



Does asymmetric specialization differ between mutualistic and trophic networks?

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Recently, plant–pollinator networks have been found to be highly structured in a nested pattern in which specialists interact with generalist species. This structure is often assumed to be particular to mutualistic interactions in opposition to the compartmentalized pattern expected for antagonistic networks. We investigated the presence of asymmetric specialization in a data set assembled from the literature of 20 highly resolved plant–insect herbivore networks and compared them with 24 plant–pollinator networks. Our results indicate that these two types of networks differ, but not in the way it is generally assumed. Asymmetric specialization is present in plant–herbivore networks even if it appears less frequently than in plant–pollinator networks. Indeed, mean and median percentages of species showing asymmetric specialisation in herbivory webs are 33% and 14% respectively, compared to 57% and 60% in pollination webs. Furthermore, the amount of asymmetry is linked with species diversity and not to connectance in plant–pollinator networks whereas the opposite pattern is found in plant–herbivore networks. Our results offer promising perspectives for understanding both the mechanisms that structure ecological communities and their impact on community dynamics depending on the type of interaction.

The analysis of patterns describing interactions among species in communities has been the focus of many studies and debates in ecology (May 1983, Briand and Cohen 1984, 1987, Martinez 1991, Montoya and Sole 2002, 2003, Olesen and Jordano 2002, Bascompte et al. 2003, Jordano et al. 2003, Melian and Bascompte 2004) in order to find precise characteristics common to different networks and to infer some general mechanisms responsible for the structure, function and evolution of ecological systems (Martinez 1994).

Networks involving plants and their pollinators or frugivores have been shown recently to exhibit a complex structural characteristic called nestedness, which particularly implies great levels of asymmetric specialization so that specialist species tend to interact with the most generalist species, (Bascompte et al. 2003, Jordano et al. 2003, Vazquez and Aizen 2003, 2004). While the degree of specialization is involved in profound ecological and evolutionary issues, the presence of asymmetrical specialization questions the assumption of tight reciprocal specialization found in models of coevolution (Waser et al. 1996, Gomulkiewicz et al. 2000). This structural property of networks can have major consequences in terms of ecological and evolutionary dynamics of communities, and an important question concerns the underlying

mechanisms responsible for it (Vazquez et al. 2005, 2007). The high prevalence of asymmetric specialization in a variety of different mutualistic networks (plant–pollinator, plant–frugivore and plant–ant networks) has led to the suggestion that this pattern may be favoured by mutualistic interactions through coevolutionary convergence and complementarity of traits in interacting species (Thompson 2005, Bascompte et al. 2006, Guimarães et al. 2006). In opposition, antagonistic interactions are assumed to favour greater symmetry and compartmentalization through the continual coevolution of defences and counter defences that generates greater reciprocal specialisation (Thompson 2005).

While two studies tend to support the idea that antagonistic networks differ from the general structure of mutualistic networks (Bascompte et al. 2003, Lewinsohn et al. 2006), the presence of similar patterns has also been highlighted in both types of networks (Vazquez et al. 2005). Particularly, host–parasite interaction networks can exhibit high levels of asymmetric specialization (Vazquez et al. 2005) and nested patterns have been found embedded in the compartments of a plant–herbivore interaction network (Lewinsohn et al. 2006). Thus, there is a need to extend these studies over a broad range of food web data and to explicitly compare antagonistic and mutualistic networks in

order to investigate if antagonistic networks organization really differs from the particular asymmetrical organization of mutualistic interactions.

Direct comparison between food webs and mutualistic networks are scarce (Bascompte et al. 2003, Lewinsohn et al. 2006): these two types of webs are by essence represented in different manners, which often prevents direct comparison of topological properties. While food webs are represented as directed graphs (Pimm 1982, Cohen et al. 1990) that is, relations depicting who-eats-whom through several trophic levels, mutualistic networks are described by means of bipartite graphs (Jordano et al. 2003). Furthermore, whereas mutualistic networks describe interactions at species taxa levels, most food webs consider interactions between aggregated set of trophically equivalent species, named trophic groups. The degree of resolution and aggregation in network data can strongly affect the analysis of networks patterns (Martinez 1991); it is therefore essential to assemble appropriate data sets of networks in order to test the impact of interaction type (either antagonistic or mutualistic) on the structure of communities and particularly on the importance of asymmetric specialization in these networks.

Here, we propose to use an original data set of both plant–pollinator and plant–insect herbivore networks to study this question. Data on plant–insect assemblages provide an ideal material in this case; both mutualistic and trophic networks concern the same type of organisms, they are described by means of bipartite graphs and their resolution are at the same level, that is at species level.

