



Research frontiers in null model analysis

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ABSTRACT

Null models are pattern-generating models that deliberately exclude a mechanism of interest, and allow for randomization tests of ecological and biogeographic data. Although they have had a controversial history, null models are widely used as statistical tools by ecologists and biogeographers. Three active research fronts in null model analysis include biodiversity measures, species co-occurrence patterns, and macroecology. In the analysis of biodiversity, ecologists have used random sampling procedures such as rarefaction to adjust for differences in abundance and sampling effort. In the analysis of species co-occurrence and assembly rules,

null models have been used to detect the signature of species interactions. However, controversy persists over the details of computer algorithms used for randomizing presence–absence matrices. Finally, in the newly emerging discipline of macroecology, null models can be used to identify constraining boundaries in bivariate scatterplots of variables such as body size, range size, and population density. Null models provide specificity and flexibility in data analysis that is often not possible with conventional statistical tests.

Key words assembly rules, biodiversity, species co-occurrence, macroecology, null hypothesis, null model, rarefaction, taxonomic ratios.

‘When you have a new hammer, everything looks like a nail’

Old Russian proverb

Null models are statistical tests widely used in ecology and biogeography (Nitecki & Hoffman, 1987; Manly, 1991; Gotelli & Graves, 1996). They have had a long and controversial history, but they continue to be a useful tool for describing patterns in ecological and biogeographic data (e.g. Colwell & Lees, 2000), particularly when conventional statistical analyses fall short. In this essay, I discuss three active research fronts where null models are (or should be) figuring prominently.

DEFINING THE NULL MODEL

A null model is ‘a pattern-generating model that is based on randomization of ecological data or random sampling from a known or imagined distribution’ (Gotelli & Graves, 1996). In contrast to most other modelling approaches (Caswell, 1988),

the null model strategy is to construct a model that deliberately *excludes* a mechanism being tested. We want to know how well the data can be fitted by such a model (Hilborn & Mangel, 1997) — in other words, can the patterns in the real data be reproduced in a simple model that does not incorporate biologically important mechanisms? Or, do the data appear non-random with respect to the null hypothesis? If so, the analysis provides some evidence in support of the mechanism (although it never can be taken as a ‘proof’ of the mechanism in a strict Popperian framework).

Null models are rarely theoretical abstractions (e.g. Colwell & Hurtt, 1994); they usually begin and end with a real data set. To build a null model, an index of community structure, such as the amount of niche overlap (Winemiller & Pianka, 1990), is first measured for the real data. Next, a null community is generated according to an algorithm or set of rules for randomization, and this same index is measured for the null community. A large number of null communities (typically 1000

or more) are used to generate a frequency histogram of index values expected if the null hypothesis is true. The position of the observed index in the tails of this null distribution is then used to assign a probability value to the pattern (Manly, 1991), just as in a conventional statistical analysis.

In this essay, I am focusing on randomization tests that involve reshuffling, bootstrapping, or resampling from an observed data set, and Monte Carlo techniques that involve sampling from a specified parent distribution (Manly, 1991). Such tests can be tailored to address specific hypotheses about pattern, and to reflect sampling limitations and the spatial scale at which the data were collected. For these sorts of null models, many of the innovations have come from ecologists and biogeographers, rather than from statisticians.

Constructing and testing a null model is straightforward in theory and closely resembles hypothesis testing in conventional statistical analysis. Nevertheless, null models were highly controversial in the 1970s and 1980s (see reviews in Harvey *et al.*, 1983; Wiens, 1989; Gotelli & Graves, 1996; Weiher & Keddy, 1999). Extended, and sometimes acrimonious, exchanges in the literature precipitated around philosophical and statistical issues.

The philosophical issues boiled down to whether the strict Popperian framework of falsification and parsimony (Popper, 1959) should be adopted by ecologists and biogeographers. An important subtext was a debate over the then-reigning competitive paradigm in ecology (Wiens, 1977; den Boer, 1981; Strong *et al.*, 1984). These issues have largely subsided, even though the role of competition in structuring the assembly of communities is still unresolved (Gotelli, 1999). As with cladistics, null models are now viewed as a useful tool for revealing pattern (or the lack thereof) in natural communities, rather than as a *Zeitgeist* of the 1970s and 1980s debates over competition theory.

