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SPECIAL TOPIC ON FUNCTIONAL TRAITS

How phylogeny shapes the taxonomic and functional structure of plant–insect networks

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Abstract Phylogenetically related species share a common evolutionary history and may therefore have similar traits. In terms of interaction networks, where traits are a major determinant, related species should therefore interact with other species which are also related. However, this prediction is challenged by current evidence that there is a weak, albeit significant, phylogenetic signal in species' taxonomic niche, i.e., the identity of interacting species. We studied mutualistic and antagonistic plant–insect interaction networks in species-rich alpine meadows and show that there is instead a very strong phylogenetic signal in species' functional niches—i.e., the mean functional traits of their interactors. This pattern emerges because related species tend to interact with species bearing certain traits that allow biotic interactions (pollination, herbivory) but not necessarily with species from all the same evolutionary lineages. Those traits define a set of potential interactors and show clear patterns of phylogenetic clustering on several portions of plants and insect phylogenies. Thus, this emerging pattern of low phylogenetic signal in taxonomic niches but high phylogenetic signal in functional niches may be driven by the interplay between functional trait convergence across plants' and insects' phylogenies and random sampling of the potential interactors.

Keywords Plant–pollinator · Plant–herbivore · Phylogenetic signal · Functional niche · Taxonomic niche

Introduction

A central aim in ecology is to unravel the ecological and evolutionary processes that shape the structure of ecosystems (Lavergne et al. 2010; Schoener 2011). In this context, the question of just how complex interaction networks emerge in species-rich communities has received increasing attention from ecologists in recent years (Bascompte and Jordano 2007; Ings et al. 2009; Heleno et al. 2014), with the result that several causes of interaction networks have been identified, including such factors as small-scale biogeography, abundance effects combined with random sampling (Vázquez and Aizen 2003; Vázquez et al. 2009), and species traits (Brose et al. 2006; Stang et al. 2006; Honek et al. 2007; Ibanez et al. 2013a; Dehling et al. 2014). Of these factors, traits are considered to be very important causes of interaction networks because they not only mediate the ecosystem processes triggered by species interactions, but they also drive the response of ecosystem structure under environmental changes (Violle et al. 2007).

Traits also have an evolutionary history, and part of this history can be shared by species depending on their phylogenetic relatedness—i.e., common ancestry (Kraft et al. 2007; Webb et al. 2008; Cadotte et al. 2013)—although phylogenetic dispersion does not always reflect trait dispersion (Gerhold et al. 2015). Researchers use several metrics to detect the relatedness of traits—i.e., when traits of closely related species are more similar than those of

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unrelated species. Such metrics correspond to the phylogenetic signal (hereafter trait PS) of the species. (For a recent review and a test of the metrics currently used to quantify the PS, the reader is referred to Münkemüller et al. 2012). Significant trait PS have been found in a diversity of niche-related traits (Cornwell et al. 2014; Zanne et al. 2014; Chalmandrier et al. 2015), including pollination-related traits in insects (Pellissier et al. 2013) and frugivory-related traits in birds (Rezende et al. 2007a). This has led to the proposal that if traits show a PS and if they play a major role in determining interaction networks, then interaction networks themselves should show a PS (Ives and Godfray 2006; Gómez et al. 2010; Minoarivelo et al. 2014). In other words, closely related species should interact with identical species or with closely related ones, a pattern hereafter referred to as "taxonomic niche PS", where "taxonomic niche" corresponds to the identity of the interacting species (Wiens and Rotenberry 1979; Schmitt and Coyer 1982; Polidori et al. 2011). Taxonomic niche PS has been found in a variety of networks (Vacher et al. 2008; Rezende et al. 2009; Verdú and Valiente-Banuet 2011; Jacquemyn et al. 2011; Eklöf et al. 2012), and statistical tools have been designed specifically for the purpose of identifying taxonomic niche PS in networks (Ives and Godfray 2006; Rafferty and Ives 2013; Hadfield et al. 2014). The concept of taxonomic niche PS is not only used to study interaction networks, but also to investigate how shared evolutionary history shapes community assembly (Kraft et al. 2007; Pillar and Duarte 2010; Mouquet et al. 2012).