Methods

Data sets

We collected in the literature studies of plant–insect herbivores communities which describe plant–herbivore interactions at species levels. To be included in our analysis, a study had to meet the following criteria: (1) the data set should include ten or more plant species, this criteria was made in order to focus on community-wide networks; (2) a direct evidence of the feeding relation between plants and herbivores should be provided by relying either on insect's gut/crop content analysis or on observation in situ with experimental verification of insect feeding and insect rearing. We found twenty data sets from studies of plant–insect herbivores communities that met these criteria. We compared these networks with 24 data sets from published community-wide studies of plant–pollinator interactions which included also ten or more plant species. A list of the data sets analyzed in this article can be found in Appendix S1 in the Supplementary material. Each data set was converted to a binary interaction matrix, in which rows represented insect species and columns represented plant species. In these matrices, a cell ij containing a "1" represented an interaction between insect species i and plant species j , while a cell with a "0" represented no interaction. For part of our data set (9 herbivory networks and 10 pollination networks), we had information on

interaction frequencies through the number of visits or feeding events recorded. For these quantified data, we also constructed quantified interaction matrices where a cell ij contains the frequency of interaction between insect species i and plant species j .

Measure of species connectivity and asymmetric specialization

Asymmetric specialization considers the asymmetry in terms of degree (the number of links per species), it is therefore a qualitative descriptor of network structure, in opposition to quantitative descriptors which take also into account the interaction strengths in the networks (Bersier et al. 2002). For each species, we calculated both the species degree s , and p that is the mean number of interactions of its partners. Thus, low s means high specialization whereas large s means generalization. In parallel, a species with a low p then interacts with species that are relatively specialized while a species with a high p interacts with generalists (Vazquez and Aizen 2004, Vazquez et al. 2005). Asymmetrical specialization will be represented by species that have a low s and a high p or a high s and a low p . Asymmetric specialization can be calculated as the connectivity correlation (s – p correlation), a well-known measure in the study of the structure of complex networks (Melian and Bascompte 2002). It can also be measured as the proportion of species in a network which are significantly more asymmetrical than that would be expected by random (Vazquez and Aizen 2004). We chose to use this last measure of asymmetric specialization as it has often been used recently in studies on asymmetric specialization (Vazquez and Aizen 2004, Vazquez et al. 2005). In order to test whether s – p combination of a species is significantly more asymmetrical than that would be expected by random, we compare these values to randomly generated ones.

To do so, we used two null models employed in the previous analyses for the detection of asymmetric specialization and nestedness (Bascompte et al. 2003, Vazquez and Aizen 2004, Vazquez et al. 2005). In the first null model, interactions were randomly distributed among pairs of plant and insect species; all plant or animal species had the same probability of interacting, regardless of their identity. In the second null model, interactions were assigned proportionally to species' generalism degrees, so that generalist species had a higher probability of being assigned an interaction than more specialist species. Species with observed s – p combination more asymmetrical than predicted by null models were regarded as significantly asymmetrically specialized (Fig. 1). For each network we then calculated separately for insects and plants, the percentage of species that exhibits significant asymmetrical specialization which allows quantification of the level of asymmetric specialization in the network.

A third null model was defined in order to test the hypothesis that the detected asymmetry resulted from the distribution of abundance among species so that species interactions occur randomly among individuals (Vazquez and Aizen 2004, Vazquez et al. 2005). This null model used

