

Asymmetries in specialization in ant–plant mutualistic networks

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Mutualistic networks involving plants and their pollinators or frugivores have been shown recently to exhibit a particular asymmetrical organization of interactions among species called nestedness: a core of reciprocal generalists accompanied by specialist species that interact almost exclusively with generalists. This structure contrasts with compartmentalized assemblage structures that have been verified in antagonistic food webs. Here we evaluated whether nestedness is a property of another type of mutualism—the interactions between ants and extrafloral nectary-bearing plants—and whether species richness may lead to differences in degree of nestedness among biological communities. We investigated network structure in four communities in Mexico. Nested patterns in ant–plant networks were very similar to those previously reported for pollination and frugivore systems, indicating that this form of asymmetry in specialization is a common feature of mutualisms between free-living species, but not always present in species-poor systems. Other ecological factors also appeared to contribute to the nested asymmetry in specialization, because some assemblages showed more extreme asymmetry than others even when species richness was held constant. Our results support a promising approach for the development of multispecies coevolutionary theory, leading to the idea that specialization may coevolve in different but simple ways in antagonistic and mutualistic assemblages.

Keywords: asymmetric specialization; complex networks; extrafloral nectaries; geographic mosaic; nestedness

1. INTRODUCTION

Species interact within communities as networks, with each species connected to one or more other species (Pascual & Dunne 2006; Waser & Ollerton 2006). Analyses of network structure are allowing prediction of the consequences of species extinction and environmental perturbation to the whole community (Pascual & Dunne 2006). Additionally, comparative studies of network structure are helping to explain variation in patterns of specialization across communities (Olesen & Jordano 2002; Waser & Ollerton 2006). In this context, one of the central problems to solve in community ecology is whether different forms of interaction favour alternative structures in these networks of interacting species (Bascompte *et al.* 2003; Jordano *et al.* 2003).

A network of interacting species may have a small number of links among species, indicating an assemblage of ecological specialists, or many links, indicating ecological generalists. Mutualisms between free-living

species often form multispecies networks apparently similar to the food webs commonly described for antagonistic interactions (Jordano 1987). Recent studies of pollinator–plant and seed disperser–plant interactions, however, have suggested that mutualistic and antagonistic webs of free-living species may differ fundamentally in the structure of how specialization is distributed among interacting species (Bascompte *et al.* 2003; Jordano *et al.* 2003; Vazquez & Aizen 2004). Bascompte *et al.* (2003) found that pollination and seed dispersal networks often show a specific type of asymmetrical specialization called nested. Nested networks are characterized by (i) generalists that all interact with each other, forming a core of interacting species; (ii) specialist species that commonly interact only with generalists and (iii) the absence of specialists that interact only with other specialists (figure 1a). In contrast, antagonistic networks (e.g. predator–prey, herbivore–plant), tend to be more compartmentalized, i.e. characterized by cohesive groups of interacting species (compartments) with relatively few interactions among groups (Prado & Lewinsohn 2004; Bascompte & Jordano 2006; figure 1b).

Nested patterns of asymmetrical specialization may be more likely to develop in mutualistic interactions among free-living species than in antagonistic interactions,

