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## *Null versus neutral models: what's the difference?*

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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 values must be guessed at or fitted. 3) Most important, null models are viewed as simple statistical descriptors: unspecified "random" forces generate variation in a simple model that excludes particular biological mechanisms (usually species interactions). Although the neutral model was originally framed as a null model, recent proponents of the neutral model have begun to treat it as a literal process-based description of community assembly.

These differences lie at the heart of much of the recent controversy over the neutral model. If the neutral model is truly a process-based model, then its assumptions should be directly tested, and its predictions should be compared to those of an appropriate null model. Such tests are rarely informative, and most empirical data sets can be fit more parsimoniously to a simple log-normal distribution. Because unknown parameters in the neutral model must usually be guessed at or fit in ad-hoc ways, classical frequentist tests are compromised, and may be biased towards finding a good fit with the model. There has been little analysis of the potential for type I and type II errors in statistical tests of the neutral model.

The neutral model has recently been proposed as a specific form of more general null models in biogeography (the mid-domain effect) and community ecology (species co-occurrence). In both cases, the neutral model is qualitatively, but not quantitatively, similar to the predictions of classic null models. However, because the important parameters in the neutral model can rarely be measured directly, it may be of limited value as a null hypothesis for empirical tests.

Future progress may come from moving beyond dichotomous tests of neutral versus null models. Instead, the neutral model

might be viewed as a mechanism that contributes to pattern along with other processes. Alternatively, the fit of data to the neutral model can be compared to the fit to other process-based models that are not based on neutrality assumptions. Finally, the neutral model can also be tested directly if its parameters can be estimated independently of the test data. However, these approaches may require more data than are often available. For these reasons, simple null model tests will continue to be important in the evaluation of the neutral model.

The neutral model (Bell 2000, Hubbell 2001) has generated great interest and controversy among ecologists. Some of these debates echo earlier controversies in the 1980s over null model analysis (Gotelli and Graves 1996). Indeed, Enquist et al. (2002) have claimed that the neutral model is nothing more or less than a null model. Yet there remains considerable confusion about whether the neutral theory is only a null model, can function as a null model, or is different from traditional null models. In this commentary, we review the similarities and differences between null and neutral models, and point out that a failure to clearly distinguish between them has been responsible for some of the controversy surrounding neutral models.

### **Defining null and neutral models**

Gotelli and Graves (1996: 3) provide an operational definition of a null model as it has been applied in community ecology: "A null model is a pattern-generating model that is based on randomization of ecological data or random sampling from a known or specified distribution. The null model is designed with respect to some ecological or evolutionary process of interest. Certain elements of the data are held constant, and others are allowed to vary stochastically to create new

assemblage patterns. The randomization is designed to produce a pattern that would be expected in the absence of a particular ecological mechanism”.

The null model thus functions as a standard statistical null hypothesis for detecting pattern, in contrast to a scientific hypothesis, which is a mechanism to explain the pattern (Gotelli and Ellison 2004).

Hubbell (2001) describes a neutral model as: “By neutral I mean that the theory treats organisms in the community as essentially identical in their per capita probabilities of giving birth, dying, migrating and speciating. This neutrality is defined at the individual level, not the species level... (p. 6). [Neutral theory] examine[s] the consequences of assuming that population and community change arises only through ecological drift, stochastic but limited dispersal, and random speciation (p. 7)”.

How well does Hubbell’s (2001) description of the neutral model match the definition of a null model? Superficially, the neutral model conforms nicely to this definition. The data often consist of counts of the number of individuals of each species in a community. The model assumes that individuals are ecologically equivalent, with identical per capita rates of birth, death, migration, and speciation (Caswell 1976, Bell 2000, Hubbell 2001, Chave 2004). A repeated process of deaths followed by replacements (births) generates the expected relative abundance distribution in the absence of evolved niche differences among species. Neutral dispersal, in which per capita dispersal rates are the same for all individuals, leading to a similar degree of dispersal limitation among species, is a prominent feature of the most recent elaborations of the neutral model (Bell 2000, Hubbell 2001). Note that the assumption of identical per capita rates differs from other theories, such as island biogeography, which assume that rates per species are identical. Models with identical per species rates can also be viewed as neutral, but the term neutral is usually reserved for the per capita version (Hubbell 2001).

