Manifold influences of phylogenetic structure on a plant–herbivore network

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Ecologists are increasingly aware of the interplay between evolutionary history and ecological processes in shaping current species interaction patterns. The inclusion of phylogenetic relationships in studies of species interaction networks has shown that closely related species commonly interact with sets of similar species. Notably, the degree of phylogenetic conservatism in antagonistic ecological interactions is frequently stronger among species at lower trophic levels than among those at higher trophic levels. One hypothesis that accounts for this asymmetry is that competition among consumer species promotes resource partitioning and offsets the maintenance of dietary similarity by phylogenetic inertia. Here, we used a regional plant–herbivore network comprised of Asteraceae species and flower-head endophagous insects to evaluate how the strength of phylogenetic conservatism in species interactions differs between the two trophic levels. We also addressed whether the asymmetry in the strength of the phylogenetic signal between plants and animals depends on the overall degree of relatedness among the herbivores. We show that, beyond the previously reported compositional similarity, closely related species also share a greater proportion of counterpart phylogenetic history, both for resource and consumer species. Comparison of the patterns found in the entire network with those found in subnetworks composed of more phylogenetically restricted groups of herbivores provides evidence that resource partitioning occurs mostly at deeper phylogenetic levels, so that a positive phylogenetic signal in antagonist similarity is detectable even between closely related consumers in monophyletic subnetworks. The asymmetry in signal strength between trophic levels is most apparent in the way network modules reflect resource phylogeny, both for the entire network and for subnetworks. Taken together, these results suggest that evolutionary processes, such as phylogenetic conservatism and independent colonization history of the insect groups may be the main forces generating the phylogenetic structure observed in this particular plant–herbivore network system.

Recent advances in ecophylogenetics have facilitated the investigation of the extent of phylogenetic conservatism in different types of species interactions (Rezende et al. 2007, Gómez et al. 2010, Fontaine and Thébault 2015). The inclusion of phylogenetic relationships in studies of species interaction networks has shown that closely related species commonly interact with similar sets of species (Rezende et al. 2007, Gómez et al. 2010, Cagnolo et al. 2011, Krasnov et al. 2012, Martos et al. 2012, Naisbit et al. 2012, Elias et al. 2013). However, the strength of phylogenetic conservatism of interactions in ecological networks often differs between trophic levels in the same network. In antagonistic networks, the effect of phylogenetic relatedness on the compositional similarity of interactions is frequently stronger between resource species (i.e. species of lower trophic levels) than between consumer species (i.e. species of higher trophic levels) (Cagnolo et al. 2011, Jacquemyn et al. 2011, Krasnov et al. 2012, Martos et al. 2012, Naisbit et al. 2012, Elias et al. 2013, Fontaine and Thébault 2015). On the other

hand, in plant–pollinator and plant–frugivore mutualistic networks, closely related animal species (higher trophic level) tend to share a larger proportion of plant species when compared to closely related plant species (lower trophic level) in relation to their pollinators or seed dispersers (Rezende et al. 2007).

The mechanisms generating the observed asymmetry in the phylogenetic signal between trophic levels are still not well understood. A theoretical study by Rossberg et al. (2006) on food webs suggests that a slower rate of evolution of defensive traits in the lower level could generate this difference between trophic levels. Another explanation for this asymmetry is that the effect of competitive interactions between consumer species is stronger than the effect of indirect interactions (e.g. predator-mediated apparent competition) between resource species, which then leads to a lower-than-expected similarity in the dietary composition of closely related consumers (Elias et al. 2013). These effects could drive phylogenetic patterns in the topological structure

of interaction networks, such as the formation of network modules, i.e. groups of species more densely connected among themselves than with other species from the same network (Prado and Lewinsohn 2004, Rezende et al. 2009, Krasnov et al. 2012). Finally, if asymmetry is driven by competition between consumers, it should be greater in networks of species with greater potential for competition. As phylogenetic conservatism in traits is common (Losos 2008, Wiens et al. 2010), and species with greater similarity are expected to share more resources (Fritschie et al. 2014, but see Cahill et al. 2008), the trophic-level differences in the phylogenetic conservatism of interactions should be higher in networks of closely related consumer species than in networks of phylogenetically distant species. Therefore, the asymmetry in the magnitudes of the correlations between phylogenetic and ecological similarities between trophic levels is expected to be higher for networks based on phylogenetically clustered consumers than for networks based on phylogenetically dispersed consumers.

Interactions between plants and herbivores have historically been used by ecologists as model systems to evaluate how evolution shapes current interaction patterns (Ehrlich and Raven 1964, Benson et al. 1975). For example, plant defense systems against natural enemies, such as chemical and physical barriers, tend to be phylogenetically conserved (Agrawal 2007); therefore, herbivorous insects usually consume closely related plant species (Barone 1998, Morais et al. 2011). Similarly, because herbivore adaptations to feed and develop on their host plants are, at some level, also phylogenetically conserved, host plants that are more closely related are expected to have, on average, greater similarity in their herbivore faunas when compared to phylogenetically distant host plants. Both patterns, however, can be masked to varying degrees by convergent evolution in both plant and herbivore traits (Becerra 1997).