Taxonomic niche PS is not a purely descriptive metric with limited biological interest; to the contrary, it has the potential to be used for ecological forecasting (Rezende et al. 2007b) and ecological restoration (Verdú et al. 2011), along with other network-level metrics (Devoto et al. 2012). Let us consider, for example, a focal community for which the interaction network between its species is known, and the neighboring communities with slightly different species compositions for which one would like to predict the interaction networks. If the taxonomic niche PS is strong in both the focal and the neighboring communities, their interaction networks should then be predictable using the data from the focal community. A similar approach can be applied to the study of temporal variations of the focal community, as well as to biological invasions (Vacher et al. 2010) provided the invasive species do not form outgroups with the phylogeny of the resident species (for a discussion of this, see Thuiller et al. 2010).

Alternatively, closely related species may not interact with species of certain lineages, but with species having similar traits, even if those latter species are phylogenetically distant. In other words, taxonomic niche PS may be absent, but a pattern which is referred to as "functional niche PS" may remain. Functional niche PS thus arises when closely related species interact with species that are on average functionally similar. In contrast to the taxonomic niche PS which focuses on the identity of the interacting species, the functional niche PS measures the mean trait value of the interactors (Ibanez et al. 2013b). This perspective is similar to the "pollination niche" concept which refers to the functional group of pollinators targeted by plant species (Fenster et al. 2004), with the exception that a quantitative rather than a qualitative approach is adopted with the functional niche PS concept. This use of the term "functional niche" is consistent with previous definitions (Elton 1927; Whittaker et al. 1973; Rosenfeld 2002) and transposes this concept into the context of interaction networks.

The purpose of the study reported here was to explore the potentially complex links between traits, networks and phylogenies, as a first step in a wider program that aims at predicting species interaction networks from phylogenies and/or traits. Here we tested whether trait PS, taxonomic niche PS, and functional niche PS can be detected and whether they can be considered to be associated. To this end, we studied two plant–insect networks occurring in alpine meadows located in the French Alps, of which one is a plant–pollinator network and the other a plant–herbivore network. Figure 1 depicts the studied plant–insect networks, the species phylogenies and a schematic representation of the three different PS used in this study.

Materials and methods

For both datasets (plant–pollinator network and plant–herbivore network), the field sites were located in the central French Alps, in subalpine and alpine meadows around the Lautaret pass (45.34°N, 6.34°E; elevation 1800–2200 m.a.s.l.). Data for the plant–pollinator dataset were collected from field observations, while data for inclusion in the plant–herbivore dataset were obtained from a cafeteria-type food choice experiment conducted with plants and Orthoptera species co-occurring in the study area. Both networks are quantitative; the plant–pollinator network is weighted by the number of visits and the plant–herbivore network is weighted by the dry mass eaten.

Plant–pollinator network: observations and trait measurements

Two 500-m^2 terraced fields located 1000 m apart were studied and the data subsequently merged for the purposes of this analysis. A total of 32 plant species were observed in June–July 2008 [species list given in Electronic

