N e   e a   de : _a'_ e d ffe e ce?

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The neutral model posits that random variation in extinction and speciation events, coupled with limited dispersal, can account for many community properties, including the relative abundance distribution. There are important analogies between this model in ecology and a three-tiered hierarchy of models in evolution (Hardy Weinburg, drift, drift and selection). Because it invokes random processes and is used in statistical tests of empirical data, the neutral model can be interpreted as a specialized form of a null model. However, the application and interpretation of neutral models differs from that of standard null models in three important ways: 1) whereas most null models incorporate species-level constraints that are often associated with niche differences, the neutral model assumes that all species are functionally equivalent. 2) Null models are usually fit with constraints that are measured directly from the data set itself. In contrast, the neutral model requires parameters for speciation, extinction, and migration rates that are almost never measured directly, so their

codon regions which allows for an immediate empirical
calibration of rates of drift. This inability .hic5sacalibrate

effect null models. The general strategy in null model construction is to incorporate some minimal amount of realistic biological structure, but allow other elements of the data to vary randomly. Although null models usually are not discussed in this context, often these constraints effectively preserve many of the important "niche properties" of a species that are discarded in neutral models.

There are two reasons for incorporating such constraints (niche properties) into null model analysis. The first reason is that, all other things being equal, a realistic null model should be preferred to one that is biologically naive. Indeed, the question at the heart of neutral model analysis is how much species differ in their niche characteristics, and whether those differences are necessary to account for community patterns (Gaston and Chown 2005). Of course, a useful ecological model

This duality between null versus process-based models need not be a problem for ecology. However, authors do need to be explicit about whether they are using neutral theory as a process-based, predictive model or as a null hypothesis. If the neutral model is being treated as a process-based model, then it should be compared to the predictions of a (simpler) null model, such as the log-normal. As Harte (2003) has emphasized, stronger tests of the neutral model can be made by directly testing its assumptions (e.g. species equivalence), rather than its predictions (relative abundance distributions), which can usually be fit by many statistical models.

If the neutral model is being used as a null hypothesis, as Bell (2000) suggested, then the alternative hypothesis needs to be made explicit, as Caswell (1976) did. Those advocating the neutral model as process-based predictive model rather than as a null model, cannot hide behind the apparent overlap with null models and use weaker, less explicit, tests. If the neutral model is to be treated as a process-based model, it must be subjected to the same rigor of test as any other process-based theory (McGill 2003a, McGill et al. 2006). Specifically, the predictions of the neutral model should be compared to the predictions of an appropriate null model. Moreover, the underlying mechanistic assumptions of the neutral model (such as species equivalence and dynamic community turnover) should be tested directly (Harte 2003).

Assumptions and alternatives

The three differences between neutral and null models that we have discussed have a common theme. Predictive models are ''tested'' by deliberately trying to exclude their underlying mechanisms from a null model.(n)27.3'4.63ydel41(om)-371.1(a)-372.6(s)-593.6(ofHiom)vIeehou723.2.9(pr)6(o

distribution and make predictions only about the number of species per site (although other predicted patterns, including turnover and beta diversity, could also be derived from both MDE and neutral models).

Although the Rangel and Diniz-Filho (2005a, b) models provides an explicit mechanistic scenario for the mid-domain effect, estimating speciation, migration, and extinction rates for large species assemblages at the continental scale seems daunting. Graves and Rahbek (2005) discuss the problems and limitations of using neutral theory to explain macroecological patterns. In contrast, mid-domain effect models can be readily fit to species occurrence data that are mapped in a gridded biogeographic domain (Colwell et al. 2004).

Community ecology: species co-occurrence

Recently, Ulrich (2004) and Bell (2005) have asked whether the neutral model might account for observed patterns of species co-occurrence, which have traditionally been tested with classic null models (Connor and Simberloff 1979). Ulrich (2004) and Bell (2005) both used the neutral model to generate binary presence-absence matrices, and then used standard metrics of species co-occurrence such as the V-ratio (Schluter 1984) and the C-score (Stone and Roberts 1990), to quantify segregation of species. Both authors found that a well-tempered neutral model can cause patterns of species segregation. In other words, the neutral model does not predict neutral or random co-occurrence patterns! This result was actually foreshadowed by previous null models (Roxburgh and Chesson 1998, Roxburgh and Matsuki 1999) that preserved the patchy spatial distributions that are generated by limited dispersal in the neutral model. In contrast, most null model randomization tests do not incorporate spatial constraints in randomization tests.

Ulrich's (2004) analysis is especially interesting, because he first generated patterns with the neutral model, then tested them with standard null model protocols (Gotelli and Entsminger 2002). .226[9r374.4(s2r374.9(eal)V(200C20.snl3 TD[n41(ull)-03 ,0and)yg374md41and)]JT*[(p

statistical falsification of simple null hypotheses will continue to play an important role in the assessment of neutral theory.

Summary

Table 1 summarizes the key differences between null and neutral models that we have described. The subtle distinctions between traditional statistical null models