# ''Disentangling nestedness'' disentangled

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Analytical research indicates that the 'nestedness' of mutualistic networks facilitates the coexistence of species by minimizing the costs of competition relative to the benefits of facilitation[1]. In contrast, James *et al.*[2] 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 for these interactions to be organized in any particular manner. Here we demonstrate that these conclusions are an unintended consequence of the fact that the methodology of ref. 2 directly changed the number of 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 reconfirms the importance of nestedness in mutualistic communities[1,3]. 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 to generalist species via the degree distribution[4,5]. A network's degree distribution is of considerable importance, because studies have repeatedly highlighted the significant, positive relationship between a species' number of mutualistic partners and its survival probability[1–3,6]. This distribution alone is also capable of driving many higher-order network properties[7], not to mention the fact that the degrees of species are phylogenetically constrained themselves[8]. For these and other reasons, studies across the ecological-network literature[4,5,7] have emphasized the need to take the degree distribution into consideration when assessing the significance of the myriad patterns observed in nature[9–11].

Unfortunately, when comparing empirically observed networks to random networks, the authors of ref. 2 seem to have overlooked this critical link between changes in the degree distribution and species' survival. As a direct consequence, the specialists in their random networks became less specialist and the generalists less generalist[5]. Yes, the random networks were observed to be more persistent (Fig. 1a), but this was not in fact an indication that nestedness is unimportant[2]. Instead, this increase in persistence was a result of the random networks having more homogeneous degree distributions[5,12], and that the most vulnerable species in the empirical networks almost always had more interactions in the corresponding randomizations. Here this distinction is of critical importance because species' degrees are, in fact, "a better predictor of individual species survival"[2]. "The more the merrier" indeed[13].

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 networks with a null 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 prevailing question across the ecological literature is whether or not some ways to structure those interactions (for example, nestedness) lead to more persistent communities. Although the number of

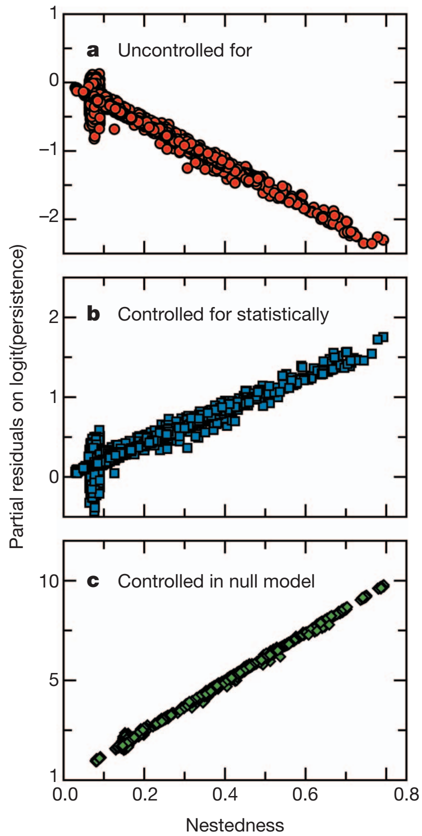


**Figure 1 | Within our regression analysis, the relationship between nestedness and persistence in mutualistic networks depends integrally on changes in the degree distributions of the networks. a**, If these distributions are allowed to change but are uncontrolled for, nestedness appears to be negatively correlated to persistence ($P < 10^{-4}$). **b**, **c**, However, when these changes are appropriately controlled for—either statistically (**b**) or in the null model for randomization (**c**)—there is a significant positive relationship between nestedness and persistence ($P < 10^{-4}$ and $P < 10^{-4}$, respectively). The same general conclusions reached here for the probabilistic null model hold for other, non-degree-preserving randomizations[3].

mutualistic interactions of a species plays an important role in its survival[2,3,6,13], we find unambiguous support for the added importance of the way in which mutualistic interactions are organized—the true architecture of biodiversity[14]. Echoing ref. 2, our findings re-emphasize the importance of carefully considering the interplay between all potential sources of variation[11] in ecological models. Otherwise, one runs the risk of further entangling models that are sufficiently tangled already.

## Methods

For 59 empirical networks, we generated 250 randomized networks and for each we simulated persistence (the fraction $P$ of surviving species in each simulation) across 250 parameterizations of a dynamic mutualistic model[1,2]. We quantified the relationship between persistence and nestedness with a mixed-effects logistic regression[15] that takes the form $\mathrm{logit}(P_{ijk}) = \beta_0 + \beta_1 M_i + \beta_2 C_i + \beta_3 W_{ij} + \beta_4 N_{ij} + n_i + r_{ij} + \varepsilon_{ijk}$. Here the indices $i$, $j$ and $k$ indicate the empirical network, network randomization and model parameterization, respectively, $\beta_0$ is a constant, the slopes $\beta_1$, $\beta_2$, $\beta_3$ and $\beta_4$ quantify the importance of network magnitude[2] $M$, connectance[2] $C$, relative degreehomogeneity[12] $W$,andnestedness[9] $N$,respectively,therandomeffects $n_i$ and $r_{ij}$ controlforvarianceacrossnetworksandrandomizations,and $\varepsilon_{ijk}$ isthe modelresidual.Varianceinflationfactorsgavenoindicationofmulticollinearityin thismodel.

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## Appendix

Werandomizedtheempiricalnetworkswithtwonullmodels:theprobabilisticand fixed(orswap)algorithms[5].Forourpurposeshere,thekeydistinctionbetweenthe twoisthattheprobabilisticmodelgeneratesrandomnetworkswithquantitatively morehomogeneousdegreedistributionsthanthoseobservedempirically( $W_{ij} > 0$) whereasthedegreedistributionisstrictlyconservedinnetworksgeneratedbythe fixedmodel( $W_{ij} \equiv 0$).ThestatisticalanalysespresentedhereweređperformedinR version 2.15.3 (http://R-project.org/) using the glmer function in package lme4 version0.999999-0(http://lme4.r-forge.R-project.org).Codetoperformthenetwork randomizations and dynamic simulations in Matlab (http://www.matlab.com/) andthemixed-effectslogisticregressionsinR(http://R-project.org/)isavailable fromtheDryadDigitalRepositoryathttp://dx.doi.org/10.5061/dryad.p2gq8.