COMMENTARY

Spatial scale resolves the niche versus neutral theory debate

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Abstract

The 50-ha long-term forest plot on Barro Colorado Island in Panama was 'ground zero' for the development of ecology's 'neutral theory' and comparisons with its 'niche theory' counterpart. In this issue, Garzon-Lopez and colleagues used tree distributions at this site to recast the unresolved (and unresolvable) debate to show that observational scale drives the perception of which processes predominate.

For more than a century, community ecologists have been embroiled in a series of disagreements that revolve around the same general question: "Are the relative abundances and distributions of species more strongly controlled by deterministic factors, such as environmental conditions and interspecific interactions? Or, are stochastic processes and/or dispersal limitation of overriding importance?" This question was evident during the earliest days of ecology as a field of inquiry (e.g. Gleason 1926 vs Clements 1936), heated up as ecology transitioned towards a more mature quantitative science in the 1970s (e.g. Diamond 1975 vs Connor & Simberloff 1979) and flared again in its most recent iteration as the 'niche vs neutral' debate as the field has become increasingly more quantitatively sophisticated (e.g. Hubbell 2001 vs Chase & Leibold 2003).

So, what's the answer? Just how 'predictable' are communities? Are deterministic processes, driven by species' niches and interspecific interactions, more important in driving the distributions of species, or are stochastic processes and dispersal limitation more important? Although I and many hundreds of other ecologists have spent an inordinate amount of time asking variations on these very questions, no clear consensus has emerged. Are we faced with another example of the much bemoaned and unsatisfactory answer that the answers to all of community ecology's questions are that "it depends?" I will argue here that although the answer might be "it depends", the study in this issue published by Garzon-Lopez et al. (2014) elegantly showed that this unsatisfactory answer is because the question itself – "are communities niche-assembled or neutral-assembled?" – is in fact too ambiguous to provide useful insights because of the overriding influence of scale.

To illustrate the ambiguity of the question, we can ask a similar question of a fair two-sided coin. Are stochastic processes or deterministic processes more important in driving whether the coin will come up heads or tails? On any given flip, the coin will turn up heads or tails as a result of a stochastic process. But after 10, 20, 30 or more flips, the percentage of times the coin comes up heads or tails will deterministically approach 50% because the coin is fair and has two sides. So, the answer is that both stochastic and deterministic processes act in concert, but the window of observation (i.e. the number of flips) influences our perception of which process is more important.

Back to ecology. We can visualize how observational scale alters our perception of the relative importance of niche vs neutral processes in a simple scenario where two species distribute themselves among two different habitat types (Fig. 1). At larger spatial scales, habitat associations are strong and determine compositional shifts when environmental conditions change (left side of Fig. 1). However, at the same time, there are a multitude of probabilistic events (birth and death rates, dispersal, etc.) that allow each species to have a large number of sporadically distributed individuals in the habitat that it finds less favourable. As sampling scale declines to encompass fewer individuals and less habitat heterogeneity, the relative contribution of those stochastic events to the overall structure of the community increases, and we perceive this system, which is highly niche-structured at larger scales, as largely neutrally structured at smaller scales. Extending this to a reasonably diverse and environmentally heterogeneous community with many species undergoing many probabilistic events, it is inevitable that our ability to predict the composition of species in any given 1 m^2, or
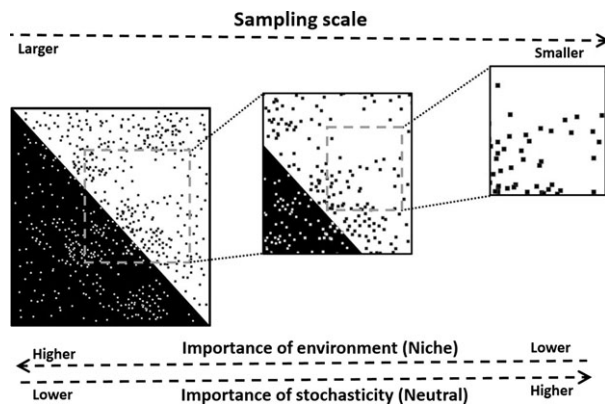
Fig. 1. Hypothetical depiction showing how sampling scale can influence the perception of the relative importance of environmental (niche) factors vs stochastic (neutral) factors. There are two species, a black species and a white species, which partition habitats in the environment. At the largest scale (left panel), the lower left half of the region has environmental conditions that primarily favour the black species and so the primarily black part of the site indicates a very high coverage of the black species; the upper right half of the region primarily favours the white species and the primarily white part of the site indicates a very high coverage of the white species. While many individuals of each species can be found in their less favoured habitats (noted by the black and white squares on the sides opposite to their favoured habitats where the species are most dense), the habitat association at the largest scale is very strong. At the intermediate scale (middle panel), the community is still influenced by habitat associations. However, because there is less of one habitat type (the black species' favoured habitat) than the other habitat type (the white species' favoured habitat), and there are fewer individuals sampled overall, the influence of stochastic processes will appear to play a stronger role. Finally, at the smallest spatial scale (right panel), one of the habitat types (the black species' favoured habitat) is completely eliminated, and the fewer remaining individuals appear to be almost entirely distributed by stochastic processes.

even 100 m^2 or 1000 m^2, would be low, and we might conclude that neutral processes were of primary importance even if niche assembly were the predominant mechanism at larger scales. Indeed, when analysing the distributions of tree species in a subtropical forest in China, Legendre et al. (2009) showed exactly this sort of pattern; as the size of the sampling plot decreased, the relative importance of environmental factors declined while the relative importance of stochastic factors increased.

