SPECIAL FEATURE: ORIGINAL ARTICLE

Comparing the conservatism of ecological interactions in plant–pollinator and plant–herbivore networks

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Abstract Conservatism in species interaction, meaning that related species tend to interact with similar partners, is an important feature of ecological interactions. Studies at community scale highlight variations in conservatism strength depending on the characteristics of the ecological interaction studied. However, the heterogeneity of datasets and methods used prevent to compare results between mutualistic and antagonistic networks. Here we perform such a comparison by taking plant–insect communities as a study case, with data on plant–herbivore and plant–pollinator networks. Our analysis reveals that plants acting as resources for herbivores exhibit the strongest conservatism in species interaction among the four interacting groups. Conservatism levels are similar for insect pollinators, insect herbivores and plants as interacting partners of pollinators, although insect pollinators tend to have a slightly higher conservatism than the two others. Our results thus clearly support the current view that within antagonistic networks, conservatism is stronger for species as resources than for species as consumer. Although the pattern tends to be opposite for plant–pollinator networks, our results suggest that asymmetry in conservatism is much less pronounced between the pollinators and the plant they interact with. We discuss these differences in conservatism strength in relation with the processes structuring plant–insect communities.

Keywords Antagonistic · Communities · Interaction network · Mutualistic · Phylogenetic signal

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Introduction

In the past decade, our understanding of the processes structuring ecological communities has gained new insights by the incorporation of species evolutionary history (Webb et al. 2002; Cavender-Bares et al. 2009; Mouquet et al. 2012). Although mainly used to understand the distribution and coexistence of species within a given trophic level (e.g., Elias et al. 2008), phylogenetic information has recently been included to study the processes shaping the structure of multitrophic communities (e.g., Rezende et al. 2007; Cagnolo et al. 2011; Krasnov et al. 2012; Naisbit et al. 2012; Elias et al. 2013). It is expected that closely related species interact with similar partners if the species traits involved in interspecific interactions are shared among related species. Such phylogenetic constraints on the way species interact can potentially determine the complex structure of food webs (Cattin et al. 2004). Meanwhile, both trait evolution and species coexistence strongly depend on local community interactions: for example competition between related species is expected to limit niche conservatism and to lead to phylogenetic overdispersion (Webb et al. 2002). Unravelling

the links between phylogeny and interaction networks should thus help to shed lights on the relative importance of phylogeny and local ecological processes on network structure (e.g., Elias et al. 2013).

Conservatism in species interaction, that is to say the tendency for related species to share interaction partner due to maintenance of ancestral ecological characteristics, appears to be a pervasive feature of ecological interactions. By compiling a large dataset across several kingdoms considering all known interactions for various clades, Gómez et al. (2010) concluded that occurrence of conservatism in ecological interactions was high and did not depend on interaction characteristics such as the intimacy (symbiotic or non-symbiotic) or the sign (mutualist or antagonist) of interactions. However, such a clade orientated perspective, by considering all interactions per clade, might not be the best suited to look for the relation between species evolutionary history of species, network structure and interaction characteristics. Interactions between species occur locally and are expected to have greater importance on the phylogenetic structure of communities at small spatial and taxonomic scales (Cavender-Bares et al. 2006). This is because interactions affect local adaptation and local community coexistence constraints. Indeed, studies at community scale often highlight variations in conservatism strength depending on the characteristics of the ecological interaction studied.

Within trophic and parasitic networks, interaction conservatism is often stronger for resources than for consumers. This means that related prey species tend to share more consumers than related consumers share prey species (Ives and Godfray 2006; Bersier and Kehrli 2008; Cagnolo et al. 2011; Krasnov et al. 2012; Naisbit et al. 2012), suggesting that "vulnerability traits" evolve slower than "foraging traits" (Rossberg et al. 2006). Lower conservatism in interaction for consumers can even turn into phylogenetic over-dispersion, where related consumers tend to have no overlap in the resources they consume (Elias et al. 2013). This negative correlation between phylogenetic relatedness and resource overlap suggests that negative indirect interactions mediated by resources or natural enemies (Denno et al. 1995; Kaplan and Denno 2007; Rezende et al. 2009; Elias et al. 2013), or such as reproductive interference (Noriyuki et al. 2012; Kishi and Tsubaki 2013) can generate strong selection for closely related consumers to shift resources.

