

LETTER

Reciprocal specialization in ecological networks

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Abstract

Theories suggest that food webs might consist of groups of species forming ‘blocks’, ‘compartments’ or ‘guilds’. We consider ecological networks – subsets of complete food webs – involving species at adjacent trophic levels. Reciprocal specializations occur when (say) a pollinator (or group of pollinators) specializes on a particular flower species (or group of such species) and vice versa. Such specializations tend to group species into guilds. We characterize the level of reciprocal specialization for both antagonistic interactions – particularly parasitoids and their hosts – and mutualistic ones – such as insects and the flowers that they pollinate. We also examine whether trophic patterns might be ‘palimpsests’ – that is, there might be reciprocal specialization within taxonomically related species within a network, but these might be obscured when these relationships are combined. Reciprocal specializations are rare in all these systems when tested against the most conservative null model.

Keywords

Ecological network, food web, host-parasitoid, mutualism, nestedness, null model, specialization, trophic level.

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INTRODUCTION

From the outset, discussions of food web structure recognized the possibility of groupings of species interactions, variously called ‘guilds’, ‘compartments’ or ‘clusters’. If trophic interactions are grouped, there are important implications for how disturbances, particularly the loss of species, propagate through communities (Pimm 1980, 1991; Jordán *et al.* 1999, 2006; Montoya *et al.* 2006).

The evidence for such ‘blocks’ – as May (1972) first called these groupings – is complex. Certainly, there are relatively fewer trophic interactions across habitat boundaries than within habitats (Pimm & Lawton 1980). Whether compartments or clusters exist within broadly similar habitats is less clear, with evidence both for and against (May 1973; May & McLean 2007; Montoya *et al.*

2006). These studies of compartments and clusters required the feeding relationships for species at three or more trophic levels (Montoya *et al.* 2006). For example, some methods used two trophic levels to define possible compartments and then the third to confirm them (Pimm & Lawton 1980).

Here, we consider the evidence for how trophic relationships might group species’ interactions at only two adjacent trophic levels – just consumers and their resources. For simplicity, we call any interaction set an ‘ecological network’. The notion that feeding relationships at adjacent trophic levels group is familiar (May & McLean 2007). ‘Guilds’ are species that exploit similar resources, implying that species outside the guild use distinct resources and perhaps belong to a different guild. Another perspective on reciprocal specializations is Ehrlich & Raven’s (1964)

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influential idea of ‘coevolution’ – the observation that taxonomically related insects might exploit taxonomically related groups of plants. Other examples of reciprocal patterns include hummingbirds (and other nectar-feeding birds) and the flowers that they exploit (Temeles & Kress 2003), and most famously, the Malagasy orchid and the moth Darwin predicted would pollinate it (Darwin 1862).

We define strict one-to-one reciprocal interactions as when a consumer exploits only a single resource and that resource has no other consumer. We ask: are such specializations more common than expected? We also count ‘close’ reciprocal patterns whereby a small set of species – ‘a guild’ – might exploit one or a small set of resources, and those resources would have no other exploiters (see Materials and methods for a definition of ‘close’ reciprocal patterns). Our analyses include both antagonistic interactions – particularly parasitoids and their hosts – and mutualistic ones – such as insects and the flowers that they pollinate. We also examine whether trophic patterns might be ‘palimpsests’ – that is, there might be reciprocal specialization within taxonomically related species within a network but these patterns might be obscured when these relationships are combined.

While stating our question is simple, testing it is not. The difficulty lies in the words ‘than expected’. We present two tests that differ in the expectations they assume. The first test involves broad comparisons of feeding relationships. It notices that there are two general visualizations – essentially caricatures – that aid thinking about the relationships between resources and consumers. One visualization that underpins much ecological thinking imagines an extreme pattern that facilitates reciprocal specialization. The other visualization apparently precludes reciprocal specialization. In our first test, we present evidence to show that existing data suggest this visualization predominates in nature.

However, this first test involves relatively crude assumptions about feeding relationships. Our second test is a considerably more subtle and quantitative one that takes into account the many factors that determine whether a species is specialized or generalized in its diet.