And this brings us to the 50-ha long-term plot at Barro Colorado Island (BCI), the veritable birthplace of the modern conceptualization and exploration of neutral theory. Hubbell's (1979) original version of the neutral theory was developed and parameterized with data from a ~13-ha plot in Costa Rica, where the stems of all trees were mapped and he could analyse their

relative abundances and spatial distributions. The following year, Hubbell and colleagues established a larger-scale (50 ha) plot on BCI, which they have repeatedly censused through time to explore these ideas in more depth, finding large agreement between the data and the theory (see e.g. Condit et al. 2012 for a recent analysis).

The success of the forest plot at BCI has spawned a 'cottage industry' of similar plots in a network of sites across the world (53 and counting), with mixed evidence for both niche and neutral processes explaining the observed patterns (e.g. De Cáceres et al. 2012; Baldeck et al. 2013; Brown et al. 2013). The current consensus from these and related studies is that both niche and neutral processes act in concert to determine the relative abundances and distributions of species, even in diverse tropical tree communities (e.g. Guèze et al. 2013; Correa-Metrio et al. 2014). Nevertheless, a primary goal is still to determine whether niche or neutral processes play a stronger role in a given community, and whether there are any local or biogeographic correlates that might explain any differences in their relative importance. To address these questions, community ecologists typically assume that analyses of pattern and process at a single spatial scale of observation (i.e. a given plot size) provide unambiguous insight into the relative importance of niche or neutral processes in driving community-level patterns in a given system. It does not.

The study by Garzon-Lopez et al. (2014) beautifully illustrates the problem of scale and our perception of the relative importance of different processes. Using high-resolution aerial photographs of the island from which they could identify species, they quantified the degree of aggregation ('clumpiness') of five widespread species of canopy tree as well as their habitat characteristic associations; stronger habitat associations would indicate increasing importance of niches in determining species' distributions. They defined the smallest spatial grain as 50 ha (the same size as the long-term mapped plot), and at this scale, found high variability in aggregations of the species across the island and only moderate habitat associations, as might be expected if the signatures of the neutral theory (ecological drift and dispersal limitation) predominated. However, as their spatial grain of observation increased, eventually towards the size of the entire island, species distributions became increasingly more aligned with variation in habitat characteristics, indicating an increasing role for niche-based processes.

While the analysis of Garzon-Lopez et al. (2014) is elegant in its ability to differentiate aggregations and habitat associations at different spatial scales within the

iconic BCI forest trees, the scale dependence in habitat associations, and the associated perceived importance of niche vs neutral processes, is in fact inevitable. At the extreme, we would not expect to find spruce trees or penguins in the tropical rain forest, just as we would not expect palm trees and hummingbirds in the Arctic (even if dispersal limitations were eliminated). Likewise, species composition clearly segregates among tropical forests with strongly different precipitation regimes and edaphic conditions. No one would doubt that niche factors, related to major morphological and physiological differences among species adapted to these divergent community types, drive these compositional shifts. On the other side of the spectrum, the vagaries of stochasticity will predictably emerge at the smallest spatial scales, where the death of a canopy individual will leave a space open for a replacement that will have as much or more to do with chance than any factor related to its specific traits.

In conclusion, we simply cannot unambiguously disentangle the relative importance of niche and neutral processes without an explicit consideration of the spatial scale on which patterns are examined. Garzon-Lopez et al. (2014) illustrate this nicely, and their use of the tree community on BCI that has played an inordinately large role in the niche vs neutral debate drives the point home forcefully. Although several analyses from decades of evidence suggest that the 50-ha plot on BCI is largely structured by neutral processes (e.g. Condit et al. 2012), this probably has as much to do with the relatively small scale of the plot and its relative homogeneity, both of which will magnify the perceived importance of neutral processes despite the simultaneous importance of niche processes at larger scales. Other fundamental problems in community ecology are similarly inexorably influenced by scale despite a general agnostic view towards scale in most studies. For example, the balance of stabilizing and equalizing processes in determining species co-existence is in fact a scaling problem; species that cannot co-exist at small scales, perhaps because there are no stabilizing factors, can do so at larger scales as habitat heterogeneity (a stabilizing factor) is encompassed (e.g. Wilson 2011). Likewise, the responses of species richness to ecological drivers, such as productivity or disturbance, will very much depend on the scale at which the data are examined (e.g. Chase & Knight 2013). As an unfortunate result of the general agnosticism towards these scale issues, the decades of investigation, and the hundreds of research papers published that have attempted to quantify the relative importance of these processes without explicitly considering spatial scale, will ultimately prove rather uninformative.

Instead, progress will only be made once we fully embrace the fact that there is, in fact, no such thing as a spatially discrete 'community' (or region, metacommunity, etc.) that can be formally defined and compared (e.g. Ricklefs 2008), and that a more continuous view of how these patterns and processes vary with scale is needed.

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