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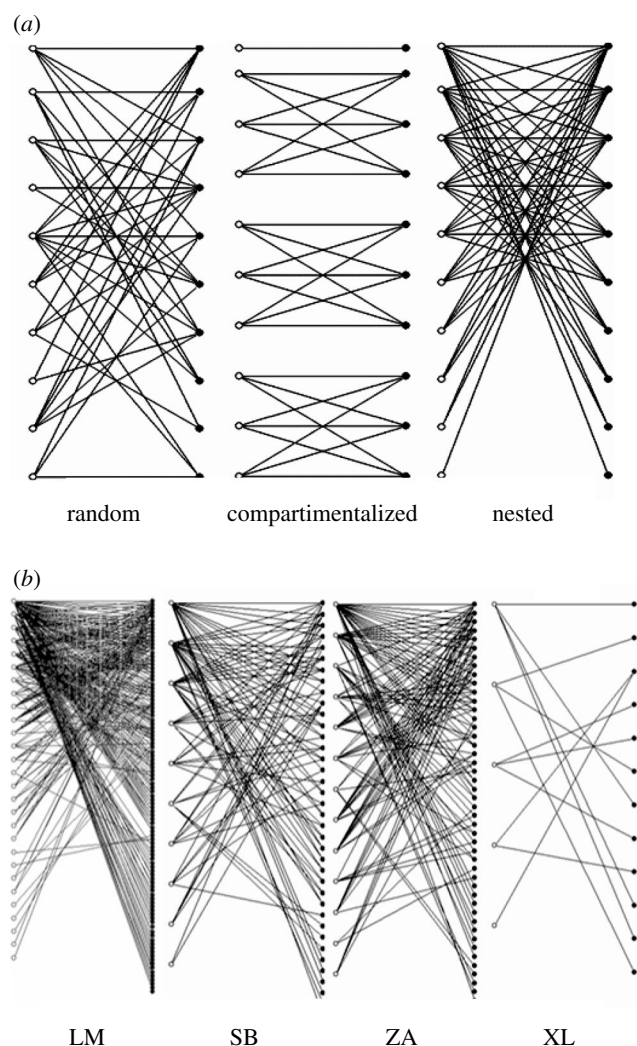


Figure 1. (a) Different types of hypothetical plant-animal networks: random networks, in which there is no community-level patterns of specialization; compartmentalized networks, in which there is symmetrical specialization; and nested networks in which there is asymmetrical specialization, i.e. specialists interact with the core of generalist species. (b) EFN networks: LM, La Mancha; SB, San Benito; ZA, Zapotitlán; XL, Xalapa. Open nodes are ant species and closed nodes are extrafloral nectary-bearing plant species. Only the first three networks (LM, SB and ZA) show high degree of nestedness. Networks were drawn in PAJEK (<http://vlado.fmf.uni-lj.si/pub/networks/pajek/>).

because natural selection on mutualisms often specifically favours the development of multispecies networks through convergence and complementarity of traits in interacting species (see Thompson 1994, 2005). In contrast, antagonistic interactions may favour greater compartmentalization through the continual coevolution of defences and counter defences that generates greater specificity (see Thompson 2005). If nested asymmetries in specialization are indeed generated by simple coevolutionary processes such as convergence and complementarity of traits, it should be a common feature of mutualisms, spanning multiple forms of interaction beyond those investigated so far for plants and their pollinators and frugivores.

Nevertheless, we currently do not know whether the nested pattern of asymmetries in specialization is common in other forms of mutualism or how different ecological conditions may shape the extent of asymmetry (i.e. the

degree of nestedness). We already know from past studies of mutualism that species commonly differ geographically in the species with which they interact (Anderson *et al.* 2004; Rudgers & Strauss 2004) and that some interactions coevolve as a geographic mosaic in which populations differ across landscapes in their adaptation and specialization to other species (Thompson 1994, 2005). Hence, the problem to solve is whether interaction networks show similar patterns of specialization in different communities regardless of the particular species involved. By exploring variation in community-level patterns of mutualistic networks, we will be able to bridge the two main approaches to explore the organization of multispecies mutualisms: geographic mosaic theory and complex network theory (Bascompte & Jordano 2006).

Here, we take a first step towards filling these gaps, by exploring whether interactions between plants with extrafloral nectaries (EFN) and ants (hereafter EFN networks), which are among the most commonly studied types of plant-animal mutualisms (Bronstein 1998), show predictable patterns of asymmetry in specialization and whether those patterns vary with ecological conditions. In a given tropical community, dozens of nectar-producing plant species may interact with ants (Díaz-Castelazo *et al.* 2004). These interactions are often defensive mutualisms, in which the ants protect plants against their natural enemies and plants reward ants with nectar (Rico-Gray *et al.* 1998b). We studied nested patterns and their variation in four EFN networks, each from a different site in Mexico, to address the following questions: do ant-plant networks show a predictable pattern of specialization within and among communities? To what extent is the pattern of specialization similar to that found in studies of other forms of interaction?

