

Disentangling nestedness from models of ecological complexity

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Complex networks of interactions are ubiquitous¹ and are particularly important in ecological communities, in which large numbers of species exhibit negative (for example, competition or predation) and positive (for example, mutualism) interactions with one another. Nestedness in mutualistic ecological networks is the tendency for ecological specialists to interact with a subset of species that also interact with more generalist species². Recent mathematical and computational analysis has suggested that such nestedness increases species richness^{3,4}. By examining previous results and applying computational approaches to 59 empirical data sets representing mutualistic plant–pollinator networks, we show that this statement is incorrect. A simpler metric—the number of mutualistic partners a species has—is a much better predictor of individual species survival and hence, community persistence. Nestedness is, at best, a secondary covariate rather than a causative factor for biodiversity in mutualistic communities. Analysis of complex networks should be accompanied by analysis of simpler, underpinning mechanisms that drive multiple higher-order network properties.

Networks of mutually beneficial interactions are an important and widespread phenomenon⁵. In many cases, these mutualistic interactions are bipartite, with each participant (species, individual or organization) from one class benefitting through interactions with participants from the other class. Among the most important ecological examples are mutualistic interactions between plants and animal pollinators: the animal receives nutrients from the plant while providing the plant with increased reproductive fitness through pollination⁶. These relationships form networks in which specialist animal species (that is, those with few mutualistic partners) tend to pollinate plant species that are subsets of those pollinated by more generalist animal species (that is, those with more partners)⁷. Put more simply, specialists tend to interact with generalists, whereas generalists interact with specialists and with other generalists. This phenomenon is referred to as nestedness and can be quantified using a variety of methods; for example, methods based on counting the number of partners that are shared by two species² or on measuring how close the interaction matrix is to being upper triangular (Fig. 1), which would correspond to a perfectly nested network⁸ (see Supplementary Information for the mathematical definition of nestedness).

To construct and parameterize detailed models for particular ecological networks is impractical at best. Research has instead focused on understanding the statistical properties of large ensembles of theoretical communities, using simple but plausible modelling frameworks and assigning random parameter values from biologically motivated probability distributions. For mutualistic networks, this methodology has been used to argue that nestedness increases biodiversity³. However, this argument relies on a predicted upper bound for the maximum number of species that can survive in a given network, which is not necessarily representative of the actual number of surviving species.

To test the relationship between nestedness and biodiversity, we used a model³ that includes intrinsic growth, intraspecific and interspecific

competition, and mutualistic interactions that are defined by empirical plant–pollinator networks⁹ (Supplementary Information). Each species competes with all other species in its own class (plant or pollinator) and interacts mutualistically with a subset of species, determined by the empirical network, from the opposite class. We used community persistence (the proportion of species surviving after the system has reached equilibrium) as a measure of biodiversity³ but, in contrast to other studies^{3–5}, we used a combination of direct numerical integration and a root-finding algorithm to determine the community equilibrium. We calculated a range of potential predictors of community persistence, including nestedness², relative nestedness (which compares nestedness of the network to that of randomized null models) and connectance (the number of mutualistic interactions divided by the total possible number of mutualistic interactions) of each network (Methods). To isolate the effects of mutualism, the mutualistic interactions were then switched off. In this case, the plant and pollinator communities are completely independent, competition-only systems. Figure 2 shows the change in persistence between the mutualistic model and the competition-only model, as a function of the nestedness and relative nestedness of the mutualistic network. All points lie on or below the horizontal axis, showing that mutualism is detrimental to persistence under this model. This decrease in persistence is driven by mutualisms increasing the abundance of a benefitting species, which then excludes other species by competition. Importantly, there is no significant correlation between change in persistence and either nestedness ($P = 0.999$, $r^2 < 0.001$) or relative nestedness ($P = 0.472$, $r^2 = 0.009$).