The statistical issues in those debates centred around the precise details of null model construction. Did certain algorithms inadvertently 'smuggle in' the effects they were designed to reveal (the 'Narcissus Effect' of Colwell & Winkler, 1984)? Conversely, were some algorithms predisposed to rejecting the null hypothesis for data sets that were entirely random (the 'Jack Horner Effect' of Wilson, 1995)? Using drier, more conventional labels, these are really controversies over whether

particular null model tests are predisposed to Type II error — incorrectly accepting a false null hypothesis (the Narcissus Effect), or Type I error — incorrectly rejecting a true null hypothesis (the Jack Horner Effect). This is an active area of research, and recent studies have quantified the frequencies of Type I and Type II errors by testing null model algorithms with random and structured data sets (e.g. Losos *et al.*, 1989; Garvey *et al.*, 1998; Shenk *et al.*, 1998; Gotelli, 2000).

Although the point has been made elsewhere (Connor & Simberloff, 1986), it bears repeating that the null hypothesis is *not* that communities are entirely random or have no structure (Roughgarden, 1983). Rather, it is that community structure is random with respect to the mechanism being tested. The null model can include as much structure as is warranted by the data and the biology, as long as the mechanism of interest can be carefully excluded from the randomization. In practice, most null models are fairly simple in their randomization structure, if only because the kinds of data and biological information needed to construct more sophisticated null models (e.g. Graves & Gotelli, 1983) are usually lacking.

TAXONOMIC RATIOS AND THE MEASUREMENT OF BIODIVERSITY

Null models got their start in biogeography in the analysis of the species/genus and other such taxonomic ratios, which have long been used to describe community patterns and to infer levels of competitive interactions (reviews in Simberloff, 1970; Järvinen, 1982). A low species/genus ratio was interpreted as a product of strong intrageneric competition (Elton, 1946), which might limit congeneric coexistence (Darwin, 1859). Consistent with this hypothesis was the widespread observation that species/genus ratios were usually smaller for island than mainland communities (Elton, 1946). But what was the correct null hypothesis? In other words, what is the expected species/genus ratio in a community that is not structured by competition? The answer can be determined by establishing species/genus ratios for random communities that differ only in the total number of species they contain.

Such a null model was first explored for plant communities by Maillifer (1929), who used draws of species from a deck of shuffled cards to calculate

the expected generic richness in small communities. For animal communities, Williams (1947, 1964) elucidated these same patterns using statistical models and computer simulations. Although their work was ignored by ecologists for several decades (Järvinen, 1982), re-analyses of species/genus ratios now suggest that island communities harbour slightly more species per genus than expected by chance, in spite of the lower absolute number of species per genus expected in smaller samples (Simberloff, 1970). This finding is the opposite of what competition theory predicts, perhaps reflecting instead the similar dispersal potential and ecological requirements of congeneric species (the 'Icarus Effect' of Colwell & Winkler, 1984).

In a parallel, but independent effort, ecologists developed rarefaction as a method for comparing species richness of samples that differ in the number of individuals collected (Sanders, 1968; Hurlbert, 1971; Heck *et al.*, 1975; Tipper, 1979). Although the motivation was quite different, the statistical problem is the same — how meaningfully to compare category/subcategory taxonomic ratios such as individuals/species or species/genus. Statistical methods (and software) have now been well developed to allow for meaningful comparisons that control for differences in both sampling effort and abundance (Gotelli & Colwell, in press).

Nevertheless, such well-understood sampling effects are frequently ignored in biodiversity studies. Ecologists have repeatedly made the error of comparing richness per quadrat (species density) among sites differing in overall plant or animal density (e.g. Hubbell *et al.*, 1999). These comparisons have confounded or equated differences in density with the differences in disturbance, successional, or productivity regimes that are being compared (Chazdon *et al.*, 1999; Stevens & Carson, 1999). Even in small-scale experimental studies in which sampling effort is carefully controlled, standardization on the basis of number of individuals collected can completely change diversity patterns in experimental treatments (McCabe & Gotelli, 2000). Species density (standardized by effort or area) and species richness (standardized by the number of individuals) may yield fundamentally different patterns of biodiversity; it is not yet clear under which circumstances each of these measures is most appropriate. Although rarefaction represents the most basic (and least controversial) null

model, it needs to be more widely applied in biodiversity studies at all spatial and temporal scales (Gotelli & Colwell, in press).