## Null and neutral models in evolution

In the study of evolution, there is a long history of constructive roles for null and neutral models (Nitecki and Hoffmann 1987). Can this experience be used to benefit in ecology? Evolutionary theory can be organized as a sequence or ladder of progressively stronger statements and models. The lowest rung is the Hardy-Weinberg equilibrium, which states that genotypic frequencies in the next generation are determined only by random mating and the laws of probability acting on an infinitely large population; no mechanism of evolution (change in allelic frequencies) is incorporated. The next rung up is that drift changes gene frequencies due to finite population sizes (Fisher 1930, Wright 1931).

Because the long-run outcome of drift is fixation, meaningful drift models include mutation and result in an equilibrium allelic frequency that reflects the opposing forces of mutation and drift (Kimura 1983). However, drift models still exclude all forces of selection (differential survival or reproduction of genotypes). The highest rung represents models that incorporate natural selection, either alone, or in concert with other evolutionary mechanisms.

Although the “first-rung” Hardy-Weinberg equilibrium is widely taught as a conceptual null model, and it is sometimes used to detect nonrandom mating patterns (selfing or assortative mating), it is rarely used anymore as a test for evolutionary change because its assumptions are known to be rarely met in natural populations. However, “second-rung” neutral drift models are often used in evolutionary studies to ask whether population genetic structure can be explained by drift or if it is necessary to invoke natural selection (“third rung” models). In essence, neutrality is used as a null hypothesis for selection. In evolution, this framework is operational because it is possible to empirically measure rates of neutral evolution in the synonymous (often third codon) regions of DNA sequences. One can then test whether rates of change in the non-synonymous (adaptive) regions are greater than in the synonymous (neutral) regions (McDonald and Kreitman 1991).

Can this approach be borrowed from evolution into ecology? The existence of three progressive rungs of models certainly carries over. The Hardy-Weinberg equilibrium, essentially a theory about sampling, corresponds to a null model in which the local community is merely a random sample of the metacommunity or regional source pool. Random sampling from a regional source pool has been used as a null model in ecology (Graves and Gotelli 1983, Cornell and Lawton 1992, McGill 2003c, Dolman and Blackburn 2004) and paleoecology (Holterhoff 1996), but ecology would probably benefit from further research into the application of this first rung model. The neutral model occupies the second rung, stating that local communities change, but only through drift. The neutral model contains the first rung (random sampling) model as a special case when  $m=1$  or all individuals are replaced by immigrants. The third rung contains niche theory or other theories based on adaptive (functionally significant) differences between species (Chase and Leibold 2003).

One implication of this sequencing is that drift is probably ever present, so that niche theories should be built on top of drift (neutrality). The interesting question is not whether drift occurs, but whether adaptive processes also occur and dominate community patterns (Tilman 2004, Chase 2005, McPeck and Gomulkiewicz 2005). Unfortunately, this is much harder to test in ecology than in evolution, because ecology does not have (or has not yet discovered) an analogue of synonymous

codon regions which allows for an immediate empirical calibration of rates of drift. This inability to calibrate rates of neutral drift has led to much of the difficulty in rigorously testing neutral theory. Evolutionary studies have used the predictions of neutral theory as a baseline and have tested for change over and above the baseline (i.e. change attributable to “third-rung” natural selection processes equals total change minus change attributable to “second-rung” neutral processes). In contrast, ecology has mostly viewed niche theory as an either/or alternative to neutral theory rather than as an incremental extension of neutral theory (but see McGill et al. 2005 for an example in which neutral theory is used as a baseline in ecology). In summary, the three rung sequence of evolutionary models suggests that drift should be incorporated into ecological models as a null model to test for adaptive niche differences. However, ecologists should probably spend more time exploring simple first-rung models (random sampling from a regional source pool), and will have to overcome substantial methodological challenges in calibrating the drift model.

### Differences between null and neutral models

In spite of the fact that neutral models appear to be a particular form of an ecological null model, there are three important ways in which the neutral model has been implemented and interpreted differently.