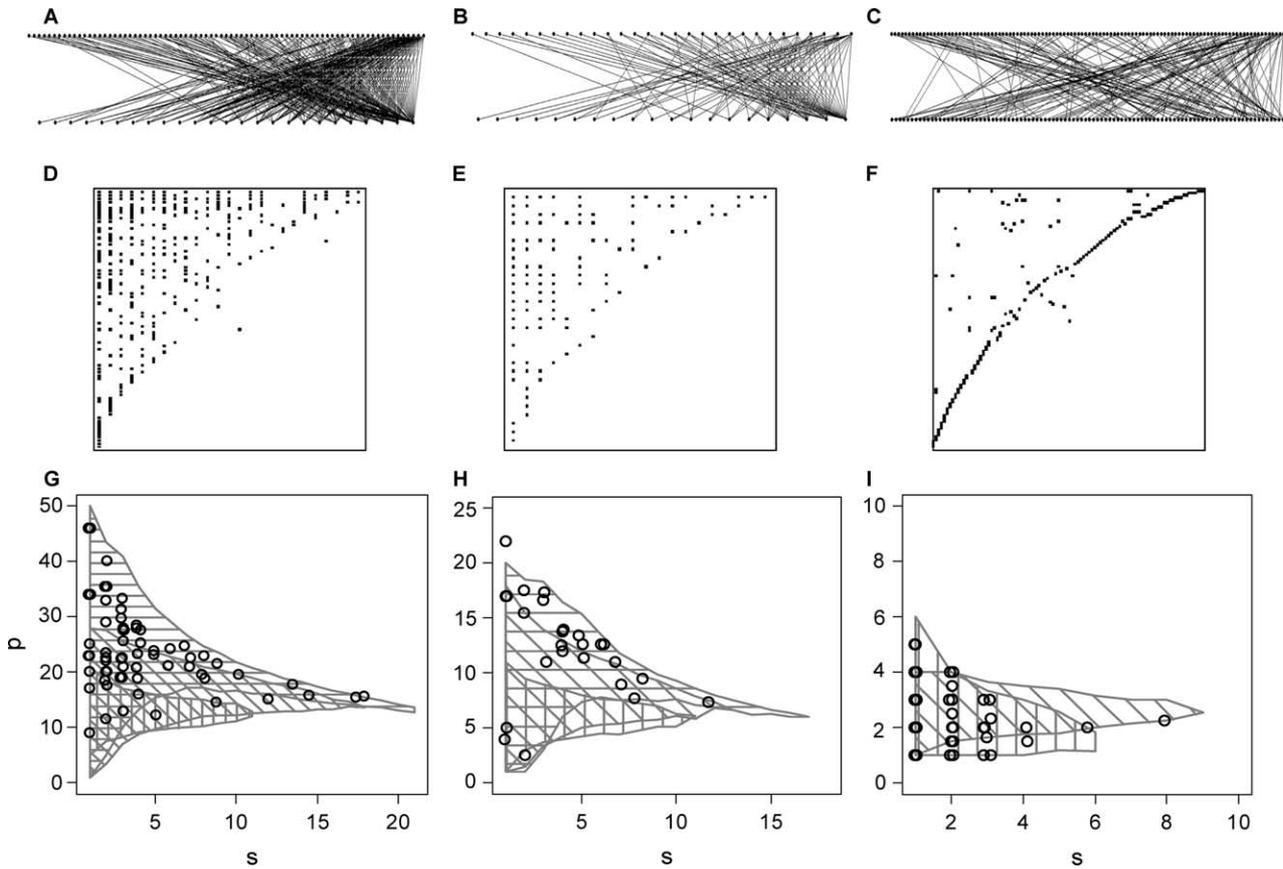


Fig. 1. Comparison between observed s - p combinations and randomly generated ones in plant-pollinator and plant-herbivore networks. Each column corresponds to the representation and the analysis of a given network, left: plant-pollinator network from Memmott (1999), middle: plant-herbivore network from Nakagawa et al. (2003) and right: plant-herbivore network from Janzen (1980). In panels (A)–(C), the networks are represented as bipartite graphs where insect species are the nodes above and plant species are below. Panels (D)–(F) corresponds to the matrices version of the networks with insect species in rows and plant species in columns, rows and columns are arranged to maximize nestedness. In panels (G)–(I), open circles represent the observed s - p values of insect species. In each panel, the vertical hatched area indicates the null space from the null model 1, the diagonal hatched area indicates the null space from the null model 2 and the horizontal hatched area indicates the null space from the null model 3 when quantitative information is available for the network. Open circles that are above or to the right of a null space represent species that are significantly asymmetrically specialized (Vazquez and Aizen 2004, Vazquez et al. 2005). Networks in panels (A)–(C) were drawn in Pajek <<http://vlado.fmf.uni-lj.si/pub/networks/pajek/>>.

information on the frequency of interaction as a surrogate for species abundance; it was thus only applicable for datasets that have quantitative information. Interactions were assigned proportionally to a species' observed interaction frequency, so that frequently interacting species had a higher probability of being assigned an interaction than rarely interacting species. Species with observed s - p combination more asymmetrical than predicted by this null model were regarded as significantly more asymmetrically specialized than predicted from the distribution of abundance in the community.

We also analysed the relation between the proportion of asymmetric interactions and two main network metrics: web size and connectance. Web size corresponds to the total number of species present in the network while connectance measures the number of realized links expressed as a proportion of the total number of possible feeding links in the network (connectance = number of links in the network / (number of plants \times number of insects)).

Statistical analysis

All statistical analyses were performed using R statistical software (ver. 2.21). Connectance was analysed with a linear model (gls function of nlme package) that included the effect of interaction type, the web size as a covariate and the interaction of both. The proportion of asymmetric interactions was analysed with a linear model (gls function of nlme package) that included the effect of interaction type, the web size and the "residual connectance" as covariates, and the second order interactions between interaction type and both covariates. Since there is a strong correlation between web size and connectance, we used as a covariate the residuals of the regressions of the model previously used to analyse connectance (noted residual connectance). This covariate allowed the identification of webs with higher or lower connectance than expected from their size (respectively, positive and negative residuals). When it was necessary, we use the varIdent function of nlme package