In this study, we investigated the phylogenetic structure in the interactions of a well-studied system comprising plants of the family Asteraceae and their associated flower-head endophagous insects in remnants of Brazilian Cerrado (Fonseca et al. 2005, Almeida et al. 2006, Almeida-Neto et al. 2011). This was done by evaluating the phylogenetic patterns for both plants and herbivores at four organizational levels – within species, between species, within network modules and between network modules. The use of the entire set of herbivores, as well as phylogenetic subsets of herbivores, also allowed us to ascertain whether the asymmetry in the strength of the phylogenetic signal between plants and animals depends on the overall degree of relatedness among the herbivores. Specifically, we tested the following hypotheses: 1) host ranges of herbivore species tend to be phylogenetically clustered, while the herbivore assemblages associated to plant species tend to be phylogenetically dispersed; 2) the strength of phylogenetic conservatism in species interactions is greater among plants (resources) than among herbivores (consumers); and 3) for herbivores, phylogenetic conservatism in species interactions will be weaker when evaluated for subsets of the network containing only a given lineage, because of the higher potential for resource partitioning due to competition among closely related herbivores.

Methods

Interaction network sampling

The Asteraceae and their flower-head endophagous insects comprise a well-defined and species-rich plant–herbivore system. In the Brazilian Cerrado savannas, flower-heads of the Asteraceae are used especially by Diptera (Tephritidae, Agromyzidae, and Cecidomyiidae), microlepidoptera (Tortricidae, Pterophoridae, Pyralidae, Gelechiidae and Blastobasidae), and apionid weevils (*Apion* spp.) (Lewinsohn 1991, Fonseca et al. 2005, Almeida et al. 2006, Almeida-Neto et al. 2011).

Associations between Asteraceae and flower-head endophagous insects were assessed quantitatively in 20 remnants of Cerrado vegetation in southeastern Brazil (Almeida-Neto et al. 2011). The regional climate is characterized by rainy summers and dry winters and is classified as CWA in Köppen's (1948) system. The sampled sites were spaced from 0.6 to 41.4 km apart (mean distance = 16.3 km), at elevations ranging from 600 to 950 m.

Plants and insects were sampled from April to May 2003. The sampling design consisted of 15 transects of 30×5 m, randomly allocated in relation to the edge of the areas. We sampled flower heads from at least 20 individuals of each Asteraceae species, collecting about 80 ml of flower-heads per individual plant whenever available. In the laboratory, the flower-head samples were kept in plastic containers covered with a mesh lid. Adult herbivore emergence was checked at least weekly for a period of two months. We spent about four person-hours collecting flower-heads in each period and site. Further information on sampling, vegetation and studied areas can be found in Almeida-Neto et al. (2010, 2011).

For the purpose of this study, both species and their interactions were integrated into a single regional plant–herbivore network, depicting the presence or absence of interactions between each plant–herbivore pair. We only included in the regional interaction network the plant and insect species that occurred in at least five (25%) of the sampled areas. By constructing the network in this way, we aimed to minimize the effect of spatial mismatch on the structure of plant–herbivore interactions. Among the 1210 plant–herbivore pairs included in our network, only 12 do not co-occur in at least one site.

Plant and insect phylogenies

Plant phylogeny was constructed by combining the information from a composite tree of the Asteraceae family (Funk et al. 2009) for most genera, with taxonomy serving as a surrogate for phylogenetic relationships of nodes for which no information was available. When even the taxonomy was unable to provide relationships, unresolved nodes were left as polytomies. Species were also attached as polytomies deriving from each genus.

Difficulties in the specific identification of the insect species, and the lack of a comprehensive phylogenetic hypothesis for the insect families comprising this study, led us to use an informal tree constructed by taxonomic substitution (sensu Bininda-Edmonds et al. 2002) of the available phylogenetic information. Starting with a purely taxonomic

tree, we added information on the relationships between taxa whenever available (Supplementary material Appendix 1 Fig. A1). We rendered both trees ultrametric by applying Grafen's transformation (Grafen 1989). We obtained similar results either by arbitrarily defining branch length as 1 (i.e. using the number of nodes between species as a measure of phylogenetic distance) or using Grafen's transformation on both phylogenies, so we only present the results of the branch lengths obtained by Grafen's transformation (Supplementary material Appendix 1 Table A1–A4). We generated 300 trees with randomly resolved polytomies (RRT) for each group (plants and insects) in order to assess the degree of phylogenetic uncertainty arising from polytomies (Rangel et al. 2015). All analyses were performed in the original hypothesis containing the polytomies and also on the 300 trees with randomly resolved polytomies. Final results from the RRT were used to compute 95% confidence intervals associated with phylogenetic uncertainty. Confidence intervals for DSI analysis are shown in the Supplementary material Appendix 1 Table A1.

Data analysis

All analyses were applied to the entire data set and the following subsets: 1) interactions between tephritids (Diptera: Tephritidae) and their hosts, 2) interactions between cecidomyiids (Diptera: Cecidomyiidae) and their hosts, and 3) interactions between lepidopterans (Blastobasidae, Gelechiidae, Pyralidae, Pterophoridae, Tortricidae) and their hosts. Defining a subnetwork comprising the weevil species was not possible, due to the small number of species present. All procedures were implemented in the R environment (<www.r-project.org>) using original code and functions from the packages *picante* (Kembel et al. 2010) and *bipartite* (Dormann et al. 2008).

