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On nestedness in ecological networks

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ABSTRACT

Questions: Are interaction patterns in species interaction networks different from what one expects by chance alone? In particular, are these networks nested – a pattern where resources taken by more specialized consumers form a proper subset of those taken by more generalized consumers?

Organisms: Fifty-nine and 42 networks of mutualistic and host–parasitoid interactions, respectively.

Analytical methods: For each network, the observed degree of nestedness is compared with the distribution of nestedness values derived from a collection of 1000 random networks. Those networks with nestedness values lower than 95% of all random values are considered 'unusually nested'. The analysis considers two different metrics of nestedness and five different network randomization algorithms, each of which differs in the ecological assumptions imposed.

Results: Most ecological networks are unusually nested when compared with loosely constrained random networks. Comparisons with highly constrained networks temper these findings, but we still report a significant preponderance of nested networks (typically those with the most species).

Conclusions: Bascompte *et al.* (2003) previously showed most observed mutualistic networks to be unusually nested. Later work using more ecologically realistic randomization algorithms cast doubt on those results. Across the largest set of species interactions considered to date, we conclude that an unexpectedly large number of interaction networks are patterned in a non-random manner.

Keywords: ecological network, food web, host–parasitoid, mutualism, nestedness, null model.

INTRODUCTION

Inspired by physical analogies, Atmar introduced the idea of *nestedness* to describe the incidence matrix of the presence of different species on different islands. A nested pattern is where the species composition on islands with fewer species is a proper subset of those on

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islands with more species. Atmar provided the computational tools to calculate nestedness – which he called 'temperature' – and, with Patterson, analysed a variety of biogeographic patterns and their likely causes (Patterson and Atmar, 1986; Atmar and Patterson, 1993, 1995; Wright *et al.*, 1997). The study of nestedness in ecology has inspired a significant volume of literature, and the original 'temperature' metric has been joined by many others (Rodriguez-Girones and Santamaria, 2006; Almeida-Neto *et al.*, 2008). Ulrich *et al.* (2009) provide a recent and comprehensive overview of the topic.

Although nestedness is most familiar in biogeography, its extension to food webs is obvious. Food webs depict in similar binary form consumer species and the resource species on which they feed. Bascompte *et al.* (2003) applied the idea of nestedness to food webs and analysed mutalistic networks – food webs that depict generally mutualistic interactions between, for example, flowers and the species that pollinate them. Bascompte *et al.* (2003) concluded that most networks were 'highly nested'. Several other more recent studies have concluded the exact opposite (Ulrich and Gotelli, 2007; Almeida-Neto *et al.*, 2008). Here, we re-visit these conclusions, incorporating additional data and comparing the observed matrices with more tightly constrained null models.

Once one has settled upon the appropriate measure of nestedness, the key question in claiming that observed patterns are nested is: 'compared to what?' Bascompte *et al.* (2003) compared the 'temperature' of the observed interaction network with a distribution of null models, created using an algorithm that assigned an interaction between each consumer–resource pair proportional to the generalization of both the consumer and resource species. The chance that a given consumer will feed on a given resource increases as the product of the number of species on which the consumer feeds and the number of consumers that consume the given resource. Other studies using similar algorithms have examined a variety of other networks (Dupont *et al.*, 2003; Ollerton *et al.*, 2003; Guimarães *et al.*, 2007a, 2007b).

It has long been argued in biogeography that many null models have unacceptably loose constraints (Sanderson *et al.*, 1998). There are well-understood constraints on how many species occur on islands – generally larger islands have more species than smaller ones. And there are constraints on which species islands receive – some species can disperse far more than others. When one creates null models of incidence matrices that retain the exact totals of species on islands and islands with species, nested patterns are no longer unusually common (Brualdi and Sanderson, 1999). In studies of island biogeography, the reasons to constrain the incidence matrix are unassailable and no longer contested (Sanderson, 2000).