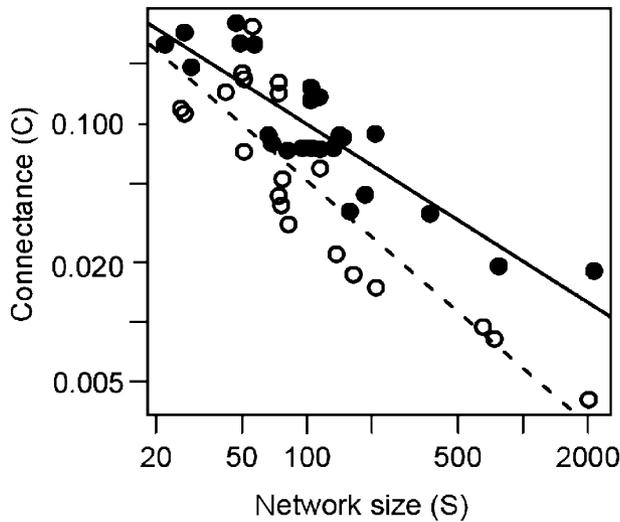


Fig. 2. Connectance of plant-herbivore and plant-pollinator webs according to the network size. Black points correspond to plant-pollinator webs and white points to plant-herbivore webs. Solid and dotted lines represent fitted regression for plant-pollinator webs and plant-herbivore networks respectively.

in order to take into account unequal variance between network types.

Results

As often found in both food webs and mutualistic network studies, connectance was negatively correlated with web size (Fig. 2 and Table S1 in the Supplementary material). In addition, we observed a marginally significant interaction between interaction type and network size (S) ($F_{1,40} = 3.24$, $p = 0.0795$) which indicates that connectance tends to decrease faster in plant-herbivore webs than in plant-pollinator webs (Fig. 2). In other words, large herbivory webs tend to be less connected than equivalent pollination webs.

If we consider first the results with null model 1, our results show that for both plant-herbivore and plant-pollinator networks, a proportion of the species establishes interactions that are significantly asymmetric, having $s-p$ combinations more asymmetrical than predicted by this first null model (Fig. 1, 3). The proportion of such

asymmetric interactions within a community can be very high in both types of networks (mean \pm SE; 0.46 ± 0.04).

The interaction type had a marginally significant effect on asymmetry for the insect side of the networks (mean proportion: 0.57 and 0.24 respectively for pollination and herbivory networks; Table 1, null model 1, $p = 0.0924$). This indicates a tendency for lower asymmetry in plant-herbivore networks. Although interaction type has only a marginal effect on the mean proportion of asymmetric interactions, it has a significant effect on the medians (0.60 and 0.14 respectively for pollination and herbivory networks; $\chi^2_1 = 4.49$, $p = 0.0341$). This indicates that the distribution of asymmetry was different between network types with most of the pollination networks being highly asymmetric and most of the herbivory networks being weakly asymmetric (Fig. 3A). The same was true for the plant side of the networks ($\chi^2_1 = 7.43$, $p = 0.0064$; Fig. 3D). It should be noted that the plant and insect sides of the networks have here differing levels of asymmetric specialisation as the networks are not symmetric.

Although asymmetry was significantly positively correlated with web size, the significant interaction between the type of interaction and network size indicated a more complex relation for both plant and insect sides of the webs (Table 1, null model 1). Indeed, as illustrated in Fig. 3B and 3E, network size had a positive effect on the asymmetry of plant-pollinator webs (for insects, slope: 0.15, $p = 0.001$; for plants, slope: 0.15, $p = 0.0016$) but had no effect for plant-herbivore webs (for insects, slope: 0.01, $p = 0.880$; for plants, slope: 0.04, $p = 0.387$). On the contrary, as indicated by the significant interaction between interaction type and residual connectance for the insect side of the webs (Table 1), residual connectance had a positive effect on the asymmetry of plant-herbivore webs (slope: 0.56, $p < .0001$) and had no effect on the asymmetry of plant-pollinator webs (slope: 0.09, $p = 0.53$) (Fig. 3C). For the plant side of the webs, we found a marginally significant positive effect of residual connectance (Table 1, null model 1, $p = 0.067$). However, as shown in Fig. 3F, this effect was more clear for herbivore webs than for pollination webs (for plant-pollinator webs, slope: 0.20, $p = 0.145$; for plant-herbivore webs, slope: 0.38, $p < .0001$). In other words, whereas web size but not residual connectance had an effect on asymmetry in plant-pollinator networks, we observed the opposite pattern for plant-herbivore networks.

The null model 2 predicted better the asymmetrical specialization present in our dataset than the previous null

Table 1. Analysis of the percentage of species showing interactions which are more asymmetric than predicted by the null models 1 and 2. Values in bold highlight $p < 0.05$.