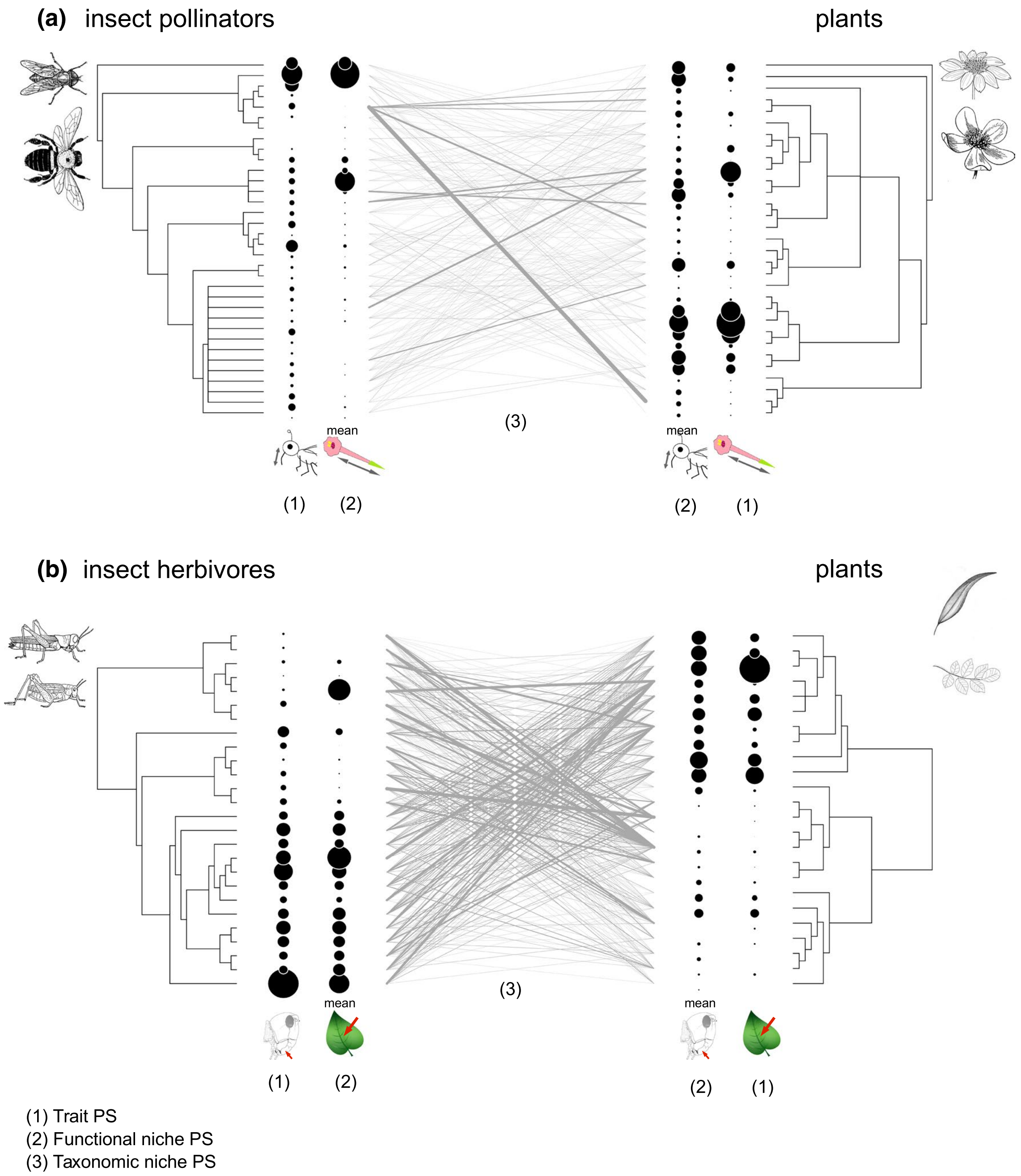

Fig. 1 Representations of the interaction networks between plants and pollinators (**a**) and plants and herbivores (**b**) in association with the phylogenies of both guilds. *Filled circles* correspond to the functional trait values of each species,and to the weighed mean value of the traits of the interactors (functional niche, see Eq. 1 for details). *Diameter of filled circles* is proportional to the trait and functional niche values. The three phylogenetic signals (*PS*) measures are calculated using different data combinations: *1* trait PS using trait values and phylogenetic data, *2* the functional niche PS using functional niche values and phylogenetic data, *3* the taxonomic niche PS using the interaction networks and phylogenetic data