Parallel arguments apply to ecological networks. Consumer species differ in how many species they exploit. The reasons why some species exploit many resources while others are more specialized are many and varied (Montoya *et al.*, 2006). Similarly, consumer species vary in the number of species that exploit them and do so for many reasons. Any null model that does not constrain column totals creates a distribution of specialist versus generalist species that does not match nature. Under null models previously used for studying nestedness (see Methods), by chance alone, the most generalized consumers may have fewer resources than observed and the most specialized consumers more resources than observed. Comparable statements apply to row totals. Excluding unrealistic null models is essential if one is to make crisply defined statements about ecological patterns.

Recently, several studies have used fixed row and fixed column constrained null models to show that nestedness in several sets of ecological networks is statistically rare (Ulrich and Gotelli, 2007; Almeida-Neto *et al.*, 2008; Dormann *et al.*, 2009; Ulrich *et al.*, 2009), contradicting the early results of Bascompte *et al.* (2003).

Here, we build upon the 2003 analysis of Bascompte *et al.*, with several modifications. First, we employ the strict null model, fixing the row and column totals, and compare our results to more loosely constrained ones. Second, we calculate nestedness using 'temperature' (as originally done by Bascompte *et al.*) and compare those results with a more recent metric, NODF (Almeida-Neto *et al.*, 2008), that claims 'better statistical properties' than 'temperature'. Finally, for comparison, we extend the analysis to include antagonistic networks of parasitoids and their hosts.

We find fixed row and fixed column constraints are sufficient to explain the patterns of nestedness in most observed mutualistic and antagonistic networks. Nonetheless, we find significantly more webs than expected that are both more nested and less nested than one expects by chance alone.

METHODS

We examine 101 networks that consist of mutualists and their resources ($n = 59$) and parasitoids and their hosts ($n = 41$). [Further details on the networks analysed can be found in Joppa *et al.* (2009).] All of those are binary matrices – showing whether a given consumer exploits a given resource, but not how extensively. We return to this distinction in the Discussion.

Without prejudice, we employ two measures of nestedness. The first is the older and more familiar measure, Atmar and Patterson's 'temperature' (Atmar and Patterson, 1995). By analogy to electrons in the orbits around an atomic nucleus, they argued the 'hotter' a matrix, the further away it is from being as nested as possible. The second measure termed 'NODF' is more recent (Almeida-Neto *et al.*, 2008). It accounts for paired overlap and decreasing fill of the matrix and claims to reduce type I statistical errors compared with 'temperature', and claims to more correctly estimate the degree of nestedness. Although 'temperature' and 'NODF' both scale from 0 to 100, 0 represents maximum nestedness using 'temperature' while 100 represents maximum nestedness using 'NODF'. To make these two metrics comparable, we re-scale the NODF results as 100 – NODF.

We used the software package ANINHADO (Guimarães and Guimarães, 2006) to calculate both measures. Our first null model (FRFC) fixes both the number of resources taken per consumer and the number of consumers that exploit each resource (i.e. fixes the marginal totals of the matrix). [Further details of the FRFC model can be found elsewhere (Joppa *et al.*, 2009).] For completeness, we also used ANINHADO to generate four additional null models that are constrained in different ways. The partially constrained models fix either the resource totals (Fixed Rows, FR) or the column totals (FC), but not the other. In the model PRC (Probable Rows and Columns), the probability that any cell a_{ij} shows a presence is: $(P_i/C + P_j/R)/2$, where P_i is the number of presences in row i, P_j is the number of presences in column j, C is the number of columns, and R is the number of rows. Bascompte *et al.* (2003) used PRC. Finally, the most loosely constrained model, P, selects each cell, with probability equal to the overall total number of presences divided by the maximum number possible ($= R^*C$).

All these models have a history of use, but all have looser constraints than the model with both row and column constraints. The FRFC model fixes both the totals of resource species (rows) and consumer species (columns) and is the most constrained model that we use here. We discuss the means to do this elsewhere (Joppa *et al.*, 2009).