We tested whether the overall network and the subnetworks show a modular pattern by using the QuanBimo algorithm (Dormann and Strauss 2013), implemented by the computeModules function in the R package *bipartite*. For the modularity analysis we included interaction frequencies, which improves the detection of modules (Schleuning et al. 2014). This simulated annealing procedure allows the detection of modules in quantitative bipartite networks, and provides a modularity measure (Q) that compares the frequency of within versus between module interactions. For each network, we applied the algorithm and the resulting Q value was used as the modularity estimate. This estimate was then compared to those obtained from 100 random networks created using a null model with fixed marginal totals in order to obtain a z-value.

We tested whether the set of plants used by a given herbivore species, and likewise the set of herbivores that develop in a given plant species, is composed of species related to a greater or lesser extent than would be expected from a null set of the same size. This is measured using an analog of the recently proposed DSI-S index (Jorge et al. 2014), which measures the degree of phylogenetic clustering in a given set of species in comparison to randomly assembled sets. The DSI-S index is computed as the z-score obtained by the comparison between the observed mean phylogenetic distance between the species in the group and the distances obtained by shuffling the species' positions along the phylogeny 999 times. The same test was applied to the set of plants in the same module, and the set of herbivores in the same module to assess the phylogenetic clustering of modules. The mean species-level and module-level DSI-S values of each subnetwork were then compared with the expected null value of 0 with one sample t-tests (Kembel and Hubbell 2006).

We also tested the effect of phylogenetic distance on counterpart dissimilarity by computing correlation coefficients between the phylogenetic distance matrices of the species and two metrics of counterpart overlap for each group. The first metric was purely compositional, defined as follows: we first computed the Jaccard dissimilarity in the counterpart composition of a given pair of plants/insects and then calculated a z-value by comparing the observed value with the mean and standard deviation of 500 null values obtained by randomly selecting two sets of the same size from all insect and plant species from the regional network. The second metric was also a null model standardized dissimilarity, calculated using the UniFrac index (Lozupone and Knight 2005). The UniFrac between two sets of species measures the proportion of evolutionary history present exclusively in each set in relation to the total amount comprised by both. In a phylogenetic tree comprising all species from the two sets, the UniFrac is defined as the ratio between the sum of branch lengths that leads to species exclusive to either set and the total sum of branch lengths in the entire tree. The UniFrac between each pair of species was compared to null values generated by the following null model: first we keep the counterparts of species A constant, randomly reassign the interactions of species B and compute the Unifrac; then we keep the interactions of species B and shuffle the interactions of species A. The null value was then defined as the mean of these two values. This procedure separates the effects of the phylogenetic pattern within the counterparts of each species from the patterns arising from the phylogenetic relationships between the species. The use of the standardized dissimilarity measures, both for the compositional dissimilarity and the UniFrac, avoids the undesired effects of counterpart richness differences between pairs of species as well as the inherent cap on maximum dissimilarity values. By looking at the phylogenetic component of counterpart sharing we aim to better explore the interaction patterns of both groups. The observed values of correlation between phylogenetic distance and each of the counterpart overlap measures were then compared to those obtained in 999 null correlations using a null model that randomly relocates species along the phylogeny. We also tested if the relatedness between a pair of species affects the probability of both species being in the same network module by adjusting binomial GLMs. Model coefficients were tested against the same null models previously described.
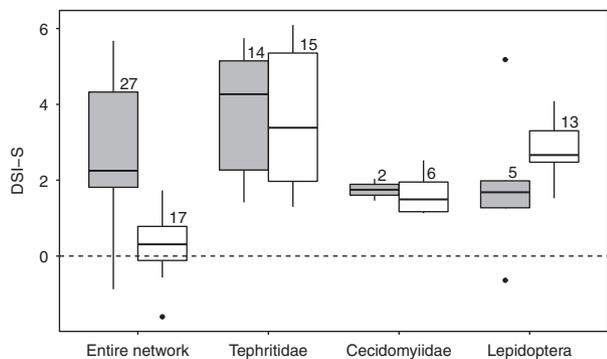
Data deposition

Figure 1. Boxplot of the DSI-S values of the counterpart of each insect species (grey boxes) and the counterparts of each plant species (white boxes), for each of the subsets considered. Positive values mean higher than expected phylogenetic clustering of the counterpart set. Horizontal lines represent the median values, boxes the interquartile range, vertical lines the 95% percentiles and dots the outliers. Sample sizes are shown above each box.

Results

A total of 13011 adult herbivores were reared from 1373 individual plants. The regional plant–herbivore network was composed of 157 interactions between 55 species of flower-head feeding insects and 22 species of host plants. The insect species belong to six families and 16 genera, while the host plants belong to six tribes and 12 genera within the Aster-aceae family. The species richness of herbivores and plants, respectively, was 23 and 19 for the Tephritidae–Asteraceae subnetwork, 6 and 17 for the Lepidoptera–Asteraceae subnetwork, and 16 and 11 for the Cecidomyiidae–Asteraceae subnetwork. The number of plant–herbivore interactions for each insect group was 67, 18 and 47, for the Tephritidae, Cecidomyiidae and Lepidoptera subnetworks, respectively.