### Unmeasured parameters

In Hubbell's (2001) formulation, there are four parameters:  $J$ , the population size of the local community,  $m$ , the rate of migration into the local community,  $J_M$ , the population size of the metacommunity and  $\theta$ , a measure of species diversity, or equivalently  $v$ , the speciation rate, where  $\theta = 2J_M v$ . Each parameter has well-defined units which in principle makes it possible to estimate all of them directly from ecological data. In practice, this rarely occurs. Although population sizes of local communities can be measured from sample data, estimating the size of the metacommunity is problematic, and speciation rates and migration rates can almost never be measured directly. Ricklefs (2003) is an exceptional study in which some of the neutral model parameters were estimated directly. Ricklefs (2003) estimated the metacommunity size ( $J_M$ ) for neotropical trees and combined this with Hubbell's estimate of  $\theta$ . The resulting neutral model predicted that the average tree species would go extinct after only 9 generations, which most would consider impossibly short.

In most neutral model analyses, one or more of the neutral model parameters must be estimated indirectly

by curve-fitting algorithms that generate best-fitting values for a particular data set. Such curve-fitting is problematic because the fit of the neutral model will depend on the value that is used for  $m$ ; using the value of  $m$  that provides a statistical “best fit” to the observed data biases the analysis in favor of the neutral model. Measuring the fit of data to a theory when the parameters were optimized to fit the data leads to an increased probability of type II statistical error (incorrectly failing to reject the neutral model; McGill et al. 2006). As discussed earlier, this difficulty in empirically calibrating levels of drift is perhaps the major difference between neutral theory in evolution versus ecology.

Null models also require “parameters” that are used to generate the model predictions. However, these parameters are simple constraints that are measured directly from the data, such as row and column totals in a presence-absence matrix (Gotelli 2000). However, more recent null model analyses have incorporated additional data constraints as weighting factors, including site-level measures of habitat variability (Peres-Neto et al. 2001), and species-level measures of population size (Gotelli and Ellison 2002); the latter can be interpreted as preserving niche properties of individual species. Of course, as more biologically specific parameters are incorporated into the null model, it will eventually “cross the line” and should be viewed as a process-based model. But most null models are simple enough that they contain only a few constraints and do not specify particular mechanisms.

### Species equivalence

Neutral models posit that consistent niche differences are not present and that community structure can be accounted for by random colonization, migration, and extinction. In contrast, null models usually hold one or more properties of a species constant, and then create a conditional distribution of null assemblages that is predicated on those constant properties. Co-occurrence analyses typically constrain the number of species occurrences (row totals) and/or the number of species per sites (column totals; Gotelli 2000). In niche overlap analysis, the niche breadth of each species is held constant, but the particular niche categories that a species utilizes are randomized in the null community (Winemiller and Pianka 1990). At the biogeographic scale, null model analyses of the mid-domain effect (Colwell and Lees 2000) typically preserve the range size frequency distribution of each species, but place the range of each species randomly within a bounded geographic domain (Colwell et al. 2004). Rangel and Diniz-Filho (2005b) introduce a hybrid model that mixes both niche-based and stochastic effects and generates patterns qualitatively similar to simple mid-domain

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 need not be "realistic," especially if realism comes at the expense of simplicity (Caswell 1988). If the community is defined in an extremely narrow way, so that only a small subset of very similar species are analyzed, perhaps neutrality is realistic for a null hypothesis. Indeed, it was just such small subsets of ecologically similar species (guilds; Root 1967) that inspired niche analyses and much early competition theory (MacArthur 1972). At the other extreme, if the definition of the community is greatly expanded to incorporate species at different trophic levels that differ vastly in body size and life history (as both Hubbell 2001 and Bell 2003 have done), it would seem essential to preserve those differences in an appropriate null model.

The second reason for incorporating constraints that reflect niche differences is statistical. In the analysis of binary presence-absence matrices, many null model algorithms are based on the row totals of the matrix (species occurrences) and column totals (species richness per site). Algorithms which allow the row totals to vary randomly are analogous to neutral models that posit random colonization and extinction probabilities. However, null models that relax the constraint of row totals are prone to type I statistical errors (rejecting the null hypothesis too frequently; Gotelli 2000). Because these null models assume species independence and do not preserve row totals of the data, they may not be able to mimic the structure of random data sets that are constructed assuming only species independence.