2. MATERIAL AND METHODS

(a) Study areas

We constructed networks using previously published data from interactions between ants and EFN-bearing plants in four different communities (Rico-Gray 1993; Díaz-Castelazo & Rico-Gray 1998; Rico-Gray *et al.* 1998a,b) and compared those with patterns found in previous studies of nestedness in pollinator-plant and seed disperser-plant networks (Bascompte *et al.* 2003). For the ant-plant networks, we evaluated four habitats with a similar number of flowering plant species (about 250–300) but with contrasting environmental characteristics: lowland tropical dry forest (La Mancha, Veracruz), coastal tropical sand dune matorral (San Benito, Yucatán), highland semiarid vegetation (Zapotitlán, Puebla), and lower montane humid forest (Xalapa, Veracruz). The vegetation in Xalapa, a mixture of tropical and temperate floristic elements (Williams-Linera & Tolome 1996), constrains the development of species-rich EFN networks because relatively few plants have EFN (Díaz-Castelazo & Rico-Gray 1998). In contrast, the other three habitats have tropical floristic elements (e.g. Leguminosae, Bignoniaceae, Cactaceae) that are abundant and frequently have nectar-producing structures (Elias 1983; Schupp & Feener 1991). See electronic supplementary material for detailed description of study sites.

(b) Nestedness in EFN networks

Typically, plant-animal interactions can be depicted as networks consisting of two sets of nodes (plants and animals;

Jordano *et al.* 2003; figure 1) and links among them that depict the interactions between any species pair. An EFN network is defined by an adjacency matrix \mathbf{R} describing trophic interactions between E extrafloral nectary-bearing plant species and A visiting ants within a well-defined ecological community, where $r_{ij}=1$ if the plant i is visited and its extrafloral nectar harvested by the ant j and zero otherwise. Thus, this matrix has non-zero r elements wherever ants visit the EFN of a plant. It is important to emphasize that visitation by ants does not necessarily imply that ants are protecting the plant. Rather, certain ant species may only explore the resource without protecting the plants or only protecting under certain ecological conditions. Therefore, only a subset of recorded interactions in these networks is unambiguously mutualistic. Future studies should focus on the importance of exploiters of mutualistic interactions to network structure. In this study, we follow the approach already used in other interactions and considering that all interacting species are part of the mutualistic network (see Jordano *et al.* 2003).

Our discussion about nested asymmetrical specialization is based on the ecological concepts of specialist and generalist (see Olesen & Jordano 2002), in which the level of generalization of a given species is equal to the number of recorded interactions. In this context, specialists and generalists are terms used to describe the endpoints of a continuum varying from species that interact with only one partner (extreme specialists) to species that interact with near all possible partners (extreme generalists). Ecological specialization may emerge as a consequence of coevolutionary processes between the plants and ants, differences in species abundance and competitive interactions among the plants or the ants.

We follow Bascompte *et al.* (2003) and define nestedness, N , as $N=(100-T/100)$, in which T is the matrix temperature, a measure of matrix disorder with values ranging from 0° (perfectly nested) to 100° (perfectly non-nested). Values of N close to one therefore indicate strong asymmetrical patterns in specialization (same as high degree of nestedness), intermediate values are usually produced assuming random interactions among species, and low values of N may indicate compartmentalization (Bascompte & Jordano 2006). Thus, by calculating nestedness we are able to investigate if a given ecological interaction can be described as one of the three main classes of networks (figure 1a). In effect, we are testing three alternative hypotheses on the structure of specialization in these assemblages.

To calculate T , the adjacency matrix \mathbf{R} is maximally packed (see Atmar & Patterson 1993 for further details). Then, an isocline of perfect nestedness is calculated and deviations from this isocline (i.e. unexpected recorded presences and absences of interactions that deviate from a perfectly nested pattern) are standardized and recorded. The average degree of deviation from this isocline is T . All nestedness analyses were performed using ANINHADO v. 1.0, C-language software based on the original code of the widely used nestedness temperature software (hereafter NTC) that allows rapid analyses of thousands of replicates (Guimarães & Guimarães 2005).

