“Disentangling nestedness” disentangled


Analytical research indicates that the “nestedness” of mutualistic networks facilitates the coexistence of species by minimizing the cost of competition relative to the benefits of facilitation. In contrast, James et al. recently argued that a more parsimonious explanation exists: the persistence of a community and its constituent species depends more on their having many interactions (high connectance and high degree, respectively) than on the interactions of each species—and hence their expected persistence. When these changes are taken into account, we find a significant, positive relationship between nestedness and network persistence that confirms the importance of nestedness in mutualistic communities. There is a Reply to this Brief Communication Arising by James, A., Pitchford, J. W. & Plank, M. J. Nature 500, http://dx.doi.org/10.1038/nature12381 (2013).

Given a network, one can robustly quantify the relative numbers of specialist generalists species with the degre distribution. A network’s degre distribution is of considerable importance because studies have repeatedly highlighted the significant, positive relationship between species’ numbers of mutualistic partners and its survival probability. This distribution alone is also capable of driving many higher-order network properties. A network’s degree distribution is often used to test for nestedness. In this sense, nestedness is an important and interesting concept. The critical point is that the network is the result of random networks having more homogeneous degree distributions and that the most vulnerable species in the network are the ones that have more interactions in the corresponding randomizations. Here this distinction is of critical importance because species’ degrees are, in fact, “better predictors of individual species’ survival.” Theorem more merrier” indeed.

To quantitatively validate these results, we repeated a key analysis of ref. 2 to measure the relationship between nestedness and persistence while paying explicit attention to changes in the network’s degree distribution (Methods). On taking the small but critical step of controlling for the increased homogeneity of the degree distributions, we observe a significant, positive relationship between nestedness and persistence (Fig. 1b). In addition, we reach the same conclusion whether we account for changes in the degree distribution statistically or by repeating the analysis while generating the randomized network with an unlabeled model that explicitly maintains the observed degree distribution (Fig. 1c, Methods and Appendix). All else being equal, our results here illustrate that, the greater the nestedness of a community, the greater indeed is that community’s persistence.

Given an observed number of species and interactions in a community, a powerful question across the ecological literature is whether or not some way structure those interactions (for example, nestedness) lead to more persistent communities. Although the number of mutualistic interactions of a species plays an important role in its survival, we find ambiguous support for the idea that the way in which mutualistic interactions are organized—that the architecture of biodiversity—encompassing the importance of carefully considering the interplay between all potential sources of variation in ecological models. Otherwise, one runs the risk of further entangling models that are sufficiently tangled already.

Methods

For 9 empirical networks, we generated 250 randomized networks and forecasted the fraction of surviving species in each simulation across 250 parameterizations of a dynamical mutualistic model. We quantified the relationship between persistence and nestedness with mixed-effects logistic regression that takes the form (logit $P_{\text{surv}}$) $= \beta_0 + \beta_1 M + \beta_2 C + \beta_3 W + \beta_4 N + \beta_5 r + e$, where $M$, $C$, and $W$ quantify the importance of network magnitude, connectance, and relative
degree homogeneity \(^4\) and nestedness \(^5\) \(N_r\) respectively, the random effects \(\nu_3\) and \(\nu_4\) control for variance across networks and randomizations, and \(\epsilon_{ijk}\) is the model residual. Variance inflation factors given no indication of multicollinearity in this model.

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Appendix

For randomized empirical network with two null models, the probabilistic and fixed (or swap) algorithms. ¹ For our purpose here, the key distinction between the two is that the probabilistic model generates random network with quantitatively more homogeneous degree distribution than the observed empirically (\(W_0 > 0\)) whereas the degree distribution is strictly conserved in the network generated by the fixed model (\(W_0 = 0\)). The statistical analysis presented here was performed in R version 2.15.3 (http://R-project.org/) using the glmer function in package lme4 version 0.999999-0 (http://lme4.r-forge.r-project.org), Codetop perform the network randomizations and dynamic simulations in Matlab (http://www.mathworks.com/) and the mixed-effects logistic regression in R (http://R-project.org/) is available from the Dryad Digital Repository at http://dx.doi.org/10.5061/dryad.p2gq8.