

# Statistical ecology II: data analysis

Nicola J. Gotelli and Wilfried Ulrich

N. J. Gotelli, Dept of Biology, University of Vermont, Burlington, VT 05405, USA. W. Ulrich (ulrich@umk.pl), Dept of Animal Ecology, Nicolaus Copernicus University in Toruń/Gagarina 9, PL-87-100 Toruń, Poland.

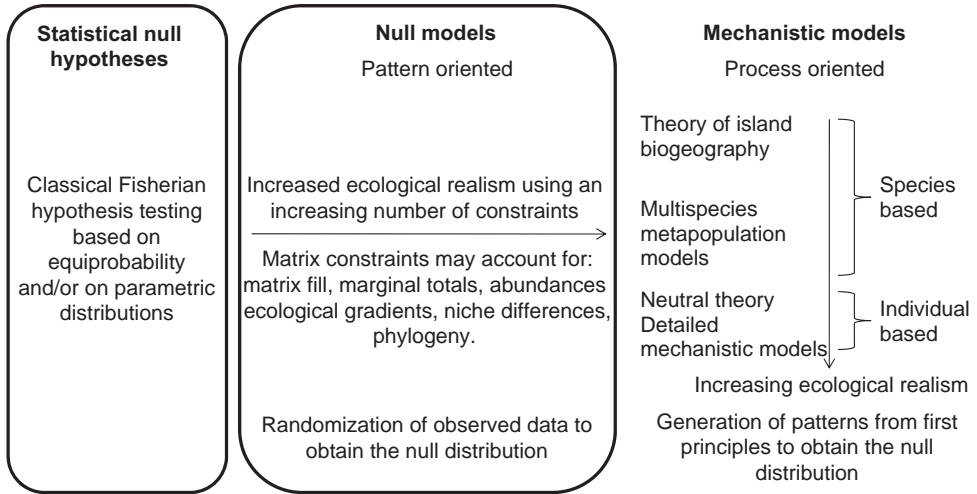
This review identifies several important challenges in null model testing in ecology: 1) developing randomization algorithms that generate appropriate patterns for a specified null hypothesis; these randomization algorithms stake out a middle ground between formal Pearson–Neyman tests (which require a fully-specified null distribution) and specific process-based models (which require parameter values that cannot be easily and independently estimated); 2) developing metrics that specify a particular pattern in a matrix, but ideally exclude other, related patterns; 3) avoiding classification schemes based on idealized matrix patterns that may prove to be inconsistent or contradictory when tested with empirical matrices that do not have the idealized pattern; 4) testing the performance of proposed null models and metrics with artificial test matrices that contain specified levels of pattern and randomness; 5) moving beyond simple presence–absence matrices to incorporate species-level traits (such as abundance) and site-level traits (such as habitat suitability) into null model analysis; 6) creating null models that perform well with many sites, many species pairs, and varying degrees of spatial autocorrelation in species occurrence data. In spite of these challenges, the development and application of null models has continued to provide valuable insights in ecology, evolution, and biogeography for over 80 years.

*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. The null model is designed with respect to some ecological or evolutionary process of interest.* (Gotelli and Graves 1996)

From its origins in the analysis of species/genus ratios (Järvinen 1982), there is a long history of using null models to analyze patterns and test hypotheses in ecology, evolution and biogeography (Harvey et al. 1983). Although the general controversy in the 1970s over null models and competition has died down (Gotelli and Graves 1996), there are still many disputed aspects of testing and implementing null models. In this paper, we review some of the more recent challenges and controversial issues in the implementation and interpretation of null models in ecology. We focus primarily on the use of null models in biogeography, ecology, and macroecology.

## How to read this paper

Classical Pearson–Neyman hypothesis testing (Graves 1978) addresses the dichotomy between a null hypothesis ( $H_0$ ) and its alternative ( $H_1$ ). If these hypotheses are mutually exclusive and collectively exhaustive, then the probability that  $H_0$  is true, given the data ( $P(H_0|\text{data})$ ), is  $P(H_0) = 1 - P(H_1)$ .



leads to excessive type II errors (Grant and Abbott 1980, Colwell and Winkler 1984). For this reason, Presley et al. (2010) recently advocated the use of the equiprobable–equiprobable model for testing for patterns of species distributions. However, the poor performance of this algorithm in the context of nestedness (Ulrich and Gotelli 2007a) and species co-occurrence (Gotelli 2000, Ladau 2008), suggests there is a real danger in overestimating the frequency of significant patterns by taking such a liberal approach.

Recently Kullback–Leibler information-based model choices have become popular as complementary approaches to classical hypothesis testing (Akaike 1973, Burnham and Anderson 2002). Information criteria assign probabilities to competing models with different numbers of free parameters and thus allow for a ranking of models from best to worst (Anderson 2008). In the context of null model analysis, we might ask whether information criteria are capable of quantifying the information content of differently constrained null models. However, a simplistic use of information criteria is problematic because we cannot equate the number of null model constraints with the number of free parameters necessary for calculating information metrics. Moreover, null models cannot simply be ranked additively by the number of constraints they contain, but should instead be

reformulated in terms of the number of parameters. However, a simplistic use of information criteria is problematic because we cannot equate the number of null model constraints with the number of free parameters necessary for calculating information metrics. Moreover, null models cannot simply be ranked additively by the number of constraints they contain, but should instead be reformulated in terms of the number of parameters.

between the formal definition of a pattern and the working definition based on the index.

The history of the nestedness concept (Almeida-Neto et al. 2007, 2008, Ulrich et al. 2009) is a good example of how this mismatch of pattern and metric can cause confusion. Patterson and Atmar (1986) originally defined nestedness as *'that the species comprising a depauperate fauna should constitute a proper subset of those in richer faunas'*. This definition of nestedness focuses on the species composition among sites, but does not consider the site composition among species. A proper nestedness metric should measure the











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