We assessed the significance of nestedness, using two null models. The first null model was based on NTC's null model and tested if the observed nested pattern is expected by the average level of generalization. Null model I assumes that each randomly assigned pair of ants and plants interacts with

constant probability, p . This probability is related to the average level of generalization observed in the network and was estimated as $\hat{p}=E/AP$, in which E is the number of observed interactions and AP is the maximum possible number of interactions in a network with A ant and P plant species. This model generates networks in which differences in the number of interactions among species of the same assemblage is small. Different nested patterns, in turn, may result from differences in the number of interactions among species. In pollination and seed dispersal networks, however, the degree of nestedness is often higher than expected by the heterogeneity of number of interactions (Bascompte *et al.* 2003). As we are interested in whether EFN networks show patterns of nestedness similar to those recorded in other mutualistic networks, we also used null model II from Bascompte *et al.* (2003), which assumes that the probability that a plant i interacts with an ant j depends on the observed number of interactions of both species, such that

$$p(r_{ij}=1)=\left(\frac{k_i}{A}+\frac{k_j}{E}\right)\frac{1}{2}, \quad (2.1)$$

in which k is the observed number of interactions for the species. As k is correlated with species abundance in plant-animal interactions (Jordano 1987; Jordano *et al.* 2003), this model also controls for potential sampling bias, in which asymmetrical patterns of interactions are generated only by differences in species abundance.

We compared the proportion of networks that show significant values of N with those recorded for pollination ($n=25$), seed dispersal networks ($n=27$) and with a set of antagonistic networks that include predator-prey, consumer-producer and herbivore-plant interactions ($n=14$, all values recorded from Bascompte *et al.* 2003).

(c) Comparisons among communities

We also investigated how ecological variables affect nestedness patterns. The degree of nestedness is thought to be a measure independent of matrix properties (Atmar & Patterson 1993). For pollination and seed dispersal networks, however, the degree of nestedness increases with species richness (Bascompte *et al.* 2003), indicating a biological pattern. Thus, we investigated whether the degree of nestedness is related to species richness in EFN networks. Then, we contrasted our four EFN networks to investigate how ecological variables affect nestedness. We assessed whether the four EFN networks showed differences in nested pattern after controlling for total number of species (network size) and the ratio between the number of ant and plant species (network form). We predicted that, if network size and form were solely responsible for the nested pattern, then the observed nestedness of a small EFN network would be equal to the nested pattern of a sub-network with equal size and form randomly sampled from a larger network. We tested this hypothesis using the following algorithm to compare pairs of networks in which L is the larger network and I is the smaller network: (i) assuming that the probability of a plant species being removed is equal in all plant species, randomly remove plant species of L until $E_L=E_I$; (ii) assuming that the probability of an ant species being removed is equal in all ant species, randomly remove ant species of L until $A_L=A_I$; (iii) record nestedness of the rarefied L network; (iv) repeat (i-iii) for 999 times; (v) calculate the probability p that a rarefied L shows a degree of nestedness equal to or more extreme than I . We only consider rarefied networks in which

all species at the end have at least one interaction, because species without any interaction lack biological meaning. If other factors besides network size and form affect the nestedness pattern of the smaller network, we expect that $p < 0.05$. It is important to note that differences in nestedness may be a result of sampling (Fischer & Lindenmayer 2002). Small networks may indeed be small datasets in which more generalists are recorded, since generalists are usually the most abundant species (Jordano 1987). To investigate if differences in nestedness among communities are a result of simple sampling bias, we used a rarefaction procedure identical to the above one, except for the fact that the probability of a plant or ant species being removed is proportional to $1/k$ in which k is the number of interactions of the species.