Test 1: broad patterns of niche overlaps

In our experience, ecologists often assume a ‘string of beads’ model (Pimm 1991) for niche overlaps [see, for example, figure 10.3 in Townsend *et al.*'s (2003)]. In this model, each consumer tends to exploit a unique core of resources, overlapping with other consumers only in its use of less important resources. Not only does each consumer have a unique core of resource species, reciprocally, a unique set of consumer species threatens each resource species. One can imagine those overlaps as being along some ‘dimension’. Body size is one possible example: with largest bodied consumers

taking the largest resources, smaller species taking smaller resources, and so on, but it could also be something more abstract (Cohen *et al.* 1993; Cohen *et al.* 2003). Such a model underlies May's (1986) work on the limits to niche overlaps. Ecological theory and analysis that accept that two or more species differ in the resources they prefer – for example, Rosenzweig (1981) – encompass this ‘string of beads’ model.

Despite the popularity of the ‘string of beads’ model it is likely *not* the description that most commonly applies to niche overlaps in nature. Increasing evidence supports a very different ‘flower petal’ model (Pimm 1991) of niche overlaps (Bascompte *et al.* 2003; Vázquez & Aizen 2004; Bluthgen *et al.* 2007; Thébault & Fontaine 2008; Ings *et al.* 2009) as being the most common pattern in nature. Consumers exploit a shared, rather than distinct, core of resource species (the ‘base of the flower’), even as they exploit a few idiosyncratic resources (the petal tips). This model underpins ecological theory and analysis that assumes two or more species are likely to have the same preferences for the prey that they exploit (Pimm & Rosenzweig 1981). Previous studies document this pattern by showing that trophic interactions are *nested* (Bascompte *et al.* 2003). Nestedness measures the tendency for consumer A to feed on resources that are mostly a subset of those B feeds on, B to feed on mostly a subset of C's resources, and so on.

Figure 1 shows these two broad models. Figure 1 shows six representations of networks, and Fig. 1a is the observed one. All six networks have the same number of birds (15, top row), fruits (21, bottom row) and trophic interactions (51). In all but Fig. 1b, the number of fruits each bird species exploits and the number of birds that consume each fruit species are the same; in Fig. 1b, they are different.

In Fig. 1a (the observed network), fruit #1 is exploited by 11 of 15 bird species, and species #2 by seven of them. Relatively specialized consumers – those which exploit only one or two species (bird species nos, 8, 10, 12, 13 and 14) – consume the resource species #1 or #2. Simply, most other consumers exploit these resource species as well. They are not distinctive ones, as expected under the ‘string of beads’ model (Fig. 1b).

If the ‘string of beads’ model provided a commonplace description of nature, one could readily imagine how coevolution might lead to ever-tighter reciprocal specialization. For example, there might be mutual convergences in morphologies – as in the Darwin's moth–orchid case. In a study Grant & Grant (1965) referred to this as the ‘lock and key’ model. In Fig. 1b, the removal of only a few linkages could quickly produce mutual specializations.

This ‘flower petal’ pattern of niche overlaps might seem to preclude extensive reciprocal specialization. While eliminating or moving a few interactions in Fig. 1b could produce numerous pairs of species with reciprocal specialization, this is less easy to achieve in Fig. 1a.