Phylogenetic clustering of host plant ranges and herbivore assemblages

In the entire network, as expected, the host-plant species used by each herbivore species comprised, on average, a subset of species more closely related than random subsets of host-plant species of the same size ($t = 7.98$, DF = 26, $p < 0.001$,

Fig. 1). A similar pattern was observed in the Tephritidae subnetwork, with a strong degree of phylogenetic cluster-ing in the plants consumed by the tephritid species ($t = 8.9$, DF = 13, $p < 0.001$, Fig. 1). The species in the Lepidoptera and Cecidomyiidae subnetworks also showed consistent positive DSI-S values, but their mean phylogenetic aggregation could not be tested due to the small sample sizes.

The subsets of herbivore species on each host-plant species did not show phylogenetic clustering when all insect groups were combined ($t = 1.6$, DF = 16, $p = 0.100$, Fig. 1). However, contrary to what would be expected if more closely related herbivores showed resource partition-ing, separate analyses of the three subnetworks revealed significant clustering of the herbivores sharing the same host species (Tephritidae: $t = 7.28$, DF = 14, $p < 0.001$; Lepidoptera: $t = 12.67$, DF = 12, $p < 0.001$; Cecidomyiidae: $t = 7$, DF = 5, $p < 0.001$; Fig. 1).

Compositional and phylogenetic similarity of host plants and herbivore assemblages

The overall influence of phylogenetic relatedness between herbivores on the compositional (i.e. taxonomic) similarity of their host plants was positive but marginally non-significant across the entire network (Table 1, Fig. 2a). A significant pattern was found, however, for the effect of phylogenetic closeness between herbivores on the phylogenetic similarity of their host plant species (Table 1, Fig. 2b). In subnetworks we found significant positive relationships between the phylogenetic relatedness of the herbivores and the phylo-genetic similarity of their host plants for the subnetworks composed of the Tephritidae and Cecidomyiidae, but not for the Lepidoptera subnetwork (Table 1, Fig. 2d–f). Thus, both Tephritidae and Cecidomyiidae showed a pattern contrary to our hypothesis, with increased phylogenetic conservatism of interactions when analyzed as subnetworks.

Host plants showed a different pattern than herbivores in the entire network, with a positive correlation between host-plant phylogenetic relatedness and both the composi-tional and phylogenetic similarity of their herbivore assem-blages (Table 1, Fig. 3). Both the subnetwork composed of the Tephritidae and that composed of the Lepidoptera showed significant positive relationships between host-plant

Table 1. Correlations between phylogenetic distance and the two metrics of compositional overlap (Jaccard and Unifrac) for each subnetwork and trophic level. 95% confidence intervals due to phylogenetic uncertainty associated with polytomies are shown in parenthesis. Bold values are significant at the 0.05 level.