Neutral models, especially when applied to species that differ greatly in body size and along other niche axes, may suffer the same problem. To date, most of the discussion about error in neutral models has focused on the type II errors discussed in the last section. Further exploration of the risk of type I and type II statistical errors is still needed for neutral model analysis (McGill et al. 2006).

## Statistical versus process-based models

The final difference between neutral and null models is philosophical. Proponents of the neutral model seem to treat it as a literal mechanistic explanation for patterns in nature. In contrast, the null model is best viewed as a pattern-generating statistical model that does not specify the detailed mechanisms that control community structure (Gotelli 2001). Early tests of the neutral theory as a process-based model (Bell 2001, 2003, Hubbell 2001) ironically failed to include an appropriate null hypothesis (McGill 2003a, b, Wootton 2005, McGill et al. 2006). The accepted standard in most of ecology, including community ecology, is that a claim for a successful theory requires rejection of a reasonable null hypothesis. This benchmark has inspired a large number of tests of the neutral theory versus null and alternative hypotheses (reviewed in McGill et al. 2006).

The distinction that we have drawn between the neutral model as a null hypothesis and the neutral model as a process-based model has also been discussed by Bell (2000), who distinguishes between statistical null hypotheses (SNH) and dynamic null hypotheses (DNH). SNH are traditional null models based on randomization of empirical data (stochasticity applied to existing data). DNH incorporate a stochastic process into a biological model (stochasticity applied to a process-based model). Neutral theory is arguably one of the first DNH in ecology.

Tests of the drift model of population dynamics have focused on the lognormal as a statistical null hypothesis for neutral theory and have produced mixed results: the neutral theory often fits worse than the lognormal, sometimes fits better than the lognormal, but rarely is the fit significantly better (i.e.  $p < 0.05$ ) than the lognormal. Tests of the dispersal limitation neutral model for spatial patterns have primarily focused on the alternative hypothesis (not truly a null hypothesis) that environmental conditions explain the species found in different localities. These tests have indicated that environment has much greater explanatory power for spatial pattern than neutral explanations. The fact that the neutral model is itself being tested against statistical alternatives such as the log-normal or environmental control of presence-absence again signifies that it is currently being treated as a process-based model.

More recent work has returned again to the idea that neutral theory can be used as a null for other hypotheses. For example, McGill et al. (2005) tested for the constancy of abundances of multiple species within communities over time and used the neutral model predictions as the null hypothesis. Earlier tests for species constancy have relied on conventional statistical procedures (Grossman et al. 1982) or stochastic population growth models and randomizations (Ebeling et al. 1990) to frame the null hypothesis.

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. Traditional null models based on randomization of existing species data usually preserve differences between the species, such as species occurrence totals (which often reflect body mass and trophic level). However, these null models assume species occurrences are random and independent, so they are null with respect to species interactions. Neutral null models clearly exclude species interactions but they also exclude differences between species. For traditional null models, the alternative hypothesis ( $H_A$ ) is that species interactions are important, whereas, for neutral models, the  $H_A$  encompasses both species interactions and species differences. This distinction may seem subtle, but has important consequences in the logic of scientific inference.

It should be noted that the proper  $H_A$  for neutral theory (i.e. the logical negation of the null) is about the importance of species interactions and species differences. It is not about a specific model of species interactions or species differences. Specifically, rejecting the neutral null ( $H_0$ ) does not automatically support niche theory. Niche theory is only one possible model

leading to the importance of species interactions and species differences. It may well be the growing awareness of neutral theory as a null hypothesis and the proper logical deductions from this will lead to a more precise statement of niche theory as well as the generation of (or appreciation of existing) alternatives to niche theory.

### Extensions of the neutral model

Most recently, the neutral model has been extended to test for patterns in biogeography and species co-occurrence. In both cases, the neutral model serves as a specific realization of more general null models that are already well-established.