3. RESULTS

Extrafloral nectary network showed on average strongly nested patterns of asymmetric specialization among the interacting species (figure 1b, $N = 0.71 \pm 0.10$, mean \pm s.e.). As a consequence of these community-level patterns, nestedness was very high on average. The three tropical networks showed nestedness values similar to those observed in pollination and seed dispersal networks (figure 2a). Indeed, the probability of a given tropical EFN network showing a nested pattern equal to or more extreme than that observed for seed dispersal or pollination network was always non-significant (La Mancha, $N = 0.949$, $p = 0.17$; San Benito, $N = 0.748$, $p = 0.19$; Zapotitlán, $N = 0.706$, $p = 0.13$). These networks were significantly nested whether tested against null model I or II (figure 2b). Therefore, the degree of nestedness observed in these ant-plant interactions was higher than expected by random interactions or by differences in the number of interactions among species. In contrast, Xalapa showed the lowest nestedness ever recorded in the literature for a mutualistic plant-animal network ($N = 0.453$; figure 2a). Both null models reproduced the nested pattern for Xalapa (figure 2b), indicating that the patterns of asymmetrical specialization in this community are expected by random interactions. The proportion of EFN networks that showed significant nestedness was very similar to the other two types of mutualistic networks analysed and very different to the pattern observed for antagonistic networks (figure 3), although our small sample of communities leads to caution when interpreting the results.

Asymmetries in specialization increased with species richness (figure 2b). We re-analysed data from Bascompte *et al.* (2003) for plants and their pollinators and seed dispersers and found that for large networks ($S > 40$, $n = 28$), nestedness increased with the logarithm of network size ($N = 0.36 + 0.1 \log(S)$, $F = 12.98$, d.f. = 27, $R^2 = 0.33$, $p = 0.01$), indicating that only species-rich systems will show high patterns of nestedness. We used this function to control network size, computing the differences between the nestedness predicted by network size and the observed nestedness for pollination, seed dispersal, and the three significant nested EFN networks. After controlling for network size, all tropical EFN networks showed patterns of nestedness similar to those observed for pollination and seed dispersal networks (La Mancha, $p = 0.29$; San Benito, $p = 0.32$; Zapotitlán, $p = 0.14$).

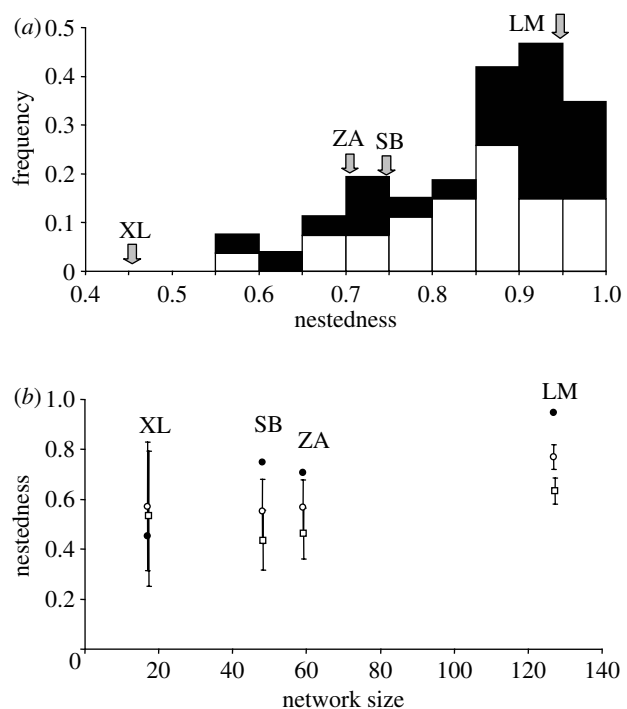


Figure 2. (a) Frequency of different degrees of nestedness observed in published studies on pollination, seed dispersal, and analysed EFN networks. Black columns indicate pollination networks, white columns indicate seed dispersal networks, and grey arrows indicate the values for analysed EFN networks (networks labelled as in figure 1). (b) The relationship between degree of nestedness and network size (i.e. number of interacting species). Closed circles indicate observed values of nestedness for each EFN network. Open squares indicate the average nested value predicted by null model I and open circles indicate the average value predicted by null model II (see text for further details). Error bars indicate 95% confidence interval (10 000 replicates for each null model).