Supplementary Material (ESM) 1]. Plant species were selected according to the abundances of their inflorescences; in both fields the selected species represented about 80 % of the total number of the inflorescences (Ibanez 2012). Each selected species was observed on two different days (two 15-min sessions per observation day) around the time of its peak flowering, under sunny conditions with no wind. During each observation session, all individuals belonging to the focal species were observed. Sixteen plant species present in both fields were observed for 120 min in total, and 16 plants species present in either one or the other field were observed for 60 min in total. Insects observed consuming nectar were counted, and five individuals per species (or morphospecies, see below) were captured for trait measurements and identification at the lowest possible taxonomic level. When insect individuals could not be identified to the species level, we attributed them to morphospecies. Morphospecies were numbered following the lowest taxonomic level identified; for example, syrphid flies belonging to different species of the genus *Eristalis* were denoted "*Eristalis_sp1*", "*Eristalis_sp2*", etc. A total of 1390 insect visits were included in the analysis, corresponding to 177 insect taxa. Sampling completeness was estimated by the Chao-2 estimator (Chacoff et al. 2012) and was 58 % for the entire pollinator fauna, 42 % for the total number of interactions and 60 ± 25 % (mean ± standard deviation) for the number of interactions per plant species.

With respect to insect traits, we measured the length and width of the proboscis, dry body mass, and the functional body length (head + thorax + hind femur) of five individuals per insect species. After the observations, ten inflorescences belonging to ten different individuals were collected for each plant species. For each inflorescence sampled, the number of flowers was counted and the size of the insect landing zone (total floral area) measured. The depth and width of the nectar holder were measured on ten flowers per inflorescence. For more details on network and trait data, see Ibanez (2012). The plant and insect traits were chosen according to their influence in the structure of the interaction web (Ibanez 2012).

Plant–herbivore network: observations and trait measurements

We studied plant preferences by Orthoptera species in a standard food-choice ("cafeteria") experiment (Pérez-Harguindeguy et al. 2003; Ibanez et al. 2013a). We placed a total of 260 individuals belonging to 26 Orthoptera species (19 grasshoppers, 7 katydids; see species lists in ESM 1) separately into 40 × 20 × 4-cm boxes where they could select between leaves belonging to 24 different plant species (21 genera and 9 families; see species lists in ESM 1). Among those 24 plant species, four were also surveyed in the pollination dataset. Both Orthoptera and plant species were collected in natural communities co-occurring in the study area. Each session lasted a minimum of 5 h (for a total of 1300 h of cafeteria experiments), at the end of which the consumed leaf dry mass (in milligrams) per each individual was quantified. For more details on the experimental set-up see Ibanez et al. (2013a).

The mandible incisive strength (IS) of the herbivores was measured on those individuals used in the cafeteria experiment after dissection of their mandibles, using a lever dynamics model (Westneat 2003; Clissold 2007). For the pollinators, we measured functional body length (as for insects: sum of head + thorax + hind femur) and body volume (product of functional body length, head width and head height). The punch toughness (PT) of plants was measured with a flat-ended cylindrical steel rod (punch diameter 2.0 mm) mounted onto the moving head of a universal testing machine (model 5942; Instron, Canton, MA) (Aranwela et al. 1999; Sanson et al. 2001). Leaf thickness was measured with a digital micrometre, and leaf dry matter content was determined using standardized protocols (Cornelissen et al. 2003). The plant and insect traits were chosen based on their function with respect to their potential role in the biomechanics of plant–herbivore interactions (Clissold 2007; Ibanez et al. 2013a).