Although less investigated, asymmetry in conservatism of interactions among interacting partners has also been documented in mutualistic networks (Thompson et al. 2013). For pollination and frugivory interactions, conservatism of animal interactions tends to be stronger than conservatism of plant interactions, meaning that related animals overlap in their set of resources more than related plants overlap in their interactions with animals (Rezende et al. 2007; but see Rafferty and Ives 2013). This pattern seems to differ from the one reported for antagonistic interactions where conservatism of interactions is weakest for species involved in active foraging—i.e., the consumers. A strong asymmetry in the strength of conservatism between two interacting groups suggests that the group with the higher conservatism has driven the evolution of the network (Jordano 2010). However, comparison between studies on mutualistic and antagonistic networks is not straightforward because they differ in the taxonomic and phylogenetic resolution of the datasets used as well as in the methods to assess interaction conservatism. We currently do not know whether the difference in conservatism observed within mutualistic networks is more important than the one observed within antagonistic networks.

There is growing evidence that network structure and related ecological and evolutionary dynamics depend on interaction type (i.e., mutualistic or antagonistic) (Fontaine et al. 2011); however, it is still far from clear how interaction type is related to the level of interaction conservatism (Jordano 2010). In any cases, differences in the level of interaction conservatism might be related to differences in the balance between the phylogenetic constraints on species traits, bounding related species to behave similarly, and a series of adaptations which allows species to diverge in their ecology (Price 2003). The adaptive value of sharing a mutualistic partner might be higher than the one of sharing an antagonistic partner since positive indirect interactions can be expected in mutualistic networks (e.g., Ghazoul 2006). Meanwhile, negative indirect interactions tend to arise in antagonistic networks. Such positive indirect interactions could promote interaction conservatism but also trait convergences. On the other hand, negative indirect interactions should promote shift in interaction partners and thus lower conservatism.

We propose here to further our understanding of the relationship between the type of interaction (mutualistic or antagonistic) and the interaction conservatism, taking plant–insect communities as a case study. Plants and insects represent an important part of biodiversity, and are interacting either mutualistically (pollination) or antagonistically (herbivory). Furthermore, both types of communities have been studied through the network lens, with a decent number of datasets available with species level resolution and similar data collection protocols (observed interactions in a community context). Using 69 highly resolved interaction networks that depict either plant–pollinator or plant–herbivorous insect interactions, we compare the relationship between the taxonomical relatedness of species and their overlap in interaction partners. Specifically, we investigate whether closely related species

overlap more (or less) in their set of interacting partners depending on whether interaction is mutualistic or antagonistic and on whether the focal species interact as a consumer or as a resource. We then discuss the implication of our findings regarding the ecological and evolutionary processes shaping plant–insect interaction networks.

Materials and methods

We analysed 69 datasets from published community-wide studies of plant–pollinator ($n = 42$) and plant–herbivorous insect ($n = 27$) networks (Electronic Supplementary Material (ESM) S1) consisting in lists of insects associated with their interacting plants. To be included in our analysis, a study had to meet the following criteria: (1) the data should include a minimum of seven 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 insects should be provided by relying on direct observation and for herbivores on gut content analysis or experimental verification of insect feeding via insect rearing.