Effects	DF	Null model 1				Null model 2			
		Insects		Plants		Insects		Plants	
		F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
Interaction type	1,38	2.11	0.0924	0.70	0.4076	1.72	0.1972	8.83	0.0051
Network size	1,38	14.15	0.0001	13.98	0.0006	4.48	0.0408	24.47	<0.0001
Residual connectance	1,38	0.58	0.3752	3.57	0.0665	0.00017	0.9897	1.23	0.2748
Inter. type \times network size	1,38	6.16	0.0085	5.25	0.0275	3.02	0.0903	15.48	0.0003
Inter. type \times res. connectance	1,38	12.66	0.0003	2.34	0.1341	8.58	0.0057	0.44	0.5133

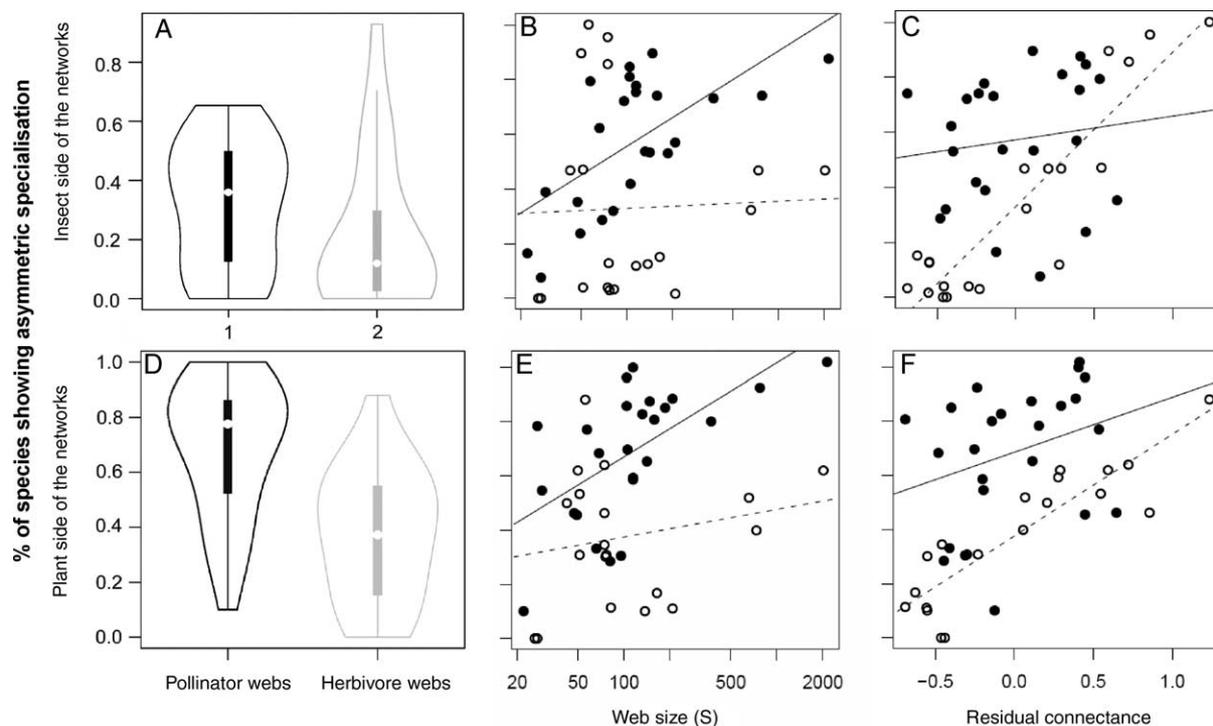


Fig. 3. Percentage of species showing asymmetric interactions of plant–pollinator and plant–insect herbivore webs predicted by null model 1, for the insect and the plant side of the networks (upper and lower part of the graph respectively). Panels (A) and (D) represent the distribution of data points for pollination and herbivory networks separately (black and grey, respectively). Vertical straight lines represent the range of the distribution, vertical rectangles range from the lower to the upper quartile, white points represent the median and the width of the surrounding shape is proportional to the number of networks that have a given percentage of asymmetric interactions. Panels (B) and (E) represent the relationships between the percentage of asymmetric interaction and web size. Panels (C) and (F) represent the relationships between the percentage of asymmetric interaction and residual connectance. For panels (B), (C), (E) and (F), each point is a network. Black points correspond to plant–pollinator webs and white points to plant–herbivore webs. Solid and dotted lines represent the regression lines fitted by the linear model for plant–pollinator webs and plant–herbivore networks respectively.

model. Indeed constraining the randomization process to fit the distribution of generalism degree of the data leads to a global decrease of the percentage of significant asymmetric interactions in both types of networks (Fig. 3, 4). However, the same overall pattern as with the null model 1 arises from the remaining asymmetry (Fig. 4). The interaction type had a significant effect on asymmetry for the plant side of the networks (Table 1, null model 2, $p=0.0051$) which indicates again a lower frequency of asymmetric specialization in plant–herbivore networks. For the insect side of the webs, we found again a significant interaction between the type of interaction and residual connectance as well as a marginally significant interaction between the type of interaction and network size. For the plant side of the webs, the interaction between the type of interaction and network size was highly significant (Table 1, null model 2).