SPECIES CO-OCCURRENCE AND COMMUNITY ASSEMBLY RULES

No other issue in the history of ecology has been as contentious as the analysis of species co-occurrence patterns. Diamond's (1975) monograph on the birds of the Bismarck Archipelago popularized the idea of using 'assembly rules' based on competitive interactions to interpret species co-occurrence patterns. In many ways, this monograph represents the apogee of the competition paradigm that was so heavily influenced by the work of G.E. Hutchinson and R.H. MacArthur.

In a sharply worded response, Connor & Simberloff (1979) attacked the logic of Diamond's (1975) assembly rules and presented a pioneering null model analysis to determine the expected pattern of species co-occurrence in the absence of competitive interactions. This pair of papers sparked off a debate over the statistical analysis of presence-absence matrices that has continued unabated for over 25 years (e.g. Diamond & Gilpin, 1982; Gilpin & Diamond, 1982; Connor & Simberloff, 1983; Wilson, 1987; Roberts & Stone, 1990; Stone & Roberts, 1990; Manly, 1995; Sanderson *et al.*, 1998; Gotelli & Entsminger, in press; Zaman & Simberloff, in press). For many ecologists, these baroque exchanges are synonymous with null models. No wonder that many have been wary to adopt null models for their own analyses!

Although the debate has become more focused, controversy persists. Connor & Simberloff (1979) introduced an important null model that randomizes presence-absence matrices, but maintains a fixed set of row (= species occurrences) and column (= island species number) totals. It has been a computational challenge to develop an algorithm that samples such matrices randomly and equiprobably (Roberts & Stone, 1990; Manly, 1995; Sanderson *et al.*, 1998; Gotelli & Entsminger, in press; Zaman & Simberloff, in press). Unfortunately, some authors have made sweeping, premature claims about the validity of their methods, sometimes based on the analysis of a single data matrix. To evaluate these methods properly, the algorithms have to be tested with artificial data sets of two kinds: random data sets that contain no pattern,

and structured data sets that contain a mixture of structure and random noise (Gotelli *et al.*, 1997). In this way it is possible to quantify the tendency towards Type I and Type II error in null model analysis (Roxburgh & Matsuki, 1999; Gotelli, 2000). Such analyses are tedious and not very exciting, but they are essential if null models are to have a solid statistical foundation.

Other innovations in the study of species co-occurrence patterns include: the development of the 'favoured states' assembly rule for functional groups (Fox, 1987; Fox & Kirkland, 1992; Fox & Brown, 1993; Fox, 1999), incorporation of intra-specific spatial patterns into null models (Wilson & Gitay, 1995; Roxburgh & Chesson, 1998; Wilson, 1999), and development of explicit biogeographic criteria for designating realistic species source pools (Graves & Gotelli, 1993; Penev, 1997). In spite of continued interest in assembly rules and species co-occurrence (Weiher & Keddy, 1999), it is still unclear how general Diamond's (1975) model is because so few data sets have been analysed with comparable methods. A recent meta-analysis (Gotelli & McCabe, in press) suggests that most communities exhibit non-random co-occurrence patterns that are indeed consistent with Diamond's (1975) model, although there are intriguing differences among taxonomic groups in the degree of non-randomness.

MACROECOLOGY

Seminal papers by Brown & Maurer (1986, 1987, 1989; see also Damuth, 1981) introduced the study of 'macroecology' (Brown, 1995; Blackburn & Gaston, 1998; Maurer, 1999), which emphasizes that the way species partition energy in nature is a fundamental constraint on community structure (Brown, 1995). In many studies of macroecology, species-level variables such as body size, population size, and geographical range area are plotted in two-dimensional scatter plots in which each species represents a single data point. The plots often exhibit unusual polygonal shapes of points. However, to my eyes, they sometimes resemble the scattershot of bullet holes in rural road signs.