To investigate variation in interaction conservatism among networks, we calculated the correlation between the overlap in interacting partners and the taxonomic relatedness of species. The overlap in interaction partners between pairs of species was estimated using the Jaccard index. To calculate taxonomic relatedness, we first constructed a taxonomic tree grouping species within genus, within family, within order. We checked for all species that the taxonomical levels used were up to date using APGIII for plants and the Interim Register of Marine and Non-marine Genera (Rees 2006) as well as the Global Names Index (Patterson et al. 2010) for insects. Following Rezende et al. (2007), we then set the branch lengths using the Grafen methodology (Grafen 1989) where branch length from the common ancestor of a clade to the leaf is proportional to the number of leaves of the clade. The taxonomic relatedness between any two species is then the sum of the branch length from tip to their "common ancestor".

We tested for a correlation between the taxonomic relatedness and the overlap in interacting partners using Mantel tests. Mantel tests are appropriate because data can be expressed as pairwise distances among taxa (Harmon and Glor 2010). Further, it is commonly used in phylogenetic analyses of interaction networks (Cattin et al. 2004; Rezende et al. 2007; Bersier and Kehrli 2008; Bailey et al. 2009; Jacquemyn et al. 2011; Naisbit et al. 2012) making comparison with previous studies easier. To assess the strength of the relationship, we quantified deviation of the observed correlations from the null expectations of the Mantel test by calculating Z scores. Z score $= (x - \mu)/\sigma$,

where x is the observed Mantel's statistic value and μ and σ are its mean and SD across 1,000 permutations.

We used mixed effects models (Pinheiro and Bates 2000) to test the effects of several covariates on the r statistics and Z scores obtained for both plants and insects. First, as Mantel tests are known to be sensitive to sample size, we included the number of either plants or insects as a covariate. We log transformed this variable to insure linearity (natural log). Second, the taxonomic span of the various networks could affect the level of conservatism, with conservatism increasing as we include more distantly related clades. To control for that, we included the mean taxonomical distance among either plants or insects as a covariate in the model. Third, to investigate a potential link between network structure and interaction conservatism, we included the residual connectance of the networks after accounting for network size effect. We used residual connectance instead of connectance to insure independence among covariates, in particular with the number of plants or insects (ESM S2). Fourth, we included the interacting groups as a factor, with four levels: either plant-eaten, plant-pollinated, insect–pollinator or insect–herbivore. The full model included all covariates and the two ways interactions. We included network identity as a random factor. Finally, we accounted for heteroscedasticity using the varExp function (Pinheiro and Bates 2000). Model simplification procedures were performed using Akaike's Information Criterion (AIC, Crawley 2007).

Results

For plants, we found a positive correlation between the taxonomic relatedness and the overlap in interacting partners in 83 % of the pollination and 96 % of the herbivory networks. Mantel tests indicated that the positive correlation was significant for 51 % of the pollination and 58 % of the herbivory networks (Fig. 1). Regarding insects, we found a positive correlation between the taxonomic relatedness and the overlap in interacting partners in 98 % of pollination and 78 % of herbivory webs. The positive correlation was significant for 80 % of pollination and 43 % of herbivory networks (Fig. 1). We did not find significant negative correlation in any pollination or herbivory network.