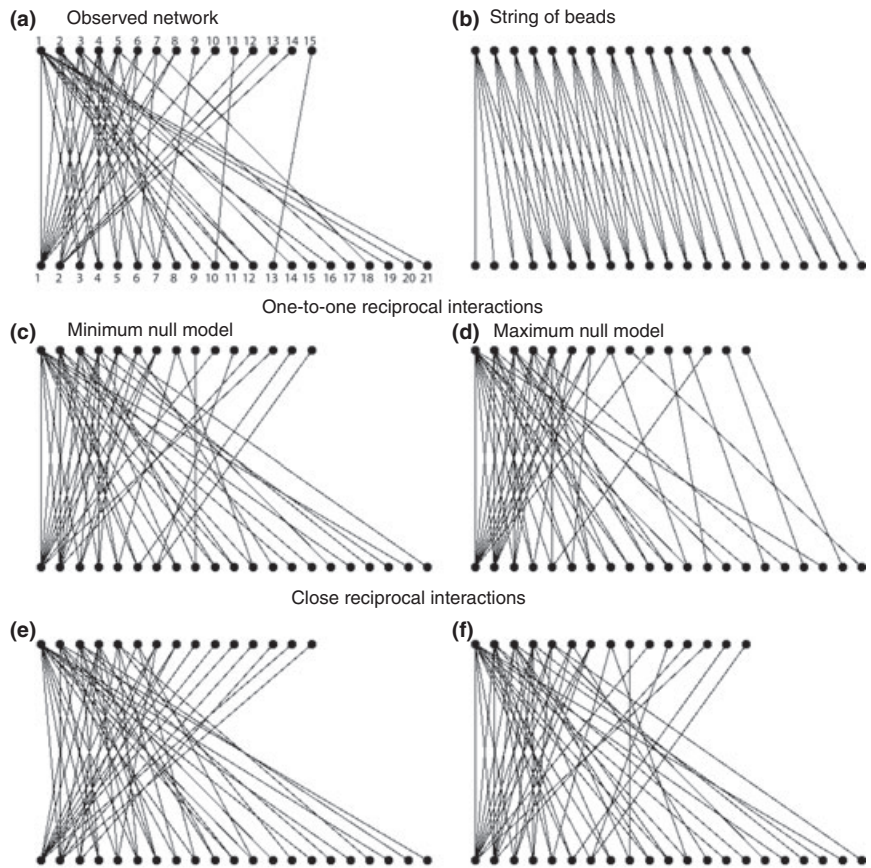


Figure 1 An example network, with row-column sum constrained randomized networks of minimum and maximum reciprocal specializations. (a) An observed network – (frugivore birds and fruiting plants, see Supporting Information for data and sources). (b) An example of a ‘string of beads’ model using the same number of interactions between consumers and resources as in (a). (c–f) Keeping exactly the same number of fruit species (bottom row) exploited by each bird species (top row) and exactly the same number of bird species using each species of fruit we show the maximum and minimum number of one-to-one interactions and close interactions (see text) in a sample of 1000 null networks (see Materials and Methods for how we produced those nulls).

Under the ‘flower petal’ model, there need be no symmetry between resources and their consumers. For example, a pollinator may be most important to a plant but get most of its resources from a different plant (Pimm 1991; Vázquez & Aizen 2004; Bascompte *et al.* 2006). One can consider Fig. 1a, where three species of birds (#12, #13 and #14), exploit only resource (fruit) #2. This fruit is likely essential to these bird species but four other bird species also take its fruits. Collectively, those four may be more important for its seed dispersal.

In graphical terms, this issue is whether observed networks more closely resemble the ‘string of beads’ illustration (Fig. 1b) or the nested, ‘flower petal’ illustrations (Fig. 1a,c–f). We conclude that nature typically rejects the ‘string of beads’ arrangement. Niche overlaps do not look like those in Fig. 1b, even in caricature.

The argument we have presented would seem to answer our question about the frequency of reciprocal trophic specialization between consumers and their resources without further analysis. ‘Such networks have typically nested trophic patterns and asymmetrical connections, so reciprocal specializations must be rare’ goes that argument. If correct, the only point of this paper would be to make this hitherto poorly made connection – and to do so largely for

the benefit of those who assume that the ‘string of beads’ model most commonly describes niche overlaps in nature.

This test, however, is only a very crude one comparing, as it does, two very general visualizations of niche overlaps. It says nothing about the subtle differences exemplified by the other parts of Fig. 1. We now consider a more conservative test that accepts the observed constraints on feeding relationships. It tests for reciprocal specialization given the expectation that these constraints will be maintained.

Test 2: a constrained test of trophic interactions

Figure 1a,c–f, not only have the same number of species of birds, fruits and interactions; *the distributions of trophic interactions per species are identical*. That is, there is still a fruit species exploited by 11 bird species and another fruit species exploited by seven species. If we depict the networks in Fig. 1c–f as binary matrices, their row and column sums would be the same as in Fig. 1a, if sorted in each case from most to fewest interactions. (Figure 1b is exceptional in that its row and column sums are *not* the same as the observed network).

Importantly, one can retain the broad structure of an observed network, yet rearrange the trophic interactions so

that there are more or fewer reciprocal mutual specializations than those observed. Figure 1c,d provide examples from strict, one-to-one specializations, Fig. 1e,f are for ‘close’ specializations.

Our second test asks: do networks have a predominance of reciprocal specialists given the observed distributions of consumer species using resource species, and resource species exploited by consumer species? In graphical terms, this asks where observed networks fall along the continuum suggested by the minimum and maximum null models shown in Fig. 1.