In any case, the next step is to draw in 'boundaries' in the two-dimensional space, beyond which real data points never occur (absolute boundaries) or rarely occur (probabilistic boundaries). Con-

ventional statistics and regression analyses are of little help here because they merely pass a line through the centre of a cloud of points and (typically) test for a slope of zero. But even if the slope of the regression is zero, the relationship between x and y may change near the edge vs. the centre of the distribution.

For example, the plot of population density vs. body size of North American birds shows a pronounced peak (Brown & Maurer, 1987), perhaps suggesting an optimal intermediate body size. However, null model analysis suggests that this pattern may not be so unusual (Blackburn *et al.*, 1990). The problem is that there are more species of intermediate body size, so the range of population sizes will tend to be greatest at intermediate body sizes. Thus, a peak may appear in the plot even if there is no constraint on the relationship between body size and population size.

Recently, sophisticated statistical methods have been proposed to analyse such data sets, including polynomial regression (Blackburn *et al.*, 1990), quantile regression (Blackburn *et al.*, 1992; Scharf *et al.*, 1998; Cade *et al.*, 1999), path analysis (Thomson *et al.*, 1996), and other techniques (Garvey *et al.*, 1998). However, a null model approach may be even more effective (Blackburn *et al.*, 1990). First, null models are often much simpler and easier to understand than some of these statistical models. Second, many of these statistical models require some arbitrary decisions to implement (e.g. which quantile should be analysed, or which path structures should be compared and by what criterion?). Moreover, some of these tests require symmetrical, Gaussian data, which are often not found with macroecological variables, even after data transformation. Finally, formulating and testing the null model lays bare two critical questions that may be hidden or implicit in sophisticated statistical models.

The first question is how can boundaries in two-dimensional plots be established objectively? One promising approach is to use simple polygons defined by midpoints, medians, and ranges of observed data distributions (Gotelli & Entsminger, 2000). These polygons define triangular and pyramid shapes, but they do not depend on subjective or visual placement of potential boundaries.

Second, and more important, what is the appropriate null distribution of points in bivariate space against which patterns should be compared? The

unstated null hypothesis in many macroecological studies is that the distribution of points is isotropic, with an even density of species throughout the bivariate space; thus, the marginal distributions for each variable would be uniform. The boundaries of that space can be defined by the endpoints of the data, by continental limits on area, or by phylogenetic extremes observed within a well-defined clade (Kochmer & Handel, 1986).

A different approach, taken by Enquist *et al.* (1995), is to use the marginal distributions of the x and y variables themselves to set the limits. As in classic randomization tests, the x and y data are reshuffled, so the null model tests for unusual patterns in the covariance of x and y (Garvey *et al.*, 1998). Thus, the observation that few large-bodied species have large population sizes might not be unusual. If large-bodied species are typically rare (Van Valen, 1973) and species with large population sizes are uncommon (Preston, 1962), we should not be surprised to find that this combination of traits is rarely found together.

These two kinds of null distributions (uniform vs. marginals) tend to give different answers. Many data sets do not appear to be isotropic, so they show significant patterns when tested against the uniform null hypothesis. However, these same data sets may not exhibit unusual covariance structure, so they appear random when tested against the marginals null hypothesis. Such contrasting results force investigators to consider explicitly how assemblages would be structured in the absence of any biological constraints. Looking to the future, other null distributions are possible. Recent synthetic work on allometric scaling and constraints on body size (West *et al.*, 1997, 1999a, 1999b; Enquist *et al.*, 1998, 1999) may prompt a different sort of null distribution for macroecological studies.

In closing, I will issue a plea for plurality, and for researchers to eschew the 'single hammer' mentality. There is no one 'correct' method for constructing and interpreting a null model! The advantage of null models is that they provide flexibility and specificity that cannot often be obtained with conventional statistical analyses. Ironically, ecologists in the 1980s became polarized over null models and argued about a narrow subset of algorithms developed for testing patterns of competitive structure. Ecologists and biogeographers

should now exercise their imaginations and develop appropriate null models for addressing other research questions.

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