The minimum adequate model for the r statistic included a significant effect of the interacting group meaning that the correlation between taxonomic relatedness and overlap in interacting partners varied among interacting partners (Table 1). The highest correlation was found for plants interacting with herbivores, followed by pollinating insects, plants interacting with pollinators and by herbivorous insects (Fig. 2). Post-hoc tests with Holm-Bonferroni
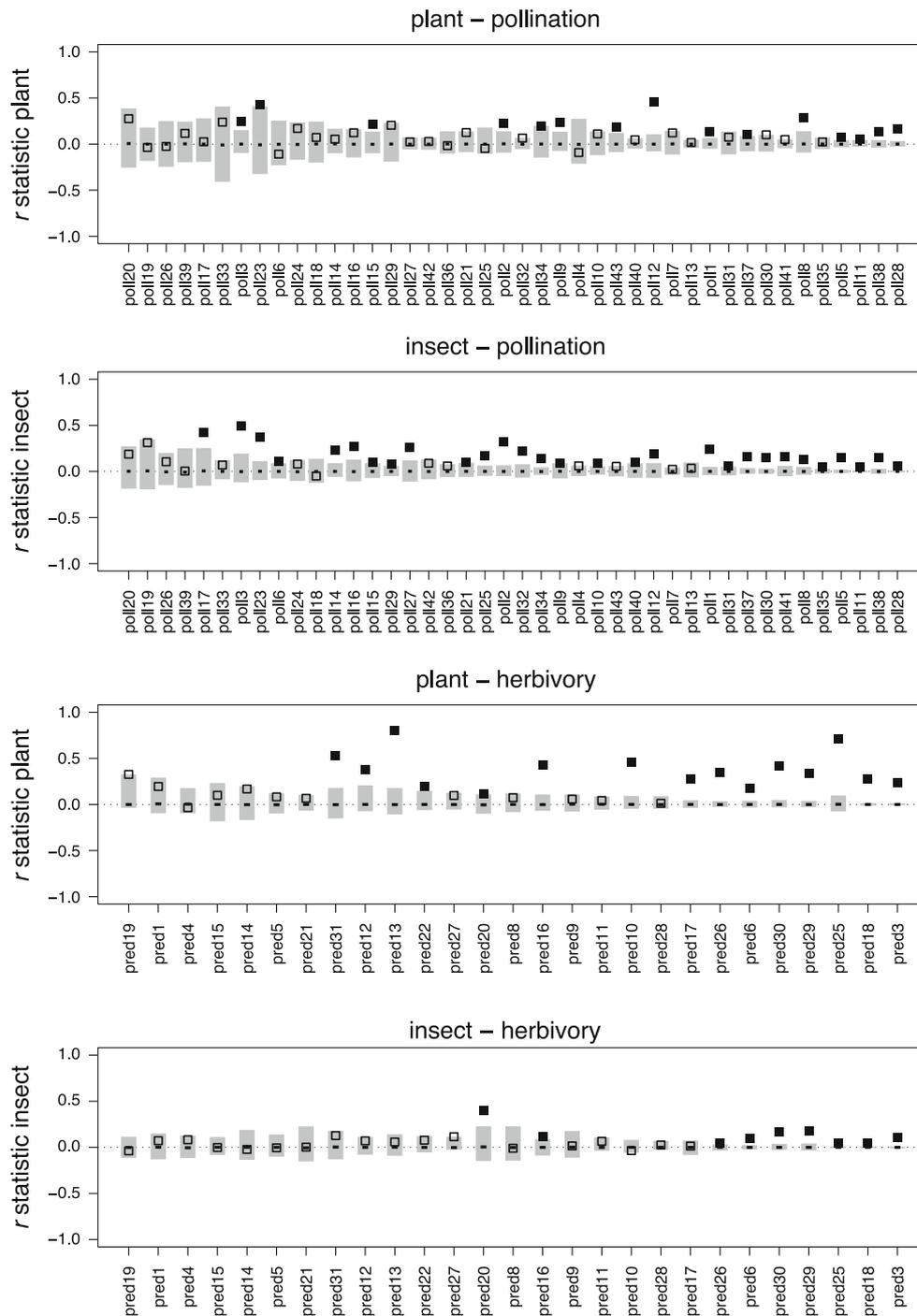
Fig. 1 *R* statistics of Mantel tests between taxonomic relatedness and overlap in interacting partners for the plant and insect levels of each network. *Squares* represent observed values for pollination and herbivory networks. *Grey bars* represent 95 % confidence intervals of the Mantel randomization. *Filled symbols* represent values that are significantly different from the randomization. Networks are ordered in increasing size

corrections indicated that plant interacting with herbivores had a significantly higher correlation between taxonomic relatedness and overlap in interacting partners than the other interacting groups. Correlation for pollinators was only marginally significantly higher than correlation for

herbivores and plants as interacting partners of pollinators (Table 2). Our analysis further revealed a significant effect of the number of species, showing a slight decrease in the mean *r* statistic with increasing number of species. The mean taxonomical distance and the connectance were