| Herbivore group	Jaccard			Unifrac		
	r	z-value	p-value	r	z-value	p-value
All herbivores						
Plant pairs	**0.40**	**4.89 (4.75–5.22)**	**<0.001**	**0.29**	**3.67 (3.63–4.20)**	**<0.001**
Herbivore pairs	**0.09**	**2.11 (1.86–2.62)**	**0.014**	**0.11**	**2.37 (2.11–2.77)**	**0.045**
Tephritidae						
Plant pairs	**0.21**	**2.65 (2.67–3.19)**	**<0.001**	**0.70**	**8.60 (8.98–10.83)**	**<0.001**
Herbivore pairs	0.10	1.36 (0.37–4.73)	0.076	**0.44**	**5.90 (3.67–8.05)**	**0.001**
Cecidomyiidae						
Plant pairs	0.14	1.03 (0.88–1.17)	0.164	**0.57**	**4.10 (3.82–4.95)**	**<0.001**
Herbivore pairs	0.13	1.44 (0.73–1.43)	0.087	**0.22**	**2.35 (1.86–3.00)**	**0.021**
Lepidoptera						
Plant pairs	**0.23**	**1.75 (1.71–1.90)**	**0.038**	**0.34**	**2.41 (2.06–2.34)**	**0.011**
Herbivore pairs	0.23	0.75 (0.03–1.15)	0.277	–0.46	–1.39 (–1.88– –0.58)	0.085
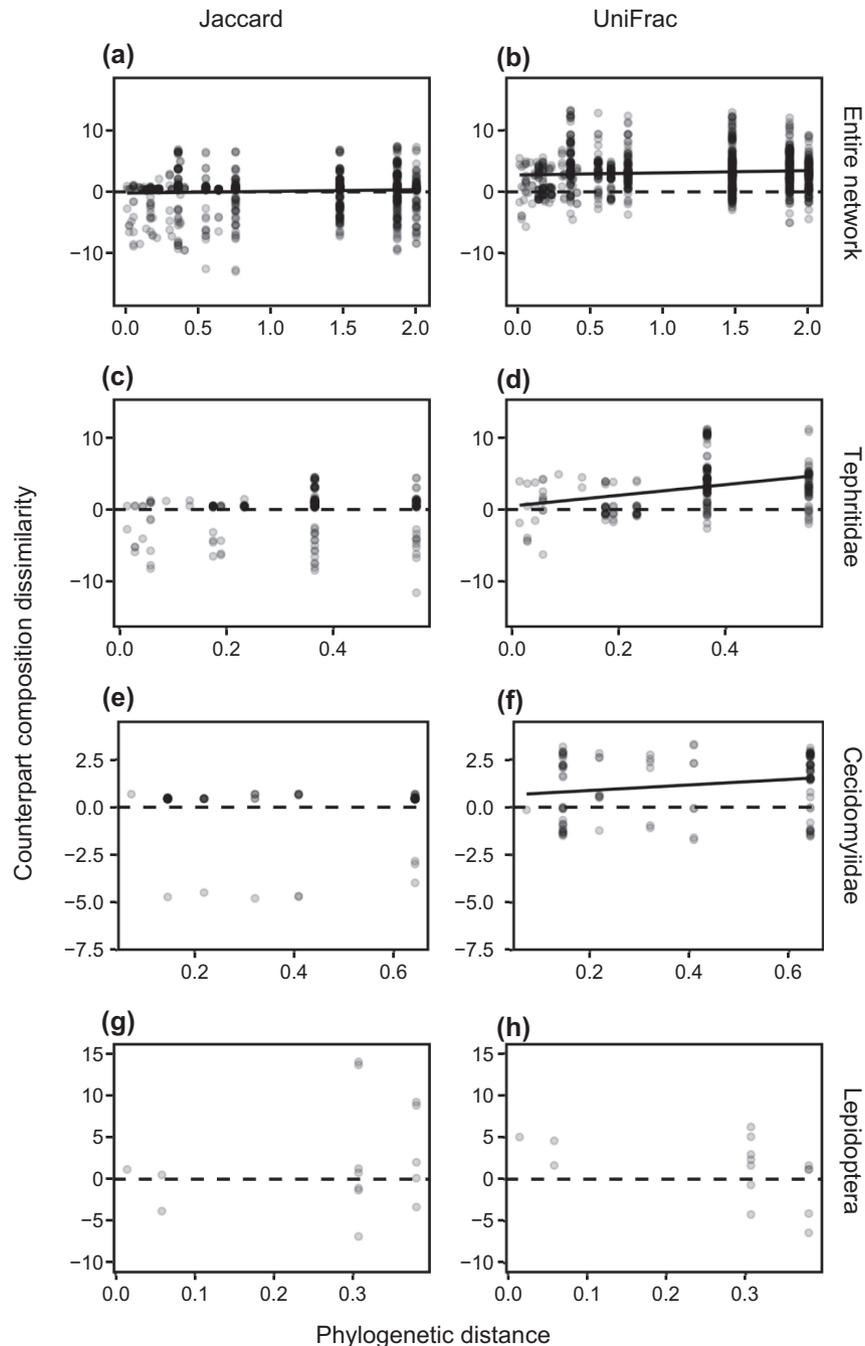
Figure 2. Correlations between phylogenetic distance between pairs of species (x axis) and the two metrics of compositional distance z-values (Jaccard: b, d, f, h; Unifrac: a, c, e, g), for the pairs of endophage species for each subset (entire network: a, b; Tephritidae: c, d; Cecidomyiidae: e, f; Lepidoptera: g, h). Significant correlations are depicted by the regression line. Dashed line at zero added for better visualization.

phylogenetic proximity and compositional and phylogenetic similarity of herbivores (Table 1, Fig. 3c–d, 3g–h). For the Cecidomyiidae subnetwork, only the phylogenetic similarity of herbivores increased with increasing phylogenetic proximity between host plant species (Table 1, Fig. 3f).