RESULTS

Against loosely constrained models, ecological networks are indeed nested (Fig. 1), as has been demonstrated previously (Bascompte *et al.*, 2003). The result holds for both measures of nestedness, even though the two are not closely correlated in the data we examine. For four loosely constrained null models (P, PRC, FR, and FC), the observed values are substantially more nested than the median values derived from 1000 null networks. In striking contrast, compared with conservative nulls that constrain the numbers of resources each consumer exploits and the numbers of consumers that each resource suffers (FRFC), the observed networks are very much closer to what one expects by chance (Ulrich *et al.*, 2009).

Figure 1 colour-codes each network according to whether the observed network falls within the top 5% or bottom 5% of the 1000 random nulls. We deem these networks to be 'unusual' with regard to their nestedness patterns. Our choice of language here is deliberate. Were we examining just a single web and were the observed web to fall in the tails of the distribution, we might deem it 'significantly' more or less nested. By chance, however, within a set of 59 mutualistic networks and 42 parasitoid networks one would expect approximately six and four networks respectively to be in the two tails of the distribution. The choice of what constitutes 'unusual' is arbitrary, of course, but we find different criteria do not qualitatively alter our results. Within the set of unusual networks, we follow Atmar and Patterson's (1993) original terminology in referring to those more nested than expected as 'cold' and those less nested than expected as 'hot'. By chance, one would expect equal numbers of unusual hot and cold webs.

Table 1 tabulates the results. That so many networks are unusually cold compared with loosely constrained models recapitulates earlier results. The comparison to the tightly constrained model is novel across the range of mutualistic and antagonistic webs we analyse. Table 1 shows that 22 and 16 of the mutualistic networks show unusual nestedness patterns with the temperature metric and NODF metric respectively. Both numbers are very much higher than expected by chance (binomial test, $P < 0.001$).

For mutualistic networks, there is a large discrepancy between the numbers of unusually hot and cold examples under the 'temperature' metric. Far more networks than expected are unusually cold ($P < 0.001$), while the number of significantly hot networks is no different than expected ($P > 0.05$). This is also true when using NODF.

Our results for antagonistic networks are similar to those for mutualistic ones. Again, we find most examples to be no more nested and no less nested than expected by chance. Nevertheless, under both the temperature and NODF metrics we find an unexpected number of unusual networks. For the temperature metric, we find 10 unusual networks and, of those, only significantly nested networks occur more often than expected ($P < 0.01$). When using NODF, we find a statistical excess of both hot ($P < 0.01$) and cold ($P < 0.05$) antagonistic networks.

Figure 2 shows that for both metrics but for temperature in particular, unusually cold (i.e. nested) networks tend to be the largest networks. Hot networks tend to be smaller, although for NODF the largest network is unusually hot. *Network size* is the product of the number of species of consumer times the number of species of resources. Given network size, neither the connectance (the number of trophic interactions divided by the size) nor the ratio of consumers to resources determines where usually hot or cold networks lie.