Finally, the percentage of asymmetric interaction revealed by the third null model that assumes random interaction among individuals is lower than for null models 1 and 2 for both types of networks (see in Fig. 1 an example of two networks). This indicates that the null model 3 predicts even better the observed patterns than the other null models. Although the dataset was half as small (10 and

9 plant–pollinator and plant–herbivore networks, respectively) the same qualitative results as with null model 1 and 2 were found but as tendencies, except for the interaction between network type and residual connectance that was not present any more (Table S2 in the Supplementary material).

Discussion

This work provides to our knowledge the first extensive comparison between mutualistic and antagonistic networks of similar format and resolution. The degree of resolution and aggregation of networks data is a problem inherent to all comparisons between networks (Martinez 1991) and it becomes even more accurate when different types of networks are considered: food webs and mutualistic networks traditionally differ greatly in their level of aggregation (trophic group vs taxa level), and in the way they are represented (directed graphs vs bipartite graphs, (Bascompte et al. 2003)). Moreover our dataset deals with the same type of organisms, plants and insects, thus limiting biological differences among network types. By using data on

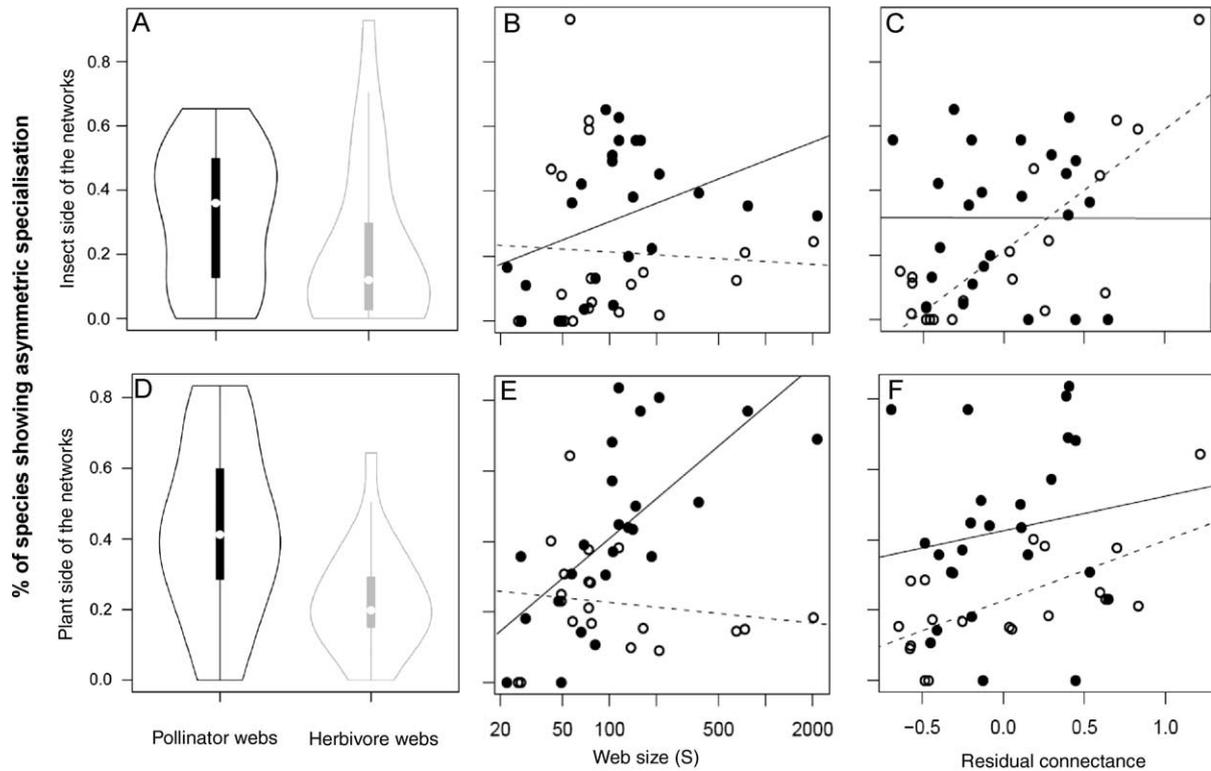


Fig. 4. Percentage of species showing asymmetric interactions of plant–pollinator and plant–insect herbivore webs predicted by null model 2, for the insect and the plant side of the networks (upper and lower part of the graph respectively). Panels (A) and (D) represent the distribution of data points for pollination and herbivory networks separately. Vertical straight lines represent the range of the distribution, vertical rectangle range from the lower to the upper quartile, white points represent the median and the width of the surrounding shape is proportional to the number of networks that have a given percentage of asymmetric interactions. Panels (B) and (E) represent the relationships between the percentage of asymmetric interaction and web size. Panels (C) and (F) represent the relationships between the percentage of asymmetric interaction and residual connectance. For panels (B), (C), (E) and (F), each point is a network. Black points correspond to plant–pollinator webs and white points to plant–herbivore webs. Solid and dotted lines represent the regression lines fitted by the linear model for plant–pollinator webs and plant–herbivore networks respectively.