### Biogeography: the mid-domain effect

The mid-domain effect (Colwell and Lees 2000) was initially proposed as a simple null model for biogeography in which the random placement of species' ranges within a bounded geographic domain generates a peak of species richness near the center of the domain. Critics have complained that MDE models do not contain an explicit mechanism for the development of geographical range limits of individual species and the cohesion of species' geographic ranges (Hawkins et al. 2005, but see Colwell et al. 2004, 2005). Recently, Rangel and Diniz-Filho (2005a) showed that, if populations are linked by short-distance dispersal, the neutral model predicts a stable peak of species richness in the middle of the domain, similar to the predictions of simple MDE null models. Rangel and Diniz-Filho (2005b) extend this model and show that a peak of richness will also emerge in a bounded domain with environmental gradients that limit range expansion. Thus, the neutral model can provide the mid-domain effect with a mechanistic basis at the population level, by generating species' range size frequency distributions and species richness gradients in the absence of environmental gradients.

However, the predictions of Rangel and Diniz-Filho's (2005a, b) neutral models differ quantitatively from the predictions of more simple mid-domain effect models. Specifically, the height of the richness peak at the center of the domain is shallower in the neutral models, which do not impose strict cohesion of species geographic ranges. As in the analysis of relative abundance distributions, the predictions of this neutral model are also sensitive to the migration parameter. The mid-domain peak is realized only for models in which migration distances are relatively short. A related issue is that Rangel and Diniz-Filho's (2005a, b) neutral models predict both the range size frequency distribution, and the number of species per site. In contrast, classic MDE models preserve the observed range size frequency

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). In effect, this analysis uses the neutral model as a null model for null models (see also Colwell and Winkler 1984). Ulrich (2004) found that the neutral model could generate segregation patterns that are statistically significant and argued that these the neutral model could generate patterns predicted by Diamond's (1975) assembly rules model, which is based on niche differences and inter-specific competition.

But can the neutral model account for the segregated patterns in the published presence-absence matrices that have been subjected to null model analysis (Gotelli and McCabe 2002)? The answer is no. Deviations from null models can be expressed as a standardized effect size (SES):  $(\text{observed} - \text{average}(\text{simulated})) /$

$\text{standard deviation}(\text{simulated})$ . SES values for non-random matrices are approximately  $>|2.0|$ . In Ulrich's (2004) tests, the SES generated by the neutral model for the C-score was only ca 0.5, whereas the average SES for 96 published presence-absence matrices was 2.67 (Gotelli and McCabe 2002). For some taxa, such as birds and mammals, average deviations from the null model were even more extreme (3.65 and 3.10, respectively). These patterns cannot be accounted for by the very weak segregation generated by the neutral model. The predictions of the neutral model are more in line with empirical patterns described for marine ectoparasites (SES = 0.35; Gotelli and Rohde (2002)), which show little evidence for competitive structuring (Morand et al. 1999). However, additional data and analysis would be needed to decide whether the neutral model actually describes the dynamics of these assemblages (Poulin 2004).

### Moving forward

Tests of data against null hypotheses lead to the familiar dichotomous evaluation of  $H_0$  versus not- $H_0$ . But there are other ways that the neutral model can be evaluated. One approach is to "partition the variance" and try to assess the relative contribution of different mechanisms simultaneously to observed patterns. For example, proponents of the mid-domain effect (Colwell et al. 2004, 2005) have recently suggested that, rather than testing MDE as a "all-or-none" dichotomy, the assumption of geographic range cohesion should be viewed as a mechanistic process (Connolly 2005) that can contribute to observed patterns along with other processes (Jetz and Rahbek 2002). It remains to be seen whether the neutral model (or mechanistic elements of it) can be fit logically into this regression model framework. A second strategy is to compare neutral model predictions not simply to a null model, but to alternative mechanistic models, such as those based on niche theory (Connolly et al. 2005). Finally, if the neutral model parameters can be estimated independently, through experimentation or direct field measurements, then the fit of the data to the neutral model can be assessed directly, without the need for comparisons to a null model or to the predictions of alternative models (Adler 2004, Wootton 2005). Although all of these approaches are promising, they often require data that are difficult to obtain, and model formulations that are difficult to achieve. Moreover, we note that evolution, which has had more time to develop its approach to neutral theory, has not taken these routes whereby niche and neutral theory are placed on an equal footing. Instead neutral drift is assumed present and serves as a baseline against which additional (e.g. niche) processes can be detected. In essence neutral theory is primarily a particular form of null hypothesis for testing other theories. For these reasons, we suspect that

