Neutral Community Ecology[1]

Interest in neutral community models has grown rapidly over the last five years. These models are provocative because they assume that all species are equivalent in their competitive ability or fitness, and yet they appear to be capable of predicting many broadly studied community patterns like rank abundance distributions and species–area relationships. Most ecologists regard the assumption of all species being equivalent as highly unrealistic, and consequently there is a risk that the models will be dismissed and will not be fully evaluated. This would be premature because the success of the models challenges us to explain what processes are responsible for patterns of distribution and abundance. It behooves us to realize that neutral models raise unanswered questions about the forces structuring communities. The models highlight questions about the role of stochasticity and transient dynamics in creating community patterns. If dynamics are sufficiently stochastic, species differences may be irrelevant to community structure and diversity patterns. While stochasticity has long been incorporated formally into population models, the neutral models discussed in this feature are among the vanguard of formal quantitative efforts for communities. The logic of community stochasticity dates back to F. E. Clements, H. Gleason, and other early ideas about succession; it deserves the rigorous framework that we have seen during the past decade. Transient dynamics in neutral community models are highlighted by the similarity between neutral community and neutral genetic models. Neutral genetic models consider random drift processes in allele frequency, whereas neutral community models consider "ecological drift" in community composition and abundance (Hubbell, S. P. 2001. The unified theory of biodiversity of biogeography. Princeton University Press, Princeton, New Jersey, USA). Transient dynamics are an emerging area of ecology and are challenging to investigate because they are not amenable to investigation using traditional equilibrium and stability analyses (see Hastings, A. 2004. Transients: the key to long-term ecological understanding? *Trends in Ecology and Evolution* 19:39–45).

Analogous to the neutralist view of evolution, we find three lines of scientific interest in neutral community theory. First, it is simple and elegant, and it provides simple relationships among existing concepts and measures, such as Fisher's index of diversity, community size, and speciation rate; as such it erects a baseline, reference point, or null model against which to pose questions about non-neutral community features. Second it forces deeper thinking about established theories of species diversity, such as those based on niche partitioning and competitive ability. Third, Hubbell's (2001) model makes linkages between ecology and evolution, and therefore it offers a potentially complete explanation for patterns of species diversity and extinction.

Much of the early work on neutral community models focused on attempting to prove or disprove that dynamics observed in natural systems are neutral. However there has also been considerable debate over the appropriate role of neutral community models. As such, the current debate has some similarities to the debates two decades ago about null models. Some of the differences between neutral theory and null models are explored by Holyoak and Loreau in this Special Feature. Bell, Hubbell, and Leibold and McPeek regard neutral theory as providing realistic mechanisms for diversity patterns (what Bell terms the "strong" version of neutral theory [see Bell, G. 2001. Neutral macroecology. *Science* 293:2413–2418]), whereas others (e.g., Leibold and McPeek, McGill et al.) regard it as a null hypothesis, reflecting with different emphasis upon the nascent efforts in this dialogue two decades ago with null models.

The contributions by Hubbell and by Leibold and McPeek argue that evolution can lead to functional equivalence. Hubbell addresses this with a general evolutionary model and tropical tree data from Barro Colorado Island, whereas Leibold and McPeek consider mechanisms of speciation

and their relevance to pond systems. By contrast, Ricklefs provides arguments against the precise mechanism of speciation being realistic in Hubbell's neutral model by means of evidence from turnover of species in bird communities. Thus, Ricklefs sees neutral theory primarily as a null model. McGill et al. also treat neutral theory as a null model and argue that more rigorous tests tend to select alternative models over neutral models. Interestingly, the conclusions of McGill et al. are almost directly opposed to those of Bell et al. who argue mainly from biological intuition.

One possibility is that the current debate will become similar to the neutralist and null model debates, resulting in integration of the two perspectives with more rigorous tests of non-neutrality. This is implied in Holyoak and Loreau's, Leibold and McPeek's, and Bell et al.'s contributions. It is clear that exploration of neutral theory has only just begun. We would hope that this Special Feature will prevent excessive enthusiasm inspired by the elegance of neutral theory and at the same time prevent excessive skepticism in other quarters where niche differences are the basis of research programs. Neutral features of dynamics can certainly arise even though all species have niche differences. Progress in the debate requires being both critical and open to new perspectives.

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SPECIAL FEATURE