Phylogenetic patterns within network modules

Both the entire network and the three subnetworks showed significant modularity with the number of modules ranging from 6 to 12 (see Fig. 5 and Supplementary material Appendix 1 Table A5 for details). However, many modules comprised only one interaction, which reduced the number of modules with sufficient data for testing. We did not find phylogenetic clustering of herbivores within the same module in the entire network (t = 0.85, DF = 3, p = 0.460, Fig. 4). However, both the Tephritidae (t = 3.71, DF = 4, p = 0.02, Fig. 4) and the Cecidomyiidae subnetworks showed significant phylogenetic clustering (t = 6.21, DF = 4, p = 0.003, Fig. 4). The Lepidoptera subnetwork had only one module with two species, which precluded statistical tests for this group (Fig. 4).
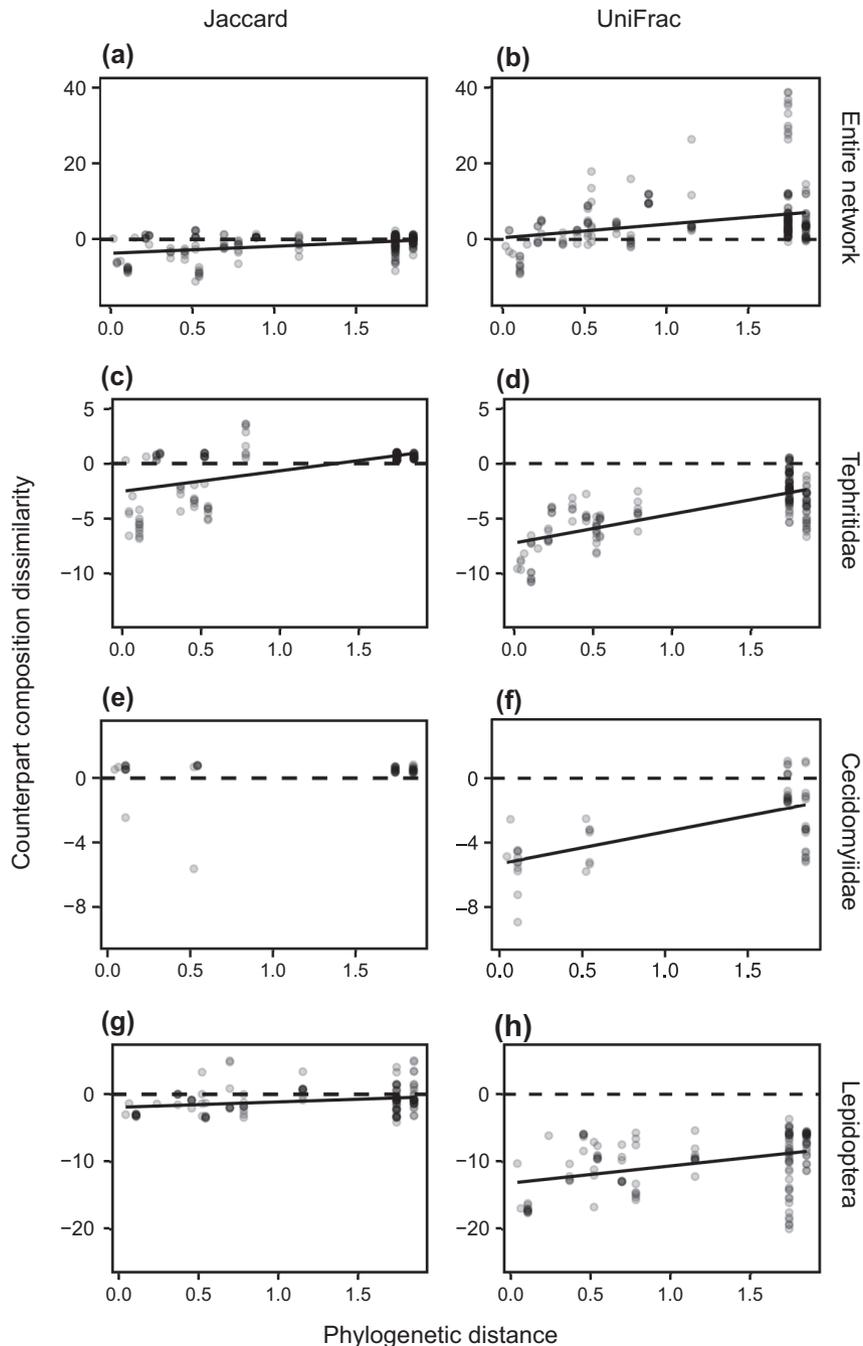
Figure 3. Correlations between phylogenetic distance between pairs of species (x axis) and the two metrics of compositional distance z-values (Jaccard: b, d, f, h; Unifrac: a, c, e, g), for the pairs of plant species for each subset (entire network: a, b; Tephritidae: c, d; Cecidomyiidae: e, f; Lepidoptera: g, h). Significant correlations are depicted by the regression line. Dashed line at zero added for better visualization.

Overall, we did not detect significant phylogenetic clustering of host plants within modules (t = 1.14, DF = 3, p = 0.35, Fig. 4). However, in accordance with our expectations, some modules had host plants that were more closely related than would be expected by chance (Supplementary material Appendix 1 Table A2). A separate evaluation of each subnetwork revealed phylogenetic clustering of the host plants only for the Tephritidae subnetwork (Fig. 4). For the Lepidoptera subnetwork, we found phylogenetic clustering of host plants in a single module. Phylogenetic

clustering of host plants within modules was not tested for the Cecidomyiidae subnetwork because only one module had more than one plant species.

Patterns between network modules

The co-affiliation of host-plant species pairs to the same module was greater between plant species that were more closely related, both for the entire network and for the Tephritidae and Lepidoptera subnetworks (Table 2, Fig. 5).
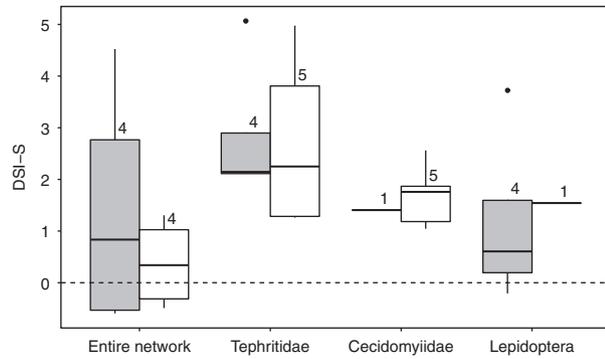
Figure 4. Boxplot of the DSI-S values of the plant species (grey boxes) and insect species (white boxes) in the same module, for each of the subsets considered. Positive values mean higher than expected phylogenetic clustering of the species in the module. Horizontal lines represent the median values, boxes the interquartile range, vertical lines the 95% percentiles and dots the outliers. Sample sizes are shown along each box. In the Lepidoptera subset there was only one module with more than one insect species and in the Cecidomyiidae subset there was only one module with more than one plant species, for these cases the horizontal lines represent the DSI-S values of that particular module.

