words, neutrality could be an emergent property of ecological systems. Ecologists have recently shown how neutrality can emerge as a byproduct of ecological and evolutionary processes (e.g. [3,14,15]). Recent papers [7,8] illustrate different but complementary ways in which emergent neutrality can arise.

Emergent neutrality in a closed Lotka–Volterra community

Scheffer and van Nes [7] begin with the classic Lotka–Volterra competition model for a spatially closed community and assume that interspecific competition reflects overlap in niches along a niche axis. If a large number of species are placed at high abundances randomly along

Glossary

Allopatric speciation: divergence of a single ancestral lineage (identified as a single species) into two or more descendent lineages (also recognized as species), mediated by the disjunct spatial separation of the evolving lineages.
Dispersal kernel: a function that describes the spatial pattern of dispersal. The word 'kernel' arises from the use of these functions in integral equations, which are used frequently in spatial ecology.
Dispersal limitation: limitation of distribution or abundance because of either constraints on dispersal or inadequate production of dispersing individuals. Empirical assessments of dispersal limitation require introductions (e.g. seed additions); distributions are dispersal limited if individuals can successfully be introduced into empty sites; abundances are dispersal limited if introductions boost the population size of an established population.
Ecological drift: by analogy with genetic drift, the relative abundance of species that are ecologically equivalent should change only owing to chance events.
Intraspecific density dependence: influence of changes in density on per capita vital rates, or dispersal rates.
Metacommunity: a set of local communities linked by dispersal of multiple potentially interacting species.
Neutrality: the hypothesis that differences in species traits do not either affect the chances of that species being present or absent in a community, or influence changes in their relative abundances.
Neutral theory: mathematical theories that formalize the assumption of neutrality, enabling quantitative predictions about species relative abundances, species–area relationships, and other aspects of community organization (see [2]).
Species sorting: a theory of community structure that assumes most species in a regional species pool can reach local communities, but that only a subset of species persist, in particular, those species whose traits match local abiotic conditions and persist in the face of interspecific interactions with other community members.

the niche axis with sufficient overlap (so that there is strong competition among most species), an intriguing pattern emerges, in which lumps of multiple species are clustered closely together, with pronounced gaps between them maintained by competition. Although in the long run, only one species in each lump persists, transient coexistence is observed for thousands of generations. This is because if species are similar, the expected time course to competitive exclusion can be long, even if one species is competitively dominant [10]. Because many extant communities might not be close to their deterministic equilibrium [12], we should expect to observe guilds of effectively neutral species for historical reasons.

The authors [7] consider several extensions of their model, such as intraspecific density dependence operating on common species. This can stabilize the 'lumps' so that they persist indefinitely (but also makes the emergent neutrality less evident). The authors mimic evolution by enabling each species to shift in its modal niche position by a small amount in the direction of increasing mean fitness. Such microevolutionary jostling, superimposed on transient competitive dynamics, can lead to sharply separated clusters of species along a niche axis; the pattern in this case is essentially permanent. When considering pairs of competitors, or species-poor assemblages, competitive divergence is expected, but when considering entire, species-rich communities, convergence among subsets of the community can generate sets of nearly competitively equivalent species. Hence, neutrality can emerge from dynamical processes within a community.

Assessing the theoretical results

To evaluate theoretical results such as these, it is helpful to consider a range of alternative model formulations. Bonsall *et al.* [14] previously examined a model for competition with quite different assumptions, which nonetheless

arrives at comparable conclusions. The authors used a discrete generation framework to examine parasitoids competing for a shared host species. Because there can be multiple infections of single host individuals, this system blends asymmetric interference competition (only one parasitoid emerges per parasitized host) with exploitative competition (ability to attack the host in the first place). Assuming a tradeoff between interference and exploitative abilities (or other life-history traits, such as longevity), and taking an adaptive dynamics approach to the introduction of variation in parasitoid traits, Bonsall *et al.* [14] show that distinct clusters of species arise, separated by substantial gaps along the tradeoff axis. Again, community processes lead to sets of species that are roughly competitively equivalent, and so effectively neutral in their dynamics within each set.