plant–insect assemblages, we aimed to minimize these potential biases in order to investigate more precisely if networks patterns differ depending on interaction type. However, differences between the ways these two types of networks are sampled remain. Particularly, plant–herbivore studies are focused on a particular taxon and they differ in the feeding categories considered (for example seed-eating or leaf-chewing insects) whereas plant–pollinator studies tend to survey all flower visiting animals regardless of the taxon. This bias might lead to emphasize the variability among the structure of plant–herbivore networks compared to plant–pollinator networks where the feeding types as well as the taxa present are more similar between the networks. As we couldn't find plant–herbivory network dataset which includes several herbivore taxa, it is difficult to predict exactly how this bias could affect our results.

Using appropriate null models is essential to highlight particular structures in networks and to test simple hypotheses to understand their occurrence. Our analysis considered three different null models. The first two models are the main null models which have been used for the detection of asymmetrical specialization and nestedness in networks (Bascompte et al. 2003, Vazquez and Aizen 2004,

Guimaraes et al. 2006). While the first one is very general and detects patterns which differ from the expectation that species interact randomly with each other, the second null model detects deeper patterns beyond the ones explained by the distribution of the generalism degree in the network (Bascompte et al. 2003). Lastly, by using information on the frequency of interaction as a surrogate for species abundance, the third null model allows to test if the detected asymmetry results from the distribution of abundance among species so that species interactions occur randomly among individuals (Vazquez et al. 2005). By the use of these three null models, we aimed to have an overview of the differences between plant–pollinator and plant–herbivore networks regarding asymmetric specialization in these networks.

Both the analysis with null model 1 and null model 2 emphasizes that several key features differ between plant–herbivore and plant–pollinator networks. First of all, they suggest that asymmetric specialization is more frequent in plant–pollinator networks than in plant–herbivore networks; this result corroborates the idea that asymmetric specialization is a major feature of mutualistic networks, as recently emphasized by the analysis of Bascompte et al.

(2003) and Vázquez and Aizen (2004). Nevertheless, the presence of asymmetric specialization is not specific to mutualistic networks contrary to what is sometimes suggested: our analyses provide the evidence that plant–herbivore networks can be highly asymmetric as already found for host–parasite interactions (Vazquez et al. 2005). Moreover, our results tend to indicate that plant–herbivore and plant–pollinator networks might differ in the mechanisms which contribute to asymmetric specialisation. Whereas asymmetry appears to be linked with the total number of species in plant–pollinator networks, it is the connectance of the web which has a major effect on asymmetric specialization in plant–herbivore networks. Indeed, for plant–pollinator networks, large assemblages tend to have a higher proportion of asymmetric interactions than smaller assemblages while for plant–herbivore networks, communities that are more connected than expected from their size tend to have a higher proportion of asymmetric interactions than communities that are less connected. Various non-exclusive hypotheses can be made to explain the observed differences between plant–pollinator and plant–herbivore networks. These hypotheses, discussed hereafter, involve either coevolutionary mechanisms or ecological mechanisms.

Several studies have proposed that the coevolutionary mechanisms which act on networks' development may differ depending on interaction type (Thompson 2005, Bascompte et al. 2006). While the development of mutualistic networks might be based on complementarity and convergence of traits in interacting species, antagonistic networks may result from the coevolution of defences and counter defences between interacting species, leading to “arms races” between these species (Thompson 2005). In this latter case, the selective pressure encourages the prey to escape the interaction, preventing predators from incorporating more species into their diets. Antagonistic coevolution may thus favour reciprocal specialisation in defences and counter-defences leading to greater symmetric specialisation in antagonistic networks. In contrast, for mutualistic interactions, the selective pressure encourages species to become more adapted to each other, which might favour the incorporation of new species in an interaction, leading to the emergence of asymmetrical specialisation (Thompson 2005). Regarding plant–herbivore networks, the importance of coevolution processes may also depend on the type of insect herbivores considered, depending on their feeding category (Tscharnkte and Greiler 1995). Internal feeders are known to be more specialized than external feeders (Novotny and Basset 2005) and tighter relations of the former with their host plants might favour coevolution processes leading to symmetric interactions, which may explain the link between residual connectance and asymmetry in plant–herbivore networks. From another point of view, the link between network size and asymmetry in plant–pollinator networks might be explained by the fact that species-poor communities might not have sufficient number of species for the evolution of species specialized in interacting with generalist species (Guimaraes et al. 2006) or, species poor communities might be degraded systems that have already lost their specialist species.