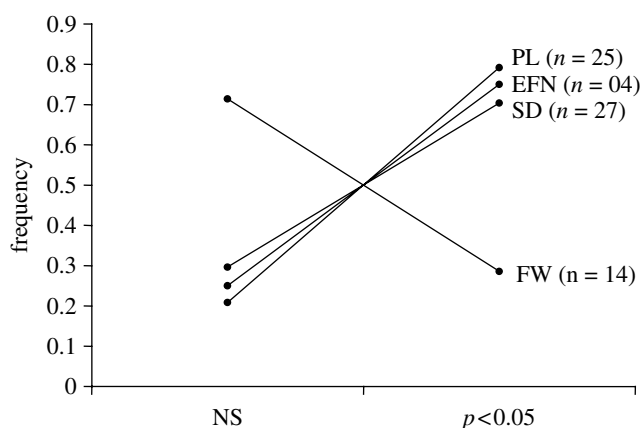


Figure 3. The proportion of significant nestedness found in different types of interaction: EFN, extrafloral nectaries; SD, seed dispersal; PL, pollination; FW, food webs (antagonistic networks). NS, non-significant nestedness; $p < 0.05$ = significant nestedness.

Species richness, however, was not the only factor affecting the degree of asymmetry in specialization. Tropical EFN networks showed larger values of nestedness than Xalapa even after controlling for network size and form (figure 4a-c). Among the tropical networks, Zapotitlán and San Benito showed a similar degree of