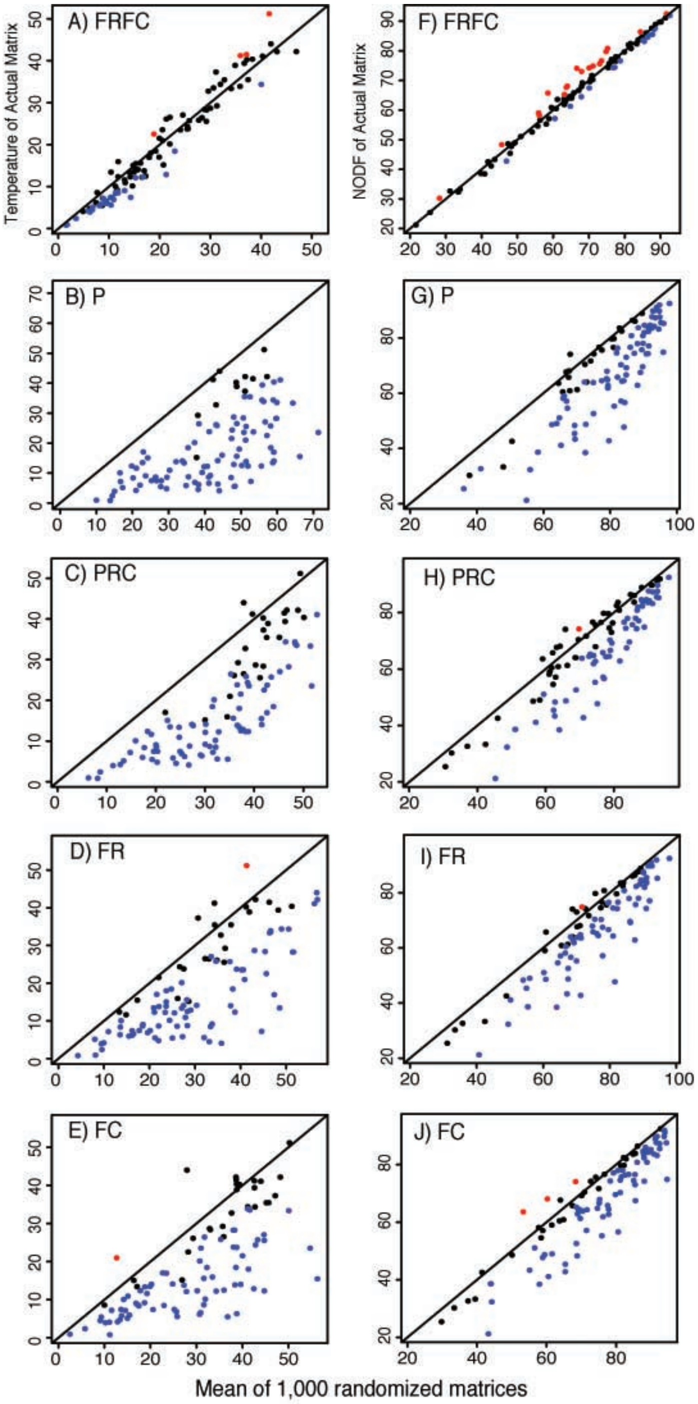

Fig. 1. A comparison of five null models and two measures of nestedness. (Left) Relationship between the observed 'temperature' of a matrix and the mean 'temperature' of 1000 null matrices under five different null models. (Right) Same as above, but for a different measure of matrix nestedness, 'NODF'. We have re-scaled NODF from its original form, so that maximum nestedness using either 'temperature' or 'NODF' is 0. 'FRFC' is the row and column constrained null model we employ in our analysis, but see the Methods section for details on each of the five null models. Blue: observed value is within the bottom 5% of 1000 nulls ('cold'), red in the top 5% of 1000 nulls ('hot').