Table 1 Results of the minimum adequate model predicting Mantel's r statistic

	df	F value	P value
Log(species number)	1, 65	7.38	0.0084
Interacting group	3, 65	12.78	<0.0001
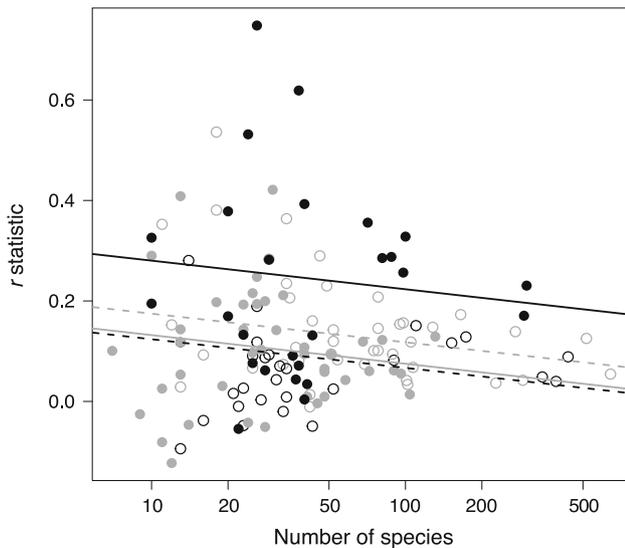
Fig. 2 Relationships between the Mantel's r statistic and species number of either plants or insects on a log scale. Pollination networks are described in *grey* and herbivory networks in *black*. *Filled symbols* represent plants and *open symbols* insects. *Solid* and *dashed lines* represent predictions of the minimum adequate model for plants and insects respectively

Table 2 Comparison of the mean r statistics among the four interacting groups

	Plants consumed by herbivores	Pollinators	Herbivores
Plants consumed by pollinator	−0.148***	−0.043*	0.008
Plants consumed by herbivores		0.106**	0.156***
Pollinators			0.051°

Numbers indicate differences in predicted mean r statistic (row minus column). Significance levels were calculated using Holm-Bonferroni correction for multiple comparisons and are noted as follow: *** $P < 0.0001$, ** $P < 0.001$, * $P < 0.05$, ° $P < 0.1$

dropped from the model during the simplification procedure.

Analysis of the strength of the relationship between taxonomic relatedness and overlap in interacting partners (measured as the Z score) gave similar results to the r statistic (ESM S3).
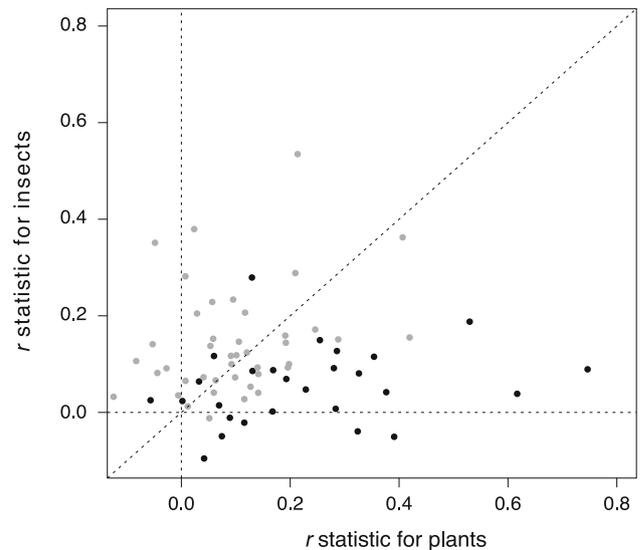
Fig. 3 Relationships between the Mantel's r statistic for plants and insects within networks. Pollination networks are in *grey* and herbivory networks are in *black*

Within networks, the correlation tended to be greater for insects than for plants in pollination networks (t test on the difference in correlation: $t = 2.12$, $df = 41$, $P = 0.045$) whereas it was the opposite for herbivory networks ($t = -4.81$, $df = 26$, $P < 0.001$) (Fig. 3).