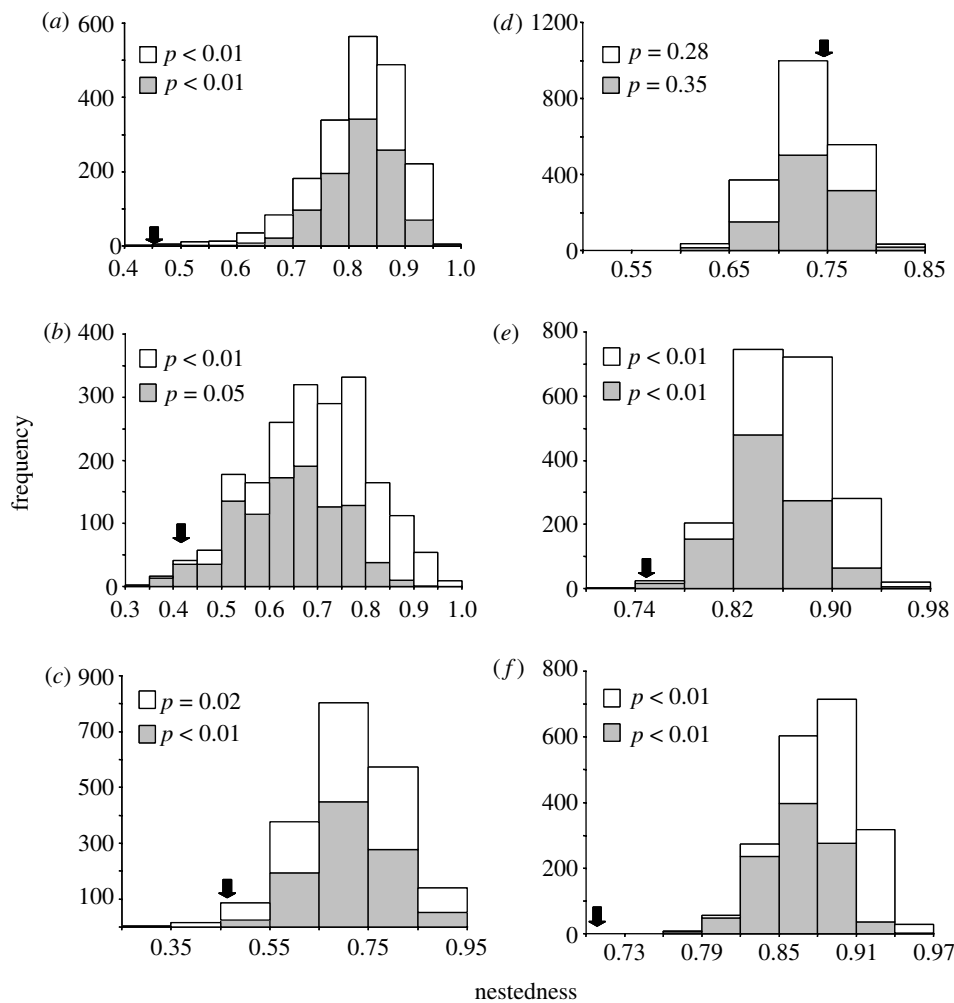


Figure 4. Nestedness for real EFN and rarefied networks. Ensembles of rarefied networks were generated by randomly removing ant and plant species using two different procedures: assuming that each plant or ant species has the same probability of removal (white columns) and assuming that the probability of a species being removed is negatively correlated with the degree of generalism (grey columns). Arrows indicate the actual degree of nestedness of the smaller network. The p indicates the probability of a rarefied network showing nestedness equal to or more extreme than the real, smaller network: Xalapa and (a) rarefied La Mancha networks, (b) rarefied Zapotitlán and (c) rarefied San Benito; San Benito and (d) rarefied Zapotitlán, (e) rarefied La Mancha and (f) Zapotitlán and rarefied La Mancha.

nestedness (figure 4d), but La Mancha showed stronger asymmetries than these other sites, even after controlling for network size and form (figure 4e,f). Hence, ecological factors other than species richness must contribute to geographic variation in the degree of asymmetry in specialization in these mutualisms, but they do not completely override the tendency of large mutualistic networks to be significantly nested.

4. DISCUSSION

The interactions between ants and plants differ in many ways from those involving pollinators and seed dispersers. In ant-EFN plant interactions, the benefit for plants is protection against herbivores. Protection, in turn, is an indirect benefit, because it depends on ants being efficient in deterring a third assemblage of species: the herbivores. In contrast, in pollination and seed dispersal interactions the benefit for plants is reproduction, and the interaction does not involve manipulating the effects of a third group of species. Yet, all these interactions show similar patterns of nestedness, in which specialist-specialist

interactions are rare and specialists interact with a core of generalist species.

Our results corroborate and extend the conclusions of recent studies suggesting that interactions among free-living species in species-rich communities show a nested pattern of asymmetrical specialization, when at least some of the interactions have potentially strong mutualistic components (Bascompte *et al.* 2003). Although, it is well known that different processes may lead to similar patterns in ecology (Levin 1992), a parsimonious possibility is that all three types of mutualism may be affected by similar evolutionary processes, such as convergence and complementarity of traits among interacting species (Thompson 2005), that differ from the processes acting on antagonistic networks. Indeed, network theory predicts that these similarities and differences are a result of simple processes (Albert & Barabási 2002). These results therefore provide support for the development of multispecies coevolutionary theory, leading to the notion that specialization may evolve and coevolve in different but simple ways in mutualistic and antagonistic interaction networks. Caution is needed since

nested patterns have been explored in only a few types of interaction. Based upon current results, however, we predict that nestedness will be observed in other interactions between free-living mutualists, such as associations between host fish and their cleaners on coral reefs (e.g. Cote 2000).

Additionally, our study highlights the potential importance of species richness and its influence on geographic variation in nested asymmetrical specialization within mutualistic networks. The logarithmic relationship between network size and nestedness suggests that only species-rich systems will be highly nested. Moreover, small networks generally do not show significant nestedness (Bascompte *et al.* 2003; this study). This feature may be a consequence of nestedness being inherently undetectable below a certain threshold of species richness, a typical problem of characterization of small networks (Guimarães *et al.* 2005). Alternatively, it may be that species-poor communities do not have sufficient number of species for the evolution of species specialized in interacting with generalist species. In fact, many mutualistic lifestyles (e.g. nectar and pollen gathering in social bees and near-obligate frugivory in some vertebrates) became possible only after local multispecies mutualistic networks came into existence (Thompson 1982).

The variation in nested asymmetrical specialization among EFN networks, however, is not totally explained by differences in species richness or by differences in the ratio between ants and plants. These differences may be a result of sampling bias, but after we controlled for preferential sampling of generalists, some communities still differed in the level of specialization (figure 4). Thus, other ecological variables may contribute to the particular degree of nestedness in any particular assemblage. Olesen & Jordano (2002) have shown that, beyond species richness, altitude and the biogeographic region affect the average level of specialization within pollination networks. We suggest that future work with mutualistic networks should focus on the role of these factors in driving regional differences in patterns of nested asymmetrical specialization.

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