Table 1. Essential differences between null and neutral models

Feature	Null model	Neutral model
Type of model	Statistical descriptor of expected pattern in the absence of a particular mechanism	Process-based mechanistic model of community structure
Assumptions	Species interactions unimportant	Species interactions unimportant and species differences unimportant (per capita demographic parameters identical)
Source of model parameters	Simulation constraints derived directly from observed data	Important model parameters often unmeasurable, and therefore estimated by optimal curve-fitting

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 (or Bell's SNH) and process-based models (or Bell's DNH) such as neutral theory are far-reaching. Because DNH contain a model, it is possible to posit them as the actual mechanisms and thus as an explanatory model, whereas SNH do not elucidate specific underlying mechanisms. Because the parameters for DNH may be difficult or impossible to measure directly, they are usually estimated through curve fitting, which optimizes the fit with the empirical data, but makes them prone to type II statistical errors (failure to reject a false hypothesis). Conversely, SNH that do not incorporate sufficient biological realism may be prone to type I statistical errors (failure to accept a true null hypothesis). The neutral model may suffer from the same problem when applied to large, diverse communities, but to date there has been little study of the relative risk of type I and type II errors in neutral model analysis.

The fact that neutral theory originated as an SNH, but is now treated as a DNH has caused considerable confusion. Neutral theory can be used either as a null hypothesis (the  $H_0$  in a statistical test) or as an explanatory model. When used as an explanatory model, the neutral theory should be compared itself to an appropriate null hypothesis. When neutral theory is used as a statistical null hypothesis ( $H_0$ ), then care must be used in specifying the appropriate alternative hypothesis ( $H_A$ ) which should describe dispersal, or relative abundance in local communities, as well as specify the importance of both species interactions and species differences, which are absent from  $H_0$ . Traditional null models that have been used to test for patterns such as the mid-domain effect or species co-occurrence may be reformulated as special cases of the neutral theory. However, the inability to measure directly many of the important parameters in the neutral model greatly limits its utility as a null hypothesis for testing empirical

patterns. Attention to the distinctions between SNH and DNH as applied to neutral theory in Table 1 should clarify further analyses of the neutral model.

*Acknowledgements* – We thank Graham Bell, Alison Brody, Rob Colwell, Alexandre Diniz-Filho, Fangliang He, Dan Simberloff, and Werner Ulrich for comments on the manuscript. Supported by NSF grant 0541936 to NJG and NSERC funding to BJM.

## References

- Adler, P. B. 2004. Neutral models fail to reproduce observed species-area and species-time relationships in Kansas grasslands. – *Ecology* 85: 1265–1272.
- Bell, G. 2000. The distribution of abundance in neutral communities. – *Am. Nat.* 155: 606–617.
- Bell, G. 2001. Neutral macroecology. – *Science* 293: 2413–2418.
- Bell, G. 2003. The interpretation of biological surveys. – *Proc. R. Soc. B* 270: 2531–2542.
- Bell, G. 2005. The co-distribution of species in relation to the neutral theory of community ecology. – *Ecology* 86: 1757–1770.
- Caswell, H. 1976. Community structure: a neutral model analysis. – *Ecol. Monogr.* 46: 327–354.
- Caswell, H. 1988. Theory and models in ecology: a different perspective. – *Ecol. Modell.* 43: 33–44.
- Chase, J. M. 2005. Towards a really unified theory for metacommunities. – *Funct. Ecol.* 19: 182–186.
- Chase, J. M. and Leibold, M. A. 2003. Ecological niches: linking classical and contemporary approaches. – Univ. of Chicago Press.
- Chave, J. 2004. Neutral theory and community ecology. – *Ecol. Lett.* 7: 241–253.
- Colwell, R. K. and Winkler, D. W. 1984. A null model for null models in biogeography. – In: Strong, D. R. et al. (eds), *Ecological communities: conceptual issues and the evidence*. Princeton Univ. Press, pp. 344–359.
- Colwell, R. K. and Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. – *Trends Ecol. Evol.* 15: 70–76.
- Colwell, R. K. et al. 2004. The mid-domain effect and species richness patterns: what have we learned so far? – *Am. Nat.* 163: E1–E23.
- Colwell, R. K. et al. 2005. The mid-domain effect: there's a baby in the bathwater. – *Am. Nat.* 166: E149–E154.
- Connolly, S. R. 2005. Process-based models of species distributions and the mid-domain effect. – *Am. Nat.* 166: 1–11.
- Connolly, S. R. et al. 2005. Community structure of coral reef fishes at multiple scales. – *Science* 309: 1363–1365.
- Connor, E. F. and Simberloff, D. 1979. The assembly of species communities: chance or competition? – *Ecology* 60: 1132–1140.
- Cornell, H. V. and Lawton, J. H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities – a theoretical perspective. – *J. Anim. Ecol.* 61: 1–12.