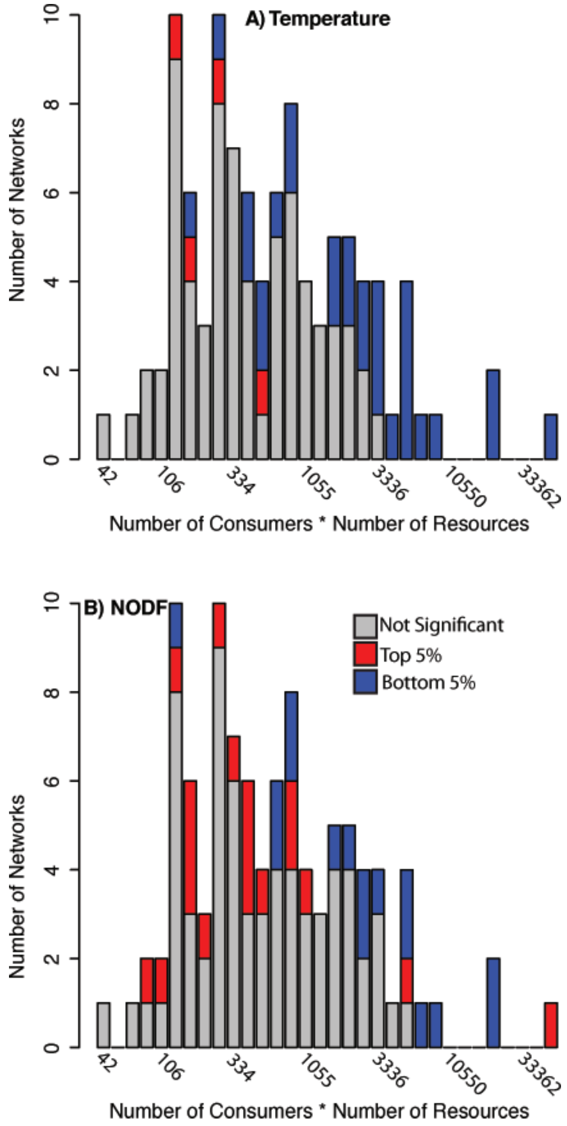

Fig. 2. Relationship between the two measures of nestedness and the size of the network (number of consumers * number of resources). Mutualistic and antagonistic network are combined. Blue: observed value is within the bottom 5% of 1000 nulls ('cold'), red in the top 5% of 1000 nulls ('hot'); grey: observed value is within the 5–95% range of the 1000 nulls ('insignificant').

DISCUSSION

Our key result is that when constrained by the observed numbers of species that a given consumer consumes and the number of species that exploit a given resource, the striking pattern of all networks being unusually nested is tempered. Only about one-third of mutualistic networks are now unusually nested, as measured by temperature, although

Table 1. Summary results for comparisons of nestedness in mutualistic and antagonistic networks with five different null models (FRFC, P, PRC, FR, FC)

	FRFC	P	PRC	FR	FC
Mutualistic					
Temperature					
Non-significant	37	3	9	9	10
Bottom 5%	20**	56	50	50	48
Top 5%	2	0	0	0	1
NODF					
Non-significant	43	8	16	11	13
Bottom 5%	10**	51	42	47	46
Top 5%	6	0	1	1	0
Antagonistic					
Temperature					
Non-significant	32	9	15	15	17
Bottom 5%	8**	33	27	26	25
Top 5%	2	0	0	1	0
NODF					
Non-significant	24	17	27	18	16
Bottom 5%	6*	25	15	24	23
Top 5%	12**	0	0	0	3

Note: Details of the models can be found in the Methods. $*P < 0.05$, $**P < 0.01$.

one-sixth if one uses the alternative measure. The comparable numbers for antagonistic networks are also low, with less than one-fifth of networks unusually nested under either temperature or NODF. Nonetheless, for both ‘temperature’ and NODF, our results show that unusual nestedness patterns are more common than would be expected by chance alone. Within those unusual networks, we find a bias towards unusually cold – or nested – networks in all cases except antagonistic networks under the NODF metric. There, we find an excess of both hot and cold examples. How does this result compare with other studies?

Binary versus quantitative networks

Rather than simple presence (1)/absence (0) information, quantitative network data include information such as the number or frequency of visits of a pollinator to a flower, allowing inference to be drawn as to the importance of that interaction to both species involved. As with binary data, there are considerable concerns with quantitative data, especially regarding the effects of sampling effort and the interpretation of the importance of a visit (Wootton and Emmerson, 2005).