The key issue is that in stating that observed networks have some unusual feature – reciprocal specialization, nestedness, or anything else for that matter, one begs the question: compared with what? Null models always have to be assessed in relation to the trade-off between type I error (false rejection of a true null hypothesis) and type II error (incorrectly accepting the null hypothesis) (Ulrich & Gotelli 2007).

Here, we decide to build a sample of randomized networks (against which to compare the observed network) that maintain the original network’s row and column sums. The rationale for row and column constraints is that this is the most conservative null model and therefore any significant result is a very robust one. To do this, the model maintains the fact that consumer species differ in the number of species they exploit – some are more generalized, some more specialized – and they do so for a variety of ecological reasons. Likewise, resource species differ in how vulnerable they are to exploitation.

Fixing row and column sums has an exact parallel in studies of the presence of species on islands, where the topic has generated extensive discussion (Sanderson 2000). Many factors determine whether an island will hold few or many species, and likewise whether a species will occur on few or many islands. Ecologically realistically constrained randomized networks have the same numbers of species on each island, and species present across the islands, as in the observed species-island network.

Prior work on specialization in networks has *not* used null models that constrained row and column sums. In performing this second test, we incidentally generate the distribution of nestedness under this constrained null model. Nestedness is an interesting network property in its own right, so we present those results elsewhere.

MATERIALS AND METHODS

From the literature, we compiled 107 networks (see Tables S1 and S2), some of which we have examined in previous studies (Montoya & Solé 2003; Bascompte *et al.* 2006; Olesen *et al.* 2007). We first classified the networks as those comprising mutualistic interactions (mutualistic), and

those of insect hosts and their parasitoids (parasitic). In the former, the networks were mainly insects and the flowers they pollinated, or birds and the fruits they exploited. We also created 35 taxonomically similar ‘daughter networks’ from the five largest mutualistic networks. When creating these ‘daughter networks’ we retained only networks that contained > 5 insect species (of the same family) and five plant species. These daughter networks are overlapping or ‘overwritten’ sub-networks within the original, mother networks.

Description of the null model

The computational problems of generating the null hypotheses involve the difficulty of generating null hypotheses that obey the constraints but are not artefactually close to the observed pattern. The issue of creating randomized interaction networks, or nulls, involves randomly assigning ones and zeros so that each of the rows and columns sums to the appropriate number. We follow Miklos & Podani (2004), but with a slight modification.

Miklos and Podani’s algorithm initiates with the original matrix and then randomizes it by performing 1000 ‘swaps’. A ‘swap’ means that the algorithm finds two rows and columns that can be transposed without altering the row and column sums. It is here that our method differs from theirs. Miklos and Podani’s method would only *attempt* 1000 swaps, while ours *completes* 1000 swaps. The reason for this is that for every iteration of Miklos and Podani’s algorithm, if the rows and columns chosen are not viable swap candidates, the algorithm simply moves on, counting that against the total number of swaps. This can result in far fewer than the expected number of actual swaps. To ensure that all swaps are actually completed, at each step, we find all possible swap candidates and select one uniform randomly. Doing this ensures that the algorithm does not become stuck in a narrowly defined range of possible swaps, as every swap is randomly chosen from the list of all potential swaps.

What is important is that the algorithm samples the null space evenly, and is appropriately constrained by the number of interactions occurring in the observed network. The algorithm accomplishes this by first selecting an index from the original binary matrix in a uniform random fashion.

We generated a sample of 1000 nulls for each network we examined, maintaining row and column sums. We then calculated the number of one-to-one and close specializations in each original network, and its corresponding 1000 nulls.

What we call a ‘one-to-one interaction’ is where a consumer feeds on only one resource while that one consumer alone exploits that resource. Second, we concede that a consumer might exploit a small number of species and

one might still consider the system to show reciprocal specialization – especially if the consumers were taxonomically close and the resources likewise (Ehrlich & Raven 1964). For the latter option, we call any combination of 1–4 consumers to 1–4 resources ‘close interactions’. For example, two species of consumer exploiting only three species of resources that are themselves only exploited by those two consumers would involve a ‘close interaction’. The limit of up to four resources or four consumers is arbitrary, but other similar thresholds do not qualitatively change our results.