- Diamond, J. M. 1975. Assembly of species communities. – In: Cody, M. L. and Diamond, J. M. (eds), *Ecology and evolution of communities*. Harvard Univ. Press, pp. 342–444.
- Dolman, A. M. and Blackburn, T. M. 2004. A comparison of random draw and locally neutral models for the avifauna of an English woodland. – *BMC Ecol.* <<http://www.biomedcentral.com/1472-6785/4/8>>.
- Ebeling, A. W. et al. 1990. Temporally concordant structure of a fish assemblage: bound or determined? – *Am. Nat.* 135: 63–73.
- Enquist, B. J. et al. 2002. Modeling macroscopic patterns in ecology. – *Science* 295: 1835–1837.
- Fisher, R. A. 1930. The genetical theory of natural selection. – Clarendon.
- Gaston, K. J. and Chown, S. L. 2005. Neutrality and the niche. – *Funct. Ecol.* 19: 1–6.
- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. – *Ecology* 81: 2606–2621.
- Gotelli, N. J. 2001. Research frontiers in null model analysis. – *Global Ecol. Biogeogr.* 10: 337–343.
- Gotelli, N. J. and Graves, G. R. 1996. *Null models in ecology*. – Smithsonian Inst. Press.
- Gotelli, N. J. and Ellison, A. M. 2002. Assembly rules for New England ant assemblages. – *Oikos* 99: 591–599.
- Gotelli, N. J. and Entsminger, G. L. 2002. EcoSim: null models software for ecology. Ver. 7.0. – Acquired Intelligence and Keesey-Bear, <<http://www.garyentsminger.com/ecosim/ecosim.htm>>.
- Gotelli, N. J. and McCabe, D. J. 2002. Species co-occurrence: a meta-analysis of J. M. Diamond's assembly rules model. – *Ecology* 83: 2091–2096.
- Gotelli, N. J. and Rohde, K. R. 2002. Co-occurrence of ectoparasites of marine fishes: a null model analysis. – *Ecol. Lett.* 5: 86–94.
- Gotelli, N. J. and Ellison, A. M. 2004. *A primer of ecological statistics*. – Sinauer.
- Graves, G. R. and Gotelli, N. J. 1983. Neotropical land-bridge avifaunas: new approaches to null hypotheses in biogeography. – *Oikos* 41: 322–333.
- Graves, G. R. and Rahbek, C. 2005. Source pool geometry and the assembly of continental avifaunas. – *Proc. Nat. Acad. Sci. USA* 102: 7871–7876.
- Grossman, G. D. et al. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. – *Am. Nat.* 120: 423–454.
- Harte, J. 2003. Tail of death and resurrection. – *Nature* 424: 1006–1007.
- Hawkins, B. A. et al. 2005. The mid-domain effect and diversity gradients: is there anything to learn? – *Am. Nat.* 166: E140–E143.
- Holterhoff, P. F. 1996. Crinoid biofacies in Upper Carboniferous cyclothems, midcontinent North America: faunal tracking and the role of regional processes in biofacies recurrence. – *Paleobiology* 127: 47–81.
- Hubbell, S. P. 2001. *A unified theory of biodiversity and biogeography*. – Princeton Univ. Press.
- Jetz, W. and Rahbek, C. 2002. Geographic range size and determinants of avian species richness. – *Science* 297: 1548–1551.
- Kimura, M. 1983. *The neutral theory of molecular evolution*. – Cambridge Univ. Press.
- MacArthur, R. H. 1972. *Geographical ecology*. – Harper and Row.
- McDonald, J. H. and Kreitman, M. 1991. Adaptive protein evolution at Adh locus in *Drosophila*. – *Nature* 351: 652–654.