This result shows that, although the presence of unrelated species in a given module may have led to an overall absence of phylogenetic clustering of the plants in each module, closely related plants are still more likely to belong to the same module. By contrast, herbivores showed no relationship between phylogenetic relatedness and module co-affiliation (Table 2).

Phylogenetic uncertainty

Phylogenetic uncertainty resulting from polytomies had no qualitative impact on the final results, since no confidence interval overlapped zero in any case that was statistically significant in the results with polytomies (Table 1, 2, Supplementary material Appendix 1 Table A1). DSI-S values for modules or species with significant aggregation varied, on average, 16.56% for the Asteraceae and 21.72% for the endophages. Likewise, statistically significant correlations

Table 2. Results from the binomial GLMs modelling the relationship between phylogenetic distance of species pairs and the probability that both belong to the same module. 95% confidence intervals due to phylogenetic uncertainty associated with polytomies are shown in parenthesis. Bold values are significant at the 0.05 level.

Herbivore group	Coefficient	z-value	p-value
All herbivores			
Plant pairs	**−0.66**	**−2.01 (−2.26 − −1.90)**	**0.028**
Herbivore pairs	0.01	−0.24 (−0.37 − −0.08)	0.494
Tephritidae			
Plant pairs	**−4.59**	**−10.86 (−12.78 − −11.19)**	**<0.001**
Herbivore pairs	−1.01	−1.29 (−3.73 − −0.59)	0.133
Cecidomyiidae			
Plant pairs	−1.52	−0.55 (−0.50 − −0.20)	0.318
Herbivore pairs	−4.01	−1.41 (−1.43 − −0.85)	0.087
Lepidoptera			
Plant pairs	**−0.62**	**−1.89 (−2.14 − −1.80)**	**0.027**
Herbivore pairs	2.84	−0.20 (−0.32 − −0.12)	0.500

across all analyses (Jaccard, Unifrac and Module co-occurrence) showed an average associated uncertainty of 16.73% for the Asteraceae and 46.68% for the endophages.

Discussion

In this study, we integrated phylogenetic/taxonomic information in a well-defined plant–herbivore network to evaluate to what extent the compositional and phylogenetic similarities of interactions between herbivorous insects or between host plants are influenced by phylogenetic relatedness of either plants or herbivores. Our results show that, in the entire network, whereas herbivores use phylogenetically clustered sets of host plants, plants are not associated to phylogenetically aggregated sets of herbivores. This asymmetry in phylogenetic clustering of interactions between herbivores and plants is probably a result of the inclusion of disparate lineages of insects that evolved this feeding mode and independently colonized this group of host plants. Evidence for this explanation comes from results for more restricted phylogenetic sets of herbivores (the Cecidomyiidae, Lepidoptera and Tephritidae), in which species sets of each insect group were, on average, more closely related than would be expected by chance. These results are consistent with a high phylogenetic conservatism of traits mediating interactions among species. Susceptibility of plants to pathogens, for example, has been shown experimentally to be phylogenetically conserved (Gilbert and Webb 2007), probably as a result of the conservatism of defense traits observed among all the angiosperms (Agrawal 2007). There are, however, examples of how convergent traits can mediate plant–herbivore interactions, independent of plant phylogeny (Becerra 1997, Kergoat et al. 2005).