Figure 1 shows the essential features of our methods. We contrast the observed network, Fig. 1a, to five null networks. Only Fig. 1b has different row and column sums than the observed. In addition to the observed network, Fig. 1c,d shows the minimum and maximum number of one-to-one specializations from a sample of 1000 randomly constructed networks that satisfy the same row and column total as the observed web. In the ‘maximum’ null model, there are five pairs of reciprocal specialists: consumers 9, 11, 12, 14 and 15 each feed on resources (fruits, bottom row) that are exploited by no other consumer. The observed network has only one such pair of reciprocal specialists (consumer 15 and resource 13), while some random networks have none at all (as in the ‘minimum’ null network shown).

Figure 1e,f shows the comparable results for close reciprocal specializations. The observed network has seven close specializations – more than the minimum we find in the nulls (five), but also less than the maximum (nine).

Using the distribution of one-to-one and close specializations in the 1000 nulls, we categorized the original networks as more reciprocally specialized, less reciprocally specialized, or no different than expectation. The categories were determined by multiplying the number of nulls with fewer specializations than the observed network by negative one, and then adding to that the number of nulls with more specializations than the observed network. Positive values from this calculation indicate the observed network is less specialized than expected. ‘Equal’ indicates that either all 1000 null models had the same degree of specialization as the observed, or there were equal numbers of nulls with more specializations as there were with fewer.

Controlling for nestedness

As mentioned, previous studies have shown that trophic interactions are nested when compared with loosely constrained null models (Bascompte *et al.* 2003). While maintaining row and column sums in our null models likely provides a sufficient control on nestedness, there are reasons why networks might be nested independent of the constraints on row and column totals (Bastolla *et al.* 2009). This raises a technical complication, with the possibility that

our results are merely artefacts of known nestedness patterns. To account for this, we ask whether reciprocal specialization is common given not only the row and column constraints, but also given the observed pattern of nestedness. For a complete description of this process, including results, see Appendix S1.

RESULTS

Common patterns across divergent networks

First, the overarching pattern is clear. Networks either show the diametrically opposite pattern to reciprocal specialization, or at the very least, are no different from what one would expect by chance in our constrained null model (Table 1). We find no evidence for reciprocal specialization to structure ecological networks. Specialist species tend to connect to generalist species, whether one looks at consumers and their resources, or resources and their consumers. This is true using strict criteria, only looking at those interactions existing between one consumer and one resource (Table 1a), or with relaxed assumptions, looking at broad groupings of up to four consumers and four resources (Table 1b).

For either measure of reciprocal specialization, our most liberal accounting finds networks to have significantly *fewer* reciprocal specialists than one would expect (Table 1a,b, second to last row). However, a network cannot have fewer than zero specializations, making it impossible for original networks with zero specializations to be more specialized than expected. It is perhaps unfair to include those networks in our comparison. Removing them does not alter our results for ‘close’ specializations, but does change ‘one-to-one’ specializations from significantly less specialized to insignificantly so (Table 1a,b, last row). Either way, we find no evidence for a preponderance of reciprocal specializations in the networks we examine. Moreover, nestedness-constrained results agree well with the unconstrained ones (Table 1a,b vs. Tables S3a,b and S4a,b).

Differences between network types

One might expect mutualistic networks to have different fractions of reciprocal specializations than antagonistic ones. The combination of coevolutionary complementarity (e.g. similar corolla and pollination tongue lengths) and coevolutionary convergence (e.g. convergence in fruit traits in plants dispersed by birds rather than animals) are thought to lead to nested, asymmetric mutualistic networks (Thompson 1994). However, in antagonistic interactions coevolutionary alternation (i.e. selection favouring parasitoids to attack hosts with weaker defences) should lead to more compartmentalized and symmetric networks (Lewinsohn *et al.* 2005;

Table 1 Summary of results for all original and daughter networks included in the analysis

	One-to-one reciprocal interactions						Close reciprocal interactions					
	(a) Unconstrained						(b) Unconstrained					
	Total	Reciprocal	Subtotals	Equal	Less	More	Total	Reciprocal	Subtotals	Equal	Less	More
Mutualistic	65	0	49	19	30		65	0	6	3	3	
		1	12	0	6	6		1–10	35	1	26	8
		> 1	4	0	3	1		11–20	14	2	11	1
							> 20	10	0	8	2	
Parasitic	42	0	40	17	23		42	0	6	5	1	
		1	1	0	1	0		1–10	21	4	9	8
		> 1	1	0	0	1		11–20	9	1	6	2
							> 20	6	0	5	1	
Daughter	35	0	16	4	12		35	0	0			
		1	8	0	3	5		1–10	18	10	6	2
		> 1	11	2	5	4		11–20	16	13	3	0
							> 20	1	1	0	0	
		Sum all networks			83*	17		Sum all networks		78*	24	
		Sum networks > 0 specializations			18	17		Sum networks > 0 specializations		74*	24	