Bluthgen *et al.* (2008) used information on marginal totals from a sample of 51 observed mutualistic networks and created large samples of simulated null models for each. The nestedness values of these null models were then compared with the observed models using Patefield’s algorithm (Patefield, 1981). It creates randomized incidence matrices with the same fixed marginal totals as the observed network. The authors found that their simulated networks were significantly nested. The results of Bluthgen *et al.* (2008) are certainly interesting, and their study encompassed much more than an analysis of nestedness. When considering how their results complement previous nestedness studies, there are several difficulties with their approach. First, while Patefield's (1981) algorithm does maintain marginal totals of the original matrix, it does not maintain the original connectance (the number of actual interactions between species divided by the maximum possible, i.e. the matrix size). This algorithm creates null models where the consumers are very much more generalized in their diets than they are in nature. So the results of such investigations are confounded by different degrees of trophic generalization.

Binary networks under different null models

Using loosely constrained models, mutualistic (Ollerton *et al.*, 2003, 2007), host–parasite (Valtonen *et al.*, 2002), plant–herbivore (Lewinsohn *et al.*, 2006), plant–epiphyte, and tree–fungus (Vacher *et al.*, 2008) are just a few examples of systems that have shown nested patterns. As our results show, loose constraints invariably lead to the conclusion of significant nestedness. The null models in these studies create consumers that differ in how generalized their diets are and this confounds the conclusion. (Once again, the parallel statement applies to the number of consumers that exploit a given resource.)

Recent studies on the nestedness of ecological networks have begun to incorporate the 'fixed rows, fixed columns' constraint. Much of this work has relied upon the data set of ecological networks that are provided as part of Atmar and Patterson's (1995) software program 'The Nestedness Temperature Calculator'. An example of these studies is Ulrich and Gotelli's (2007) analysis, which provides a comprehensive treatment of different nestedness metrics and null models to test them against. Similar to what one can see in our Fig. 1, Ulrich and Gotelli showed that the use of a fixed–fixed null model often reduces the difference between the observed value and the expected value obtained from a distribution of null matrices. Using the same loosely constrained PRC model we describe in our Methods, Ulrich and Gotelli (2007) found 75% of the networks to be significantly nested using a modified version of 'temperature'. That is in sharp contrast to the mere 7% significantly nested under their version of the 'fixed rows, fixed columns' model (described in Gotelli, 2000). When introducing the new nestedness metric 'NODF', Almeida-Neto *et al.* (2008) showed that while 83% of those same networks were considered nested under our PRC model, only 1% were considered nested using a 'fixed rows, fixed columns' null model. In another recent study, Dormann *et al.* (2009) analysed 19 ecological networks using a 'fixed rows, fixed columns' null model and a nestedness metric we do not implement here [BINMATNEST (Rodriguez-Girones and Santamaria, 2006)]. While the number of networks considered significantly nested was not reported, figures for each network's 95% confidence interval show nearly all of the 19 networks were not significantly nested (see Figure 8 in Dormann *et al.* (2009).

In short, all previous studies using the 'fixed rows, fixed columns' model found that few networks are nested. Our analysis tempers this conclusion.

Are ecological networks unusually nested?

Table 1 rejects any simplistic answer as to the role of nestedness in mutualistic and antagonistic networks. When using loosely constrained null models, we find strong evidence for nestedness to be a common pattern across networks, whether using 'temperature' or NODF as our metric of measurement. Networks with the opposite pattern of nestedness – or 'hot' networks – are rare.

This is in sharp contrast to our results when using a highly conservative null model. There, most networks are not significantly different than one would expect. However, of the networks that *are* unusually patterned, we obtain different results with different metrics. Using 'temperature' we find a significant excess of unusually nested networks, but no more unusually 'hot' examples than one would expect by chance alone. The same holds true for mutualistic networks under the metric NODF, but not for antagonistic ones. There, both hot and cold networks appear more often than expected by chance, but with no measurable difference between the two categories.