- McGill, B. 2003a. Strong and weak tests of macroecological theory. – *Oikos* 102: 679–685.
- McGill, B. J. 2003b. A test of the unified neutral theory of biodiversity. – *Nature* 422: 881–885.
- McGill, B. J. 2003c. Does Mother Nature really prefer rare species or are log-left-skewed SADs a sampling artefact? – *Ecol. Lett.* 6: 766–773.
- McGill, B. J. et al. 2005. Community inertia of Quaternary small mammal assemblages in North America. – *Proc. Nat. Acad. Sci. USA* 102: 16701–16706.
- McGill, B. J. et al. 2006. Empirical evaluation of the neutral theory. – *Ecology*, in press.
- McPeck, M. and Gomulkiewicz, R. 2005. Assembling and depleting species richness in metacommunities: insights from ecology, population genetics, and macroevolution. – In: Holyoak, M. et al. (eds), *Metacommunities: spatial dynamics and ecological communities*. Univ. of Chicago Press, pp. 355–373.
- Morand, S. et al. 1999. Aggregation and species coexistence of marine fishes. – *Int. J. Parasitol.* 29: 663–672.
- Nitecki, M. H. and Hoffmann, A. (eds) 1987. *Neutral models in biology*. – Oxford Univ. Press.
- Peres-Neto, P. R. et al. 2001. Environmentally constrained null models: site suitability as occupancy criterion. – *Oikos* 93: 110–120.
- Poulin, R. 2004. Parasites and the neutral theory of biodiversity. – *Ecography* 27: 119–123.
- Rangel, T. F. L. V. B. and Diniz-Filho, J. A. F. 2005a. Neutral community dynamics, the mid-domain effect and spatial patterns in species richness. – *Ecol. Lett.* 8: 783–790.
- Rangel, T. F. L. V. B. and Diniz-Filho, J. A. F. 2005b. An evolutionary tolerance model explaining spatial patterns in species richness under environmental gradients and geometric constraints. – *Ecography* 28: 253–263.
- Ricklefs, R. E. 2003. A comment on Hubbell's zero-sum ecological drift model. – *Oikos* 100: 185–192.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. – *Ecol. Monogr.* 37: 95–124.
- Roxburgh, S. H. and Chesson, P. 1998. A new method for detecting species associations with spatially autocorrelated data. – *Ecology* 79: 2180–2192.
- Roxburgh, S. H. and Matsuki, M. 1999. The statistical validation of null models used in spatial association analysis. – *Oikos* 85: 68–78.
- Schluter, D. 1984. A variance test for detecting species associations, with some example applications. – *Ecology* 65: 998–1005.
- Stone, L. and Roberts, A. 1990. The checkerboard score and species distributions. – *Oecologia* 85: 74–79.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. – *Proc. Nat. Acad. Sci. USA* 101: 10854–10861.
- Ulrich, W. 2004. Species co-occurrences and neutral models: reassessing J. M. Diamond's assembly rules. – *Oikos* 107: 603–609.
- Winemiller, K. O. and Pianka, E. R. 1990. Organization in natural assemblages of desert lizards and tropical fishes. – *Ecol. Monogr.* 60: 27–55.
- Wootton, J. T. 2005. Field parameterization and experimental test of the neutral theory of biodiversity. – *Nature* 433: 309–312.
- Wright, S. 1931. Evolution in Mendelian populations. – *Genetics* 16: 97–159.