Top: ‘one-to-one’ (a) and ‘close’ (b) specialization results for Mutualistic, Parasitic and Daughter webs. The first column (total) is the number of networks analysed, column two (reciprocal) indicates the number of specializations present in the original network, and column three (subtotals) is the number of networks in each of the three categories in column two. Columns four, five and six categorize the observed networks into those that are more specialized (more), less specialized (less), or no different from expectation (equal). See text for the determination of categories. The intersection between column ‘more’ and where ‘reciprocal’ equals zero is blank by default, as it is impossible for a null network to have < 0 specializations. In both (a) and (b), the second to last row is the sum of all networks in the analysis, while the last row is the sum of all networks with one or more specializations. Summary of results for all original and daughter networks included in the analysis.

*Significant under a Sign Test at $P = 0.05$.

Thompson 2005). Contrary to these differing expectations, we find a similar value of asymmetric specialization across interaction types, confirming similar results by Thébault & Fontaine (2008) for plant–herbivore networks. This means that at higher trophic levels we find a similar predominance of asymmetric specialization, confirming the generality of this pattern.

For one-to-one specialization, the 15% (7 vs. 39) of mutualistic networks that are more specialized than expected do not differ significantly from the 4% (1 vs. 25) of parasitic networks ($P = 0.30$, chi-square test). The comparable percentages for close specialization are 19% (11 vs. 48) for mutualistic networks and 34% (11 vs. 21) of parasitic networks, and similarly do not differ significantly ($P = 0.16$). These results also hold when using nestedness-constrained nulls (chi-square test, one-to-one $P = 0.07$, close $P = 0.51$).

Potential influence of network ‘modularity’

Finally, networks may be ‘modular’, that is, composed of multiple sub-networks centred around a ‘hub’ species and

linked to the greater network through species acting as ‘connectors’ (Olesen *et al.* 2007). We posited that complete networks might be palimpsests – that is, composed of smaller and over-written networks, where patterns of reciprocal specializations within a taxonomically related set of species (those in the same family, for example), might nonetheless overlap in complex ways and obscure those original patterns. If true, this might facilitate bridge major research agendas in coevolution – research focusing on the coevolution between small groups of strongly interacting species (Thompson 1999) and that analyzing networks of interactions (Bascompte & Jordano 2007).

From Table 1a,b, we can compare the percentages of mutualistic mother networks with those of the daughter networks. For one-to-one specialization, the 31% of daughter networks (9 vs. 20) that are more specialized than expected is higher, but not significantly so (chi-square test, $P = 0.18$) than the mother networks (7 vs. 39). For close specializations, the percentages are essentially the same [18% daughters, 2 vs. 9; 19% mothers, 11 vs. 48 (chi-square test, $P = 0.70$)]. Again, the results do not differ when comparing nestedness-constrained networks.

However, the daughter network idea merits further inspection. The top panel in Fig. 2 is a complete 'mother network'. Considering close interactions for this example, 1.7% of the sample null networks are the same as those observed, 97% have more specialized reciprocal interactions, and only 1.3% fewer reciprocal interactions. For one-to-one interactions, the percentages are 39%, 20% and 40% respectively. The mother network follows the general pattern of showing fewer reciprocal specializations than expected. We created six daughter networks for the insect families Calliphoridae, Muscidae, Halictidae, Tephridae, Empididae and Colletidae. For close interactions, 100% of the nulls for all daughter networks are the same as those observed, so we can draw no inferences. For one-to-one interactions, only one daughter network has 100% of the nulls the same as observed (Colletidae). Four daughter networks are more reciprocally specialized than expected, while one, Muscidae, is the reverse. The Empididae network is the most reciprocally specialized sub-network, with 58% of null models less reciprocally specialized and 42% equal to the observed network.

This is a hand-picked example, of course, but is particularly rich in both overall species and daughter networks. The contrast between the mother network, showing no evidence of mutual specializations, and the few daughter networks that do, suggests a more extensive survey of species-rich networks is required.