Ecological mechanisms might also explain the observed patterns. One of the main explanations to the patterns of asymmetrical specialization in networks is that they are linked to the distribution of abundance among species and arise from random interactions among individuals (Vazquez et al. 2005, 2007). Several studies have emphasized the link between the distribution of abundance and asymmetry for both mutualistic and antagonistic networks (Vazquez and Aizen 2004, Vazquez et al. 2005, 2007). Our results support these findings as the null model 3, which accounts for the distribution of abundance, revealed lower levels of asymmetrical specialisation for both types of networks (Fig. 1). This indicates that an important part of the asymmetry detected by the first two null models can be related with the differences in species abundance within the communities and random interactions among individuals. However, first, the last null model fails in predicting all the asymmetry present in the data, which means that other mechanisms might contribute to it. Second, although only half of the networks have been used for this analysis, part of the differences between plant–pollinator and plant–herbivore networks remain. Thus, differences in the distribution of abundance of species between plant–pollinator and plant–herbivore networks don't seem to be the only cause of the observed differences in their asymmetrical specialization.

Environmental fluctuations can also promote asymmetrical specialisation. The specialization–asymmetry–disturbance hypothesis proposes that for mutualistic networks, both generalization and highly asymmetric specialization should be favoured in unpredictable environments (MacArthur 1955, Waser et al. 1996, Vazquez and Simberloff 2002, Vazquez and Aizen 2004). Indeed, in such an environment, the more generalist a species is, the lower the fluctuations of its population might be, since it depends on several resources (MacArthur 1955). As a consequence, generalist species might provide opportunities for specialization of other species, leading to highly asymmetric specialization (Vazquez and Aizen 2004). However, if this mechanism prevails, we might expect a link between connectance (that is a measure of average generalization in a web) and asymmetric specialisation in plant–pollinator networks, which is not the case here. Turning to plant–herbivore networks, the structure of the network of Nakagawa et al. (2003) suggests that generalization and asymmetric specialization could also be both favoured in unpredictable environment in this type of networks, but through a slightly different mechanism. In this highly connected and asymmetric network, while plant composition differs strongly between the two years considered in the study, insects can show important changes in diet and interact with the abundant species present (Nakagawa et al. 2003). As emphasized earlier, patterns of asymmetric specialization can arise from interactions determined by species abundance. A link between generalization and flexibility in diet depending on species abundance might then provide a possible explanation for the link between connectance and asymmetric specialisation in plant–herbivore networks.

Other ecological processes such as indirect effects can also be an important structuring factor of the communities. In particular, in antagonistic webs such as host–parasite

networks, negative indirect effects such as apparent competition have been shown to restrict the share of interaction partners (van Veen et al. 2006), and thus may favour more symmetrical interactions. In mutualistic networks, these indirect effects might either result in apparent mutualism or competition (Ghazoul 2006, van Veen et al. 2006) and thus could favour both symmetric and asymmetric interactions. However, more studies are needed to clearly assess their impact on community structure in mutualistic networks and how it differs from that of antagonistic networks.

Another important question concerns the implications of these differences between plant–pollinator and plant–herbivore networks. From an evolutionary perspective, in asymmetric networks, generalist species might represent strong selective agents for their specialist interaction partners whereas generalists may be more influenced by a few of their generalist partners. Thus, asymmetric specialisation might lead to selective asymmetry where specialists are strongly selected by generalists but not vice versa. From an ecological perspective, asymmetry has been recently emphasized to enhance long-term coexistence and to facilitate biodiversity maintenance in mutualistic networks (Bascompte et al. 2006) but its impact on the functioning of trophic networks is more controversial and clearly needs more attention.

Our results suggest that mutualistic and trophic interaction networks differ in their structure, which tend to indicate that the mechanisms that contribute to generate them are different. While asymmetric specialization seems to be linked with web size in plant–pollinator networks, it is the connectance of the web which is related with this pattern in plant–herbivore networks. Several non-exclusive hypotheses including evolutionary and ecological processes can be made to explain these differences but it is difficult to tell the degree to which these differences are driven by evolutionary dynamics or by ecological interactions. With a few exceptions (Matsuda et al. 1996, Bascompte et al. 2006), there is a lack in theoretical studies which investigate how adaptive and ecological processes affect the architecture of mutualistic and antagonistic bipartite networks, and more work is clearly needed to understand the processes to the origin of these network patterns.

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Supplementary material available online as Appendix O16485 at www.oikos.ekol.lu.se/appendix. Table S1: analysis of the connectance; Table S2: analysis of the level of asymmetrical specialization predicted by model null 3; Appendix S1: list of the networks analyzed.