Discussion

Our analysis highlights that within plant–insect communities, the conservatism in species interaction varies depending on the type of interactions, i.e., pollination versus herbivory, and on whether we consider interaction from the resource or the consumer perspective. Overall, plants acting as resources for herbivores exhibit the strongest conservatism in species interaction of the four interacting groups. Conservatism levels are similar between insect pollinators, insect herbivores and plants as interacting partners of pollinators, even if insect pollinators tend to have a slightly higher conservatism than the two others. Our results thus clearly support the current view that within antagonistic networks, conservatism is stronger for resource species than for consumer species (Bersier and Kehrli 2008; Cagnolo et al. 2011; Krasnov et al. 2012; Elias et al. 2013). Although the pattern tends indeed to be the opposite for plant–pollinator networks (Rezende et al. 2007), our results show that the difference in conservatism between the pollinators and the plants they interact with is much smaller. Lastly, our results reveal that conservatism levels differ whether we consider plants acting as resources or as interacting partners of pollinators, whereas pollinators and herbivores show similar conservatism levels. We

discuss below the implications of these findings on our understanding of the processes structuring plant–pollinator and herbivore communities.

For plant–herbivore communities, stronger conservatism for plants than for insects indicates that plant vulnerability traits, such as mechanical and/or chemical defences, are much more conserved among related plants than foraging or detoxifying traits are among related herbivorous insects. The high conservatism of plant defences is consistent with the view that the biosynthetic pathways that produce defence compounds are complex enough that they probably can evolve only once or a few times, followed by minor modification within clades (Agrawal 2007). Such conservatism in plant defence compounds have been nicely exemplified with alkaloids (Wink 2003; Wink and Mohamed 2003; Liscombe et al. 2005). This high plant conservatism in species interaction is also consistent with previous results from Fontaine et al. (2009) showing a low phylogenetic generalism of herbivores. Indeed if herbivores consume closely related plants, it implies that closely related plants share the same consumers. The relatively lower conservatism for herbivorous insects suggests that host shifts might be relatively common among related herbivorous insects. For herbivores, host shifts more likely occur as a way to find enemy free space (Murphy 2004) or to avoid reproductive interference (Noriyuki et al. 2012; Kishi and Tsubaki 2013) rather than to escape competition for resources because green plant material (i.e., food) is plentiful (Hairston et al. 1960). However, host shifts are clearly not the rule as the mean correlation remains positive suggesting that the selection pressure for host shift is not strong enough to fully counterbalance the phylogenetic inertia that herbivores have on their foraging and/or detoxifying traits. A negative correlation would have been indicative of a stronger selection for host shift, but so far this has been shown only for trophic levels higher than herbivores (Rezende et al. 2009; Elias et al. 2013).

Turning to plant–pollinator communities, the overall level of interaction conservatism was rather low, comparable to the one for herbivorous insects. On the plant side, this result is consistent with the many studies showing convergence in floral traits related to pollinator attraction such as floral colour (Weiss 1995), scent (Andersson et al. 2002; Nielsen and Bascompte 2007; Schiestl and Dötterl 2012) and morphology (Schemske 1981), leading to few pollination syndromes (Fenster et al. 2004). On the pollinator side, relatively low levels of interaction conservatism might be explained by the same mechanisms discussed for herbivores. Pollinators are consumers as well since they actually feed on plant materials, i.e., plant rewards. Competition among pollinators for plant rewards is an important feature of plant–pollinator interactions (Zimmerman and Pleasants 1982; Fontaine et al. 2009; Staniczenko et al.