Whenever employing a null model approach, one must consider the potential influence of how that model deals with Type I and II errors. We believe our results gain more traction when one considers the relationship between the 'fixed rows, fixed columns' model and Type I and II errors. Others have shown convincingly that a variant of our 'fixed rows, fixed columns' model has a strong ability to reduce Type I errors (i.e. does not erroneously detect nestedness), and a greatly increased tendency to Type II errors (i.e. fails to detect nestedness) (Ulrich and Gotelli, 2007). That we find a statistically significant excess of networks with unusual nestedness patterns within our data set, using the conservative null model, further warrants our conclusions that these patterns are more common in ecological networks than recent studies have claimed (Ulrich and Gotelli, 2007; Almeida-Neto *et al.*, 2008; Bluthgen *et al.*, 2008; Dormann *et al.*, 2009).

It is true that row and column constraints are sufficient to explain the observed patterns in the majority of mutualistic and parasitic networks, but a null model is not a mechanistic one. A sensible question is thus, 'what mechanisms generate nested patterns?'

In examining biogeographic patterns, Colwell and Winkler (1984) argued that in addition to island size and dispersal ability – the factors that likely shape the row and column totals – which species occur where may well depend on where other, competitor species occur. Any patterns of species not co-occurring together – so-called 'checkerboards' – might be hard to detect in data where competition already shaped how many species were present on any given island.

The comparable considerations apply here. The degree of trophic generalization of a consumer likely depends, in part, on the other consumers present. Thus, for example, many consumer species might be more generalized than they appear – even if they would not be equally generalized! – in the absence of the other species. Statistically, the problem is one of creating practical null hypotheses. Ecologically, one admits the possibility that some unknown fraction of otherwise undistinguished networks might be more nested that expected given the possible (but unknown) range of resource species each consumer might exploit.

In summary, there is an ecological pattern – nestedness – that when using one measure appears to be unusually common, even when compared with null models that are highly constrained to resemble the observed networks on which they are based. Unusually non-nested networks are generally rare. That we also find an excess of significantly non-nested networks when using NODF as a measurement is a point we return to below.

How can we explain nestedness patterns?

The first approach is to look at processes that generate nestedness directly. For example, Bastolla *et al.* (2009) show that the process by which a new species enters a community will likely lead to a nested pattern of interactions. This is a direct result of the new species trying to minimize its competitive load, an action that forces it to interact with the most generalist species.

An alternative approach is to look to other mechanisms that would generate patterns that secondarily would lead to nestedness – or the lack of it. In particular, we should be alert to mechanisms that involve particular interactions between species. We worry about the underlying difficulty with aggregated metrics, of which nestedness is an example, and the number of checkerboards is another example from biogeographic studies. Such metrics miss the detail of examining species-specific interactions, lumping as they do all the species' patterns into a single index. The alternative in biogeographic studies is to examine *which* species form checkerboards (Sanderson *et al.*, 2009), a process that leads to more focused predictions.

In network studies, one particular process that would create unusually non-nested patterns is reciprocal specialization. It occurs when, say, a pollinator (or group of pollinators) specializes on a particular flower species (or group of such species) and vice versa. Perhaps the most famous example is the Malagasy orchid and the moth Darwin predicted would pollinate it. The underlying cause here is usually considered to be co-evolution. We (Joppa *et al.*, 2009), and others (Vazquez and Aizen, 2003, 2004; Bascompte *et al.*, 2006), show elsewhere that reciprocal specialization is statistically very rare in the networks examined here.

Finally, we find that typically only large networks – those where the number of consumers times the numbers of resources exceeds 400 – are unusually nested (Fig. 2). We have no definitive explanation for this result. A possible explanation is that large networks are usually more heterogeneous in their link distributions than smaller ones – they have more specialized consumers and at the same time more generalized consumers (Montoya and Solé, 2003; Montoya *et al.*, 2006). The parallel statement applies for resources. Given that reciprocal specializations are rare in these networks (Joppa *et al.*, 2009), the most generalized consumers will tend to interact with resources used by fewer consumers, and vice versa, giving rise to unusually nested large networks.

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