

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

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 find-

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

- Colwell, R.K. & Lees, D.L. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, **15**, 70–76.
- Colwell, R.K. & Winkler, D.W. (1984) A null model for null models in biogeography. *Ecological Communities: Conceptual Issues and the Evidence* (ed. by D.R. Strong Jr, D. Simberloff, L.G. Abele and A.B. Thistle), pp. 344–359. Princeton University Press, Princeton.
- Connor, E.F. & Simberloff, D. (1979) The assembly of species communities: chance or competition? *Ecology*, **60**, 1132–1140.
- Connor, E.F. & Simberloff, D. (1983) Interspecific competition and species co-occurrence patterns on islands: null models and the evaluation of evidence. *Oikos*, **41**, 455–465.
- Connor, E.F. & Simberloff, D. (1986) Competition, scientific method, and null models in ecology. *American Scientist*, **74**, 155–162.
- Damuth, J. (1981) Population density and body size in mammals. *Nature*, **290**, 699–700.
- Darwin, C. (1859) *The Origin of Species by Means of Natural Selection*. Murray, London.
- Diamond, J.M. (1975) Assembly of species communities. *Ecology and Evolution of Communities* (ed. by M.L. Cody and J.M. Diamond), pp. 342–444. Harvard University Press, Cambridge.
- Diamond, J.M. & Gilpin, M.E. (1982) Examination of the 'null' model of Connor and Simberloff for species co-occurrences on islands. *Oecologia*, **52**, 64–74.
- Elton, C. (1946) Competition and the structure of ecological communities. *Journal of Animal Ecology*, **15**, 54–68.
- Enquist, B.J., Brown, J.H. & West, G.B. (1998) Allometric scaling of plant energetics and population density. *Nature*, **395**, 163–165.
- Enquist, B.J., Jordan, M.A. & Brown, J.H. (1995) Connections between ecology, biogeography, and paleobiology: relationship between local abundance and geographic distribution in fossil and recent molluscs. *Evolutionary Ecology*, **9**, 586–604.
- Enquist, B.J., West, G.B. & Charnov, E.L. (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature*, **401**, 907–911.
- Fox, B.J. (1987) Species assembly and the evolution of community structure. *Evolutionary Ecology*, **1**, 201–213.
- Fox, B.J. (1999) The genesis and development of guild assembly rules. *Ecological Assembly Rules: Perspectives, Advances, Retreats* (ed. by E. Weiher and P. Keddy), pp. 23–57. Cambridge University Press, Cambridge.
- Fox, B.J. & Brown, J.H. (1993) Assembly rules for functional groups in North American desert rodent communities. *Oikos*, **67**, 358–370.
- Fox, B.J. & Kirkland, G.L. Jr (1992) An assembly rule for functional groups applied to North American soricid communities. *Journal of Mammology*, **73**, 491–503.
- Garvey, J.E., Marschall, E.A. & Wright, R.A. (1998) From star charts to stoneflies: detecting relationships in continuous bivariate data. *Ecology*, **79**, 442–447.
- Gilpin, M.E. & Diamond, J.M. (1982) Factors contributing to non-randomness in species co-occurrences on islands. *Oecologia*, **52**, 75–84.
- Gotelli, N.J. (1999) How do communities come together? *Science*, **286**, 1684–1685.
- Gotelli, N.J. (2000) Null model analysis of species co-occurrence patterns. *Ecology*, **81**, 2606–2621.
- Gotelli, N.J., Buckley, N.J. & Wiens, J.A. (1997) Co-occurrence of Australian land birds: Diamond's assembly rules revisited. *Oikos*, **80**, 311–324.

- Losos, J.B., Naeem, S. & Colwell, R.K. (1989) Hutchinsonian ratios and statistical power. *Evolution*, **43**, 1820–1826.
- Maillefer, A. (1929) Le coefficient generique de P. Jacard et sa signification. *Memoire Soc. Vaudoise Sc. Nat.*, **3**, 113–183.
- Manly, B.F.J. (1991) *Randomization and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- Manly, B.F.J. (1995) A note on the analysis of species co-occurrences. *Ecology*, **76**, 1109–1115.
- Maurer, B.A. (1999) *Untangling Ecological Complexity: the Macroecological Perspective*. University of Chicago Press, Chicago.
- McCabe, D.J. & Gotelli, N.J. (2000) Effects of disturbance frequency, intensity, and area on assemblages of stream invertebrates. *Oecologia*, **124**, 270–279.
- Nitecki, M.H. & Hoffman, A. (1987) *Neutral Models in Biology*. Oxford University Press, Oxford.
- Penev, L. (1997) Concrete biotas — a neglected concept in biogeography? *Global Ecology and Biogeography Letters*, **6**, 91–96.
- Popper, K.R. (1959) *The Logic of Scientific Discovery* (revised, 1965 edition). Basic Books, New York.
- Preston, F.W. (1962) The canonical distribution of commonness and rarity. *Ecology*, **43**