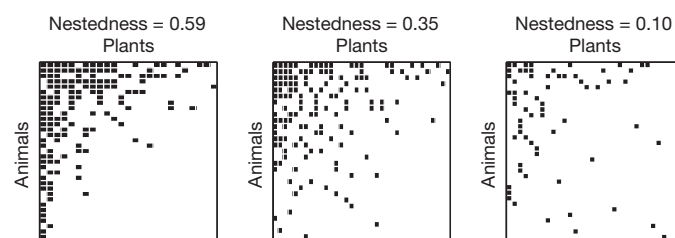
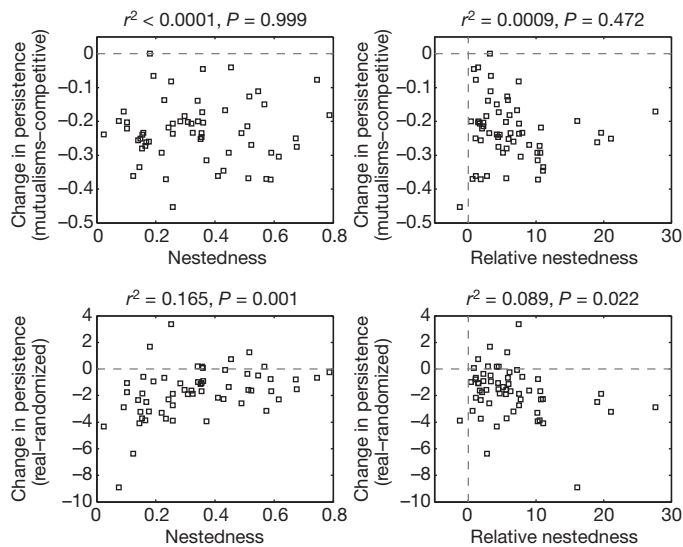


Figure 1 | Real networks exhibit a wide range of nestedness and connectance. Three example plant–pollinator networks from the 59 studied. In each of the three networks shown, each row represents an animal species and each column represents a plant species, and mutualistic interactions between a plant and animal species are represented by black squares. In each network, species have been ranked by specialization (that is, the number of mutualistic partners). In a perfectly nested network, the upper-left triangle would be full of interactions and the lower-right triangle would have no interactions. Left panel, community with high nestedness: specialist animal species (bottom rows) tend to interact with generalist plant species (left-hand columns); specialist plant species (right-hand columns) tend to interact with generalist animal species (top rows). Middle panel, community with intermediate nestedness. Right panel, community with low nestedness: specialist animal species (bottom rows) are almost as likely to interact with specialist plant species (right-hand columns) as with generalist plant species (left-hand columns). In most cases, networks with high nestedness also have high connectance (that is, a high density of black squares).

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To test how changes in network architecture affect community persistence, the mutualistic networks were then randomized (connectance and network magnitude held constant, Supplementary Information) and the resulting changes in persistence were calculated (Fig. 2). In the vast majority of networks, randomizing the interactions decreases nestedness but increases persistence. In other words, although the real networks are more nested than their randomized counterparts, this does not increase community persistence.

Figure 2 | Adding mutualistic interactions to models of real networks decreases persistence and this decrease is not related to nestedness. The change in persistence in mutualistic models for 59 empirical plant–pollinator networks is shown relative to persistence in the equivalent competition-only model (top panels). In all networks, introducing mutualisms decreases persistence. There is no significant correlation between change in persistence and nestedness ($P = 0.999$, $r^2 < 0.001$), and there is no significant correlation between change in persistence and relative nestedness ($P = 0.472$, $r^2 = 0.009$). The persistence of mutualistic models on the 59 empirical networks is shown relative to persistence on a randomized network (real network persistence minus randomized network persistence; bottom panels). In the majority of cases, the real network has a higher nestedness but a lower persistence than its randomized counterpart. There is a weakly significant positive correlation between change in persistence and nestedness ($P = 0.049$) but the correlation is extremely weak ($r^2 = 0.066$). When the same persistence change is compared to relative nestedness, there is no significant correlation ($P = 0.767$, $r^2 = 0.002$).

The claim that nestedness reduces effective interspecific competition and enhances the number of coexisting species³ does not apply to real networks (Fig. 2). The supposed link between nestedness and biodiversity is based on a theoretical value for the maximum number of species that can coexist in a mutualistic network¹⁰, rather than how many species will actually exist under a given model. A detailed exploration reveals that the paradigm that nestedness enhances biodiversity in mutualistic networks is incorrect for two reasons (Supplementary Information). First, the theoretical maximum is between 5 and 1,000 times larger than the actual number of surviving species (Supplementary Table 2) and this upper bound is unrepresentative of the actual number of surviving species (Figs 2 and 3). Second, the