DISCUSSION

We do not deny examples of reciprocal specialization (Pauw 1998) made known by the moth whose existence Darwin predicted (Darwin 1862; Rothschild *et al.* 1903), although even here the story is not as simple as it seems (Wasserthal 1998). Nor do network descriptions reject the importance of, for example, reciprocal selection, between particular hummingbirds and particular flowers. As Temeles *et al.* (2002) have argued, the former could visit many flowers and the latter be visited by many potential consumers, but only one flower may shape the hummingbird's bill and one hummingbird the flower's shape.

That said, we found no evidence that reciprocal specialization shapes ecological networks by creating an excess of reciprocally specialized trophic interactions between consumers and resources. We went to particular lengths to find such reciprocal interactions, comparing networks with mutualistic interactions and those with parasitoid-host interactions. There are no compelling differences, even when correcting for the role of nestedness in network structure. Indeed, we found ecological networks no more nested than expected given our most conservative null model (see Supporting Information) [see also Ulrich & Gotelli (2007) for the equivalent scenario in island biogeography]. Moreover, we selected taxonomic subsets to produce daughter networks from larger networks to test whether reciprocal specialization was obscured by overlap-

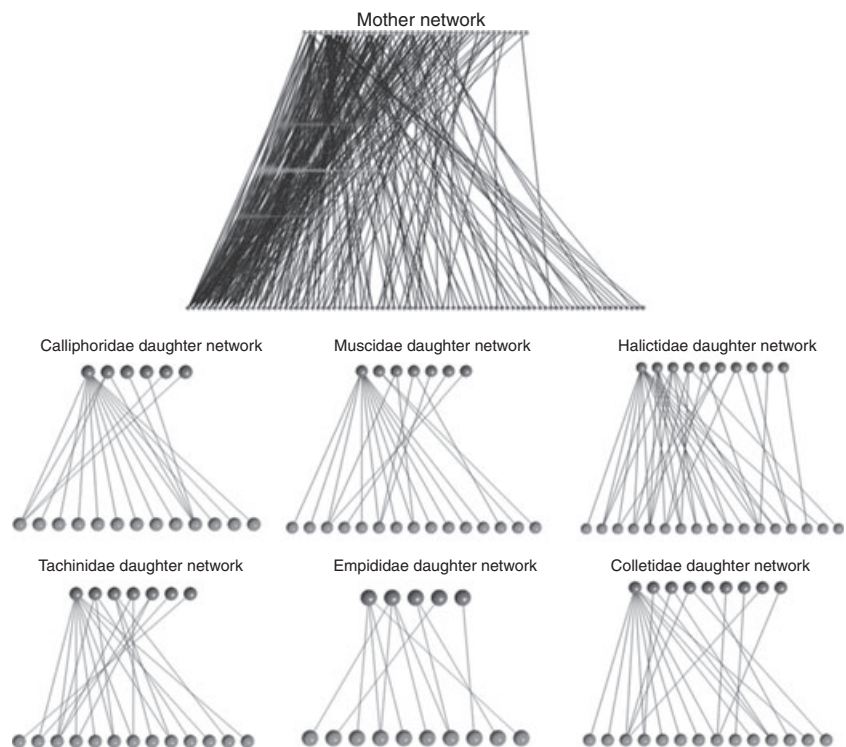


Figure 2 An example of an observed 'mother' network and its six resulting 'daughter' networks. Top panel: an observed 'mother' network (INPK, see Supporting Information) of 42 plants (bottom row) and 85 interacting insects (top row). Bottom two panels: the six 'daughter' networks created from the 'mother' network. Of 28 insect families, only six met the criteria to be analysed as a daughter network.

ping taxonomic groupings, again without finding a statistical excess of reciprocal specializations. These results suggest that common processes and universal constraints might operate across such widely different networks, and lend support to the 'flower-petal' model of network structure (Pimm *et al.* 1991).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Example of the relationship between temperature and reciprocal specialization.

Figure S2 Example of the relationship between NODF and reciprocal specialization (analogous to figure S3).

Table S1 Source, details and further temperature output for the networks used for our analysis.

Table S2 Source, details and further NODF output for the networks used for our analysis.

Table S3 Summary of all original and daughter networks included in the analysis, constrained within $\pm 1^\circ$ temperature.

Table S4 Summary of all original and daughter networks included in the analysis, constrained within $\pm 1^\circ$ NODF.

Appendix S1 Introduction, Methods, Results and Discussion for nestedness-constrained analysis.

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