2013; Fründ et al. 2013) and might lead to host shifts as a way to escape inter-specific competition.

The difference in the asymmetry of interaction conservatism between plant–pollinator and plant–herbivore webs indicates that the co-evolutionary dynamic shaping these webs differs. Co-evolutionary models for trait evolution also emphasize different co-evolutionary dynamics in mutualistic and antagonistic communities. While for antagonistic interactions, models predict escalation in defenses and counter-defense traits, or cycles in defenses and counter-defenses (Nuismer et al. 2005; Nuismer and Thompson 2006), they predict trait convergence and complementarity for mutualistic interactions (Nuismer et al. 2013). The high asymmetry we observed in plant–herbivore network further suggests that plant evolutionary history has been the main driver shaping these networks. Indeed, closely related plants tend to interact with similar sets of herbivores, but these animal species are not much taxonomically related. In other words, a plant can be consumed by a taxonomically wide range of herbivores, but an herbivore would tend to exploit a set of taxonomically restricted plant species. Such a pattern suggests that some phylogenetic constraints on plant defense traits lead to clade specific defense syndrome, while herbivore specialization on these syndromes is weakly constrained phylogenetically. Turning to plant pollinator communities, plants and animals evolutionary history seems to have contributed both to the networks evolution. This lower, but more balanced, impact of species evolutionary history on the evolution of networks is consistent with a mutualistic network evolution where both convergence and complementarity processes are favored (Jordano 2010; Guimarães et al. 2011), and this for both groups of interacting partners. Convergence among distant clades should tend to facilitate species persistence within mutualistic networks through positive indirect interactions (Guimarães et al. 2011), whereas complementarity as a result of phenotypic matching between interacting partners should be selected to facilitate how the species efficiently uses the mutualistic services provided by the partners (Jordano 2010). To sum up, although more work is clearly needed to understand the impact of species evolutionary history on interaction networks, our results suggest that herbivory networks are mainly related to plant evolutionary history whereas pollination networks are under the influence of the combined evolutionary history of both plant and insect species.

Neither the residual connectance of the networks nor the taxonomic span of the datasets had an effect on the level of interaction conservatism. Our results on connectance suggest that the strength of interaction conservatism does not depend on the level of specialization in networks. Similarly, Gómez et al. (2010) observed that occurrence of phylogenetic conservation was not related to host range in

their study. For the taxonomic span, our results contrast with a recent study showing that high taxonomical rank (kingdom to class) best explain food web structure (Eklöf et al. 2012). If this was the case here, we would observe stronger interaction conservatism in networks that include more distantly related clades. This discrepancy could originate from the fundamental difference in structure between food webs and bipartite plant–insect networks, and the much higher taxonomical span of food web datasets. Food webs typically include several trophic groups of species belonging to distant clades and these various trophic groups strongly determine the general structure of food webs (Allesina and Pascual 2009). In contrast, our analysis was restricted to bipartite networks between plants and insects, with the highest taxonomical rank at the level of the order. Our results thus suggest that when considering interaction between two trophic groups, interaction conservatism occurs at relatively low taxonomic levels, and that the strength of this conservatism may vary depending on the type of interaction. Another explanation for the absence of effects of the residual connectance or the taxonomic span could be the relatively low number of networks analysed. Although this study used a rather large set of networks in comparison to previous studies, more network datasets might be needed to explore such effects given the variability in the level of interaction conservatism among datasets, especially small ones.

More research is clearly needed to understand the mechanisms behind differences in the conservatism in interactions in plant–pollinator and plant–herbivore networks, and to evaluate the generality of these results in other mutualistic and antagonistic networks. This research effort is needed to understand and predict how novel species or interactions might integrate into existing networks (Pearse and Altermatt 2013). This is an important challenge for community ecologists given the potential for species displacement associated with climate change and with exotic species introductions (Memmott 2009; Pearse et al. 2013).

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