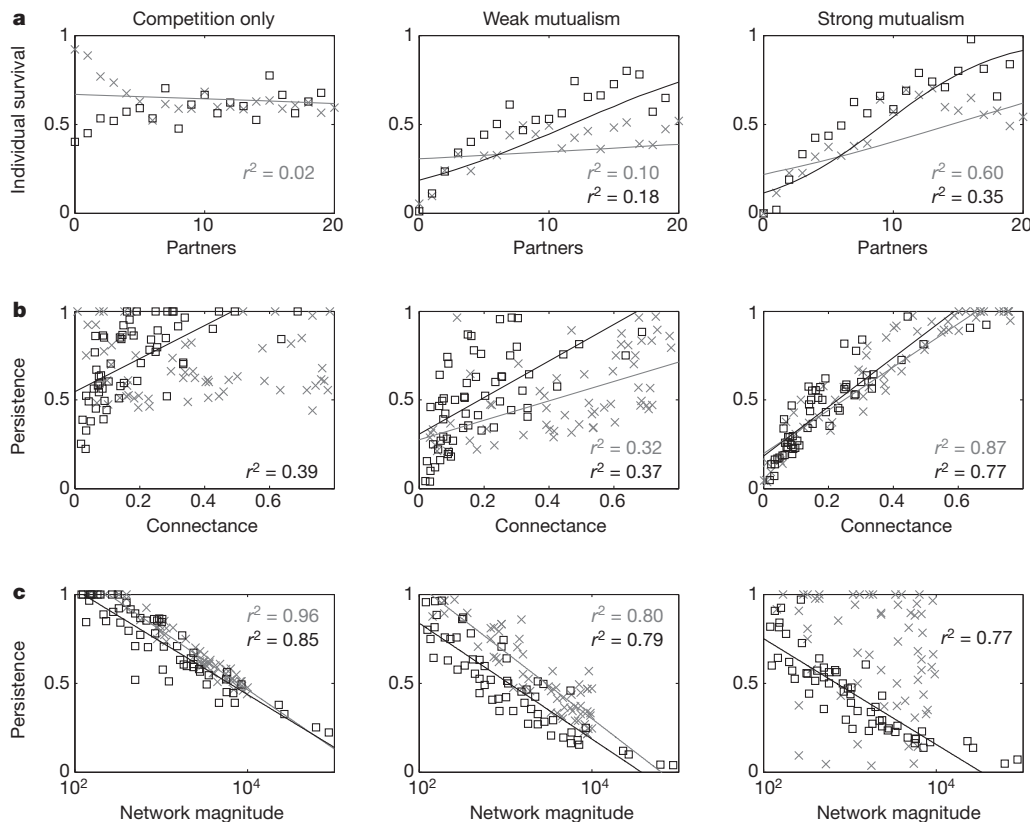


Figure 3 | The number of mutualistic partners is a robust and consistent metric of species viability in mutualistic networks. **a**, Individual species survival is highly correlated with the number of mutualistic partners. This correlation increases as the strength of the mutualistic interactions increases, but the effect is small for weak mutualisms in random networks. **b**, Community persistence is most strongly correlated with network connectance. Again this effect increases with mutualism strength. **c**, In competition-only models, network magnitude (the number of plants multiplied by the number of

animals) predicts community persistence; when mutualistic interactions are introduced, this relationship breaks down in random networks but not in empirical networks owing to the correlation between network magnitude and connectance (Supplementary Fig. 1). Black squares, empirical networks; grey crosses, randomly generated networks. Where a regression is significant ($P < 0.01$) the fitted relationship is shown and the value of r^2 is given; regressions are logistic in **a** and linear in **b** and **c** (see Methods Summary).

analytical theory only applies in a highly restricted parameter range that is very different from that used in subsequent results^{3,5}.

The roles of network properties on empirical and randomly generated networks are shown in Fig. 3. In the competition-only model, mutualistic interactions are switched off and so persistence cannot have a causal dependence on either the connectance or the nestedness of the mutualistic network (Fig. 3). The only possible factor influencing persistence is network magnitude, and this exhibits a strong, negative effect. However, because nestedness is negatively correlated with network magnitude in the empirical networks (Supplementary Fig. 1), there is a statistically significant but misleading relationship between nestedness and persistence. When mutualistic interactions are switched on (Fig. 3), the number of mutualistic links becomes the key predictor: the survival of an individual species is strongly correlated with its number of mutualistic partners. Network connectance is a basic community-level measure of the number of mutualistic partners and is strongly linked with community persistence. Nestedness is highly correlated with connectance in the empirical and random networks (Supplementary Figs 1 and 2), but when this correlation is removed there is no relationship between persistence and nestedness (Supplementary Information).