The convergence of results between the quite different models considered by Scheffer and van Nes [7] and by Bonsall *et al.* [14] is striking, and suggests that emergent neutrality arises across a wide range of assumptions about interspecific interactions.

Emergent neutrality in an open community with space competition

Gravel *et al.* [8] utilize a quite different competition model and also consider open rather than closed communities, yet end up with similar conclusions. Beginning with Hubbell's [2] model of space competition for space (when an adult dies, the probability a given species recruits into that spot depends upon its relative abundance within either a metacommunity or a neighbourhood defined by a dispersal kernel), they incorporate niche differentiation by assuming the relative survival of each species to depend upon a continuous niche axis. Different species have different optimal conditions for survival. Without immigration from an external source, competition crafts a community structured by niche differentiation. Given immigration, neutrality (as measured by variance among replicate runs) increases, and the effect is more pronounced with increasing immigration rates and high species richness. Several processes contribute to these results. With higher species richness, average abundance per species declines, hence stochasticity and dispersal limitation loom larger. Moreover, it is more likely that species sorting [13] will lead to sets of relatively similar species being present, where some weakly excluded species are maintained by immigration [10].

Conclusion

In the work reported by Scheffer and van Nes [7], Gravel *et al.* [8] and others (e.g. [3,6,14,15]), community structure reflects both niche organization and neutrality. These studies suggest that the emergence of nearly neutral suites of species is more likely in species-rich communities than in those that are species poor. In both cases, the indefinite coexistence of species requires the operation of processes outside those producing neutrality (e.g. direct density dependence in [7], and immigration from a source in [8]). In general, to understand coexistence, one must consider both forces that are stabilizing (so that each species can increase when rare) and equalizing (so that species are relatively similar in response to non-regulatory

environmental factors) [10,16]. Near-neutrality might arise when stabilizing forces are relatively weak, and equalizing forces are strong, and is likely to be more pertinent to some taxa and environmental settings, than to others.

Despite this caveat, these recent papers point to an emerging reconciliation of niche and neutral perspectives in community ecology. Ecologists should now systematically explore these issues across a wide array of community models and, perhaps more importantly, devise critical experimental tests of these ideas. For instance, in microbial communities, ecological and evolutionary dynamics occur on a manageable timescale; the quasi-species that are observed in viral evolution are not dissimilar from the clusters of species that emerge in the models of Scheffer and Nes [7] and Bonsall *et al.* [14], and so these systems might provide empirical tests of these theories. In field systems, if patterns of relative abundance are due to drift, then perturbations that change the initial patterns of relative abundances (without causing extinctions) should tend to persist, rather than rapidly returning to the initial state of the community.

Niche and neutral perspectives have quite different implications for how one should manage natural resources and craft conservation strategies. A unified theory of communities that judiciously blends both perspectives is needed if ecologists are to understand the processes governing biodiversity at a fundamental level and then apply this understanding to the urgent problem of maintaining diversity in our rapidly changing world.

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Letters

Muscling out malaria

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Recent updates in *Trends in Parasitology* [1] and *Trends in Ecology and Evolution* [2] highlighted the back-to-back articles in *Science* [3,4] that demonstrated the potential biocontrol of malaria by targeting mosquitoes with entomopathogenic fungi (*Metarhizium* and *Beauveria* spp.). The wide impact of the original articles and the need to find alternatives to pesticidal control are likely to encourage the incorporation of these fungi into biocontrol programs, although several concerns have been raised [1,2,5]. Here, we detail some of these and advocate an inclusive

approach to malarial biocontrol that proceeds with a full appreciation of the complicated biology of the pathogenic fungi concerned.

There is a long history of using *Metarhizium* and *Beauveria* in insect biocontrol [6] with 'Green Muscle', a broad consortium set up to control locusts using *Metarhizium*, as an excellent example (for more information, see http://www.lubilosa.org). Green Muscle developed from the initial conception that spores could be suspended in oil to facilitate germination in arid regions [7], which made infecting mosquitoes feasible [4]. However, failures in biocontrol have been more common than successes and are often due to the 'ephemeral and amateurish activities'

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