We also demonstrated the presence of a positive relationship between phylogenetic relatedness and the interaction similarity between species pairs from the same trophic level in most subnetworks. Additionally, our inclusion of phylogenetic information in the measures of interaction similarity resulted in an improved signal for the herbivore pairs. This was the case both for herbivore and plant partitions in the Cecidomyiidae subnetwork, an insect group that did not show correlations between pure compositional similarity and phylogenetic distance. Most cecidomyiids are highly specialized utilizing a single host plant species (Carneiro et al. 2009). Monophagy was also common among cecidomyiid species in our study system; therefore, no compositional overlap was possible between most species pairs. Even so, a greater phylogenetic similarity was observed between cecidomyiids associated to highly related plants. It is possible, therefore, that even in cases where no phylogenetic signal in ecological similarity is apparent (Rezende et al. 2007, Cagnolo et al. 2011, Elias et al. 2013) a phylogenetic signal might still exist in the shared partners' evolutionary history. The differences in signal strength between the purely compositional and the phylogenetically weighted measures of similarity can also shed some light on the detailed patterns of counterpart-sharing between species. For example, a stronger signal in phylogenetic similarity can be caused either by higher divergence in the partners of distantly related species or by higher convergence of the partners of closely related
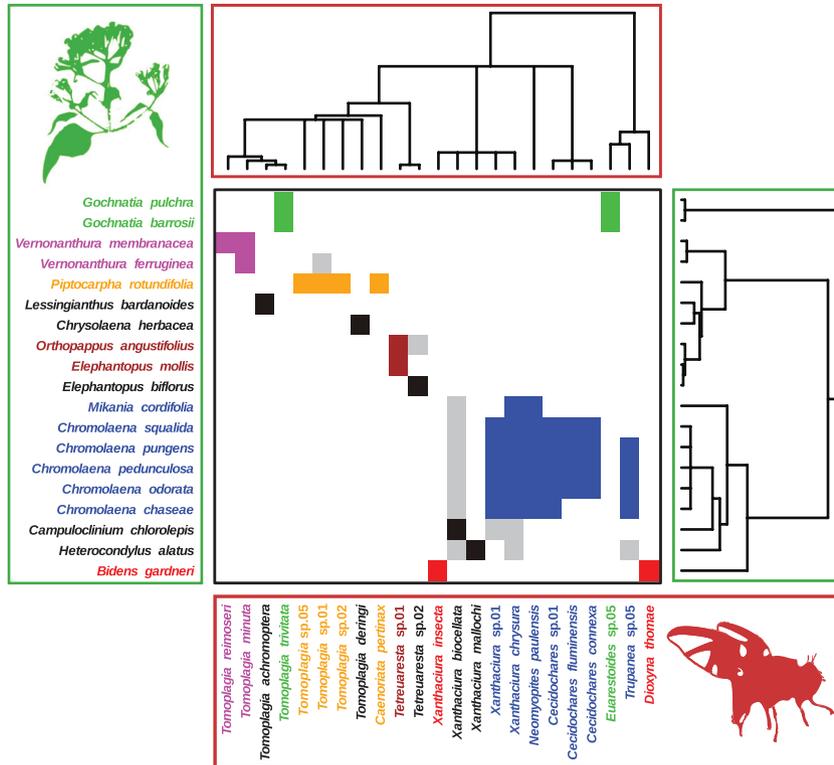
Figure 5. Module affiliations for each species in the Tephritidae subnetwork. Tephritidae species are shown on the bottom with their phylogeny shown on the top. Asteraceae hosts are shown on the left with their phylogeny shown on the right. Colors mark species and interactions that belong to each module. Species in black belong to modules that contain only one interaction. Interactions between species that belong to different modules are shown in grey.

species. Future analysis of the phylogenetic component of ecological similarity between pairs of interacting species and studies exploring additional approaches (Ives and Godfray 2006) should be helpful to further test these hypotheses.

In agreement with the patterns found in other antagonistic systems (Cagnolo et al. 2011, Krasnov et al. 2012, Elias et al. 2013, Fontaine and Thébault 2015), the strength of the phylogenetic signal was consistently greater for the host-plant species than for the herbivore insects, with higher correlation coefficients. This asymmetry was more evident when looking at the modules present in the network. Despite the phylogenetic conservatism in the ecological interactions at the species level for most insect groups tested, closely related herbivores frequently belonged to different network modules. For the plants, however, even though some modules contained distant relatives, closely related plants were more commonly found in the same module. This finding shows that the module structure is mainly driven by the plant clades and that the herbivore lineages are distributed in different modules. This result is in line with previously reported taxonomic patterns in module structure in the same system (Prado and Lewinsohn 2004).

There were, however, important differences between the entire network and the subnetworks. Contrary to what was expected if competition between consumers was the main driver of phylogenetic signal asymmetry, the observed phylogenetic conservatism in plant use was greater when we considered subnetworks composed of phylogenetically more restricted insect groups of herbivores. More closely related

herbivores in these subnetworks shared a higher proportion of hosts than was observed for the entire network. This result suggests that competition between related consumers is not a major driver of phylogenetic signal asymmetry at this scale. A recent study on the correlation between phylogenetic distance and individual level co-occurrence in flea communities (Krasnov et al. 2014) also demonstrated significant co-occurrence of pairs of closely related fleas, which indicates a prevalence of environmental, or host, filtering in determining the composition of flea assemblages on individual hosts. The parasitic lifestyle of endophagous insects also imposes numerous restrictions on host use that probably increase the influence of those kinds of filters. It seems more likely, therefore, that other processes such as differences in the colonization history between herbivore lineages and contrasting rates of evolution between resources and consumer have a greater role in determining the observed phylogenetic patterns.

Taken together, our results show the pervasive presence of phylogenetic effects in different levels of network organization. The importance of plant evolutionary history in shaping host use by herbivores has long been recognized (Ehrlich and Raven 1964, Benson et al. 1975), but the integration of phylogenetic information into plant–herbivore studies has been hampered by the scarcity of well-resolved phylogenetic hypotheses for many insect groups. Recent advances in phylogenetic methods have triggered new improvements in our understanding of how species interactions are constrained by historical processes (Symons and Beccaloni

1999, Weiblen et al. 2006, Mouquet et al. 2012, Jorge et al. 2014). Although the phylogenetic hypotheses used here were constructed by the combination of information from different sources and did not include information on branch lengths, the patterns observed are probably robust enough to withstand these shortcomings as general results were unaltered even using different branch length representations and uncertainty associated with polytomies had no qualitative impact on final results. By gaining a better understanding of the role of phylogenetic constraints in defining species interactions, many new applications, such as the prediction of novel interactions (Pearse and Hipp 2009, Ness et al. 2011, Pearse et al. 2013) will become possible.

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