Together, these results show that any apparent relationship between nestedness and community persistence is a consequence of the correlation of nestedness with simpler properties, such as network magnitude and connectance. This finding can be tested under an obligate mutualism model⁴ (Supplementary Information section 4). The results of this model for randomly generated networks seem paradoxical in the sense that nestedness is weakly negatively correlated with persistence but, after extinctions are accounted for, the network of surviving species is more nested than the original network⁴. However, the result that networks of surviving species are more nested than the original random networks can be explained by a simple mechanism: within the stated range of parameters, unconnected species (those with no mutualistic partners) and isolated pairs of species almost always go extinct in this model. Removing these species from the initial network provides a direct prediction of persistence (which is correct in over 75% of cases (Supplementary Fig. 3)). This removal of species with no links necessarily increases the network's connectance and, as connectance and nestedness are very highly correlated in random bipartite networks², this increases nestedness. Again, the key predictor for survival is the number of mutualistic partners that a species has.

The relationship between stability and complexity in networks is of enduring importance and our demonstration that mutualism can destabilize ecological networks agrees with earlier qualitative arguments¹¹. A recent study also shows that a nested architecture is detrimental to network stability in a different model of mutualistic networks without competition¹². As nestedness does not improve persistence in simple community models, the question of why real ecological networks often have a highly nested architecture remains unanswered. Many alternative theories have been proposed, including biophysical and ecological mechanisms¹³, evolutionary causes¹⁴ and behavioural switches¹⁵.

Our analysis of models of mutualism shows that simple measures (the number of mutualistic partners at the individual species-level and connectance at the community level) are better predictors of persistence than the more complex measure of nestedness. This applies equally to survival probabilities for individual species and community-level persistence. Occam's razor (the precept that, faced with competing explanations for some phenomenon, the simplest explanation should be chosen unless there are compelling reasons to do otherwise) therefore favours connectance as the most important driver of system-level behaviour. Our results for mutualistic networks complement a recent food-web analysis¹⁶ by adding nestedness to 18 empirical network properties that were found to be best predicted overall by connectance and species richness. It is notable that a simple maximum entropy distribution can provide a suitable null model to explain the distribution of connections

in both food webs¹⁷ and mutualism networks¹⁸. These simple explanations^{16–18} do not rely on differential equations and, together with the results presented here, suggest that the emphasis for future research should be shifted towards better understanding ecological complexity in terms of degree distributions and connectance rather than nestedness.

METHODS SUMMARY

Data sets. Empirical mutualistic network data were taken from previous work⁹. Network magnitude is defined as the number of plant species multiplied by the number of animal species. Connectance is the total number of links in the network divided by network magnitude.

Randomly generated networks. Random networks with the same number of species in each class (plants and animals) were generated using a method described previously⁴.

Nestedness measure. We use the NODF nestedness measure² and tested our calculations using the associated software (<http://www.home.umk.pl/~ulrichw/?Research:Software:NODF>). Relative nestedness is the *z* score relative to the nestedness of randomized versions of the network^{3,7} (Supplementary Information).

Dynamic models. The dynamic model for facultative mutualisms and the dynamic model for obligate mutualism are taken from previous work^{3,4}. We numerically integrated the equations using an adaptive step-size Runge–Kutta method (Matlab, ode45) to find an approximate steady-state solution, and then used this as the initial condition for a root-finding method (Matlab, fsolve). We tested for linear stability of the steady state by checking that the eigenvalues of the Jacobian matrix of the dynamical system at steady state all had negative real part¹⁹. The root-finding algorithm is computationally efficient and improves the numerical accuracy of our equilibrium results, but does not affect calculations of community persistence.

Statistical methods. Owing to strong multicollinearity between the potential predictors of community persistence (that is, nestedness, relative nestedness, network magnitude and connectance) (Supplementary Information), multiple regression analysis was inappropriate for both types of network. Hence, single-variable regression was used and goodness-of-fit was compared using the coefficient of determination (r^2) (ref. 20). By altering the strength of mutualisms, the different factors affecting community-level outcomes can be isolated. For binary response variables (Fig 3), logistic regression was used and McFadden r^2 values²¹ were calculated.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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