Plant and insect phylogenies

Only one plant phylogeny was inferred for both networks, and this then was pruned to the correct species samples while each network was studied. This phylogeny was built using a megaphylogeny approach as depicted in Roquet et al. (2013). To do so, we downloaded data for eight genomic regions from GenBank. Sequences were aligned with three different algorithms prior to selection of the best alignment performance. Alignments were first cleaned to remove ambiguously aligned regions and then a phylogenetic inference analysis was performed with RAxML (Stamatakis 2006). The complete procedure for tree inference can be found in Thuiller et al. (2014).

Regarding the insect pollinators' phylogeny, given that no complete molecular phylogeny was available for all of the insect taxa observed in our study, a best tree topology was assembled following the Tree of Life Web Project (Maddison et al. 2007) and the published phylogenies of Coleoptera (Hunt et al. 2007), Hymenoptera (Danforth et al. 2006), Oestroidea (Kutty et al. 2010) and Syrphidae (Stahls et al. 2003). Morphospecies were integrated into the phylogeny on the base of the lowest taxonomic level identified. To obtain a time-calibrated phylogeny, we identified a set of 19 nodes that were in common between our phylogeny and the large-scale compilation of phylogenetic divergence dates provided by Hedges and Kumar (2009). Based on this set of nodes and putative dates, we applied a pseudo-calibration procedure by interpolating undated nodes at equal intervals between dated ones (the so-called BLADJ algorithm; Webb et al. 2008).

To compile the phylogeny of the insect herbivores, we merged the Caelifera phylogeny of Rowell and Flook (1998) and the Gomphocerinae phylogeny of Vedenina and Mugue (2011) to obtain a backbone phylogeny. The relationships among the Ensifera species were elucidated using the SeaView software (Gouy et al. 2010) with 16S sequences from GenBank. The time calibration of our final phylogeny was the one of our backbone phylogenies.

Alternative arbitrary branch length transformations (Grafen 1989) were also used, with no relevant effects on the final results.

Calculation of the functional niche values

The functional niche value of a focal species corresponds to the mean trait values of the species interacting with this focal species (Ibanez et al. 2013b). For example, the functional niche of an insect species on the nectar-holder depth dimension is the weighted mean of the nectar-holder depth of the visited plants. The mean is weighted by the number of visits an insect makes to each plant species, following:

$$\text{Functional niche} = \sum_{i=1}^{n} p_i \times \text{trait}_i \tag{1}$$

where n is the total number of plant species visited, p_i the proportion of visits given to plant species i, and trait_i is the nectar-holder depth of plant species i. An example of functional niche values is given in Fig. 1. The functional niche metric is homologous to a trait community weighted mean; Lavorel et al. 2008). Our functional niche metric therefore corresponds to the niche position—and not to the niche breadth, which is also used in the context of interaction networks (Junker et al. 2013).

Estimation of the PS

For each phylogeny in the dataset, namely, the two plant phylogenies, the pollinator and the herbivore phylogenies, we computed the PS of every single functional trait of the study species on their own phylogenies (trait PS), of the strength of interaction (see below for details) with each possible interacting species (taxonomic niche PS) and the mean of all functional traits of all interacting species (functional niche PS). As a metric PS we inferred Pagel's lambda (λ; Pagel 1997), given that the results of a previous simulation study suggest that this index would perform better than other commonly used ones (Münkemüller et al. 2012). In particular, lambda estimates scale linearly with the expected phylogenetic signal in simulated data sets (Münkemüller et al. 2012). Pagel's λ allowed us to infer the closeness of the resemblance between closely related species in terms of species traits (trait PS), identity of interacting species (taxonomic PS), and functional traits of interacting species (functional PS). Interestingly, estimated λ values varied around yardstick values (0 and 1), which correspond to specific evolutionary scenarios and allowed a robust comparison of estimated PS on each study phylogeny. When λ is inferred not to differ from 0, species characteristics are considered to vary independently of their phylogenetic position, while $\lambda = 1$ fits a scenario of Brownian motion (random deviation through evolutionary time), where closely related species always resemble each other more than expected by chance due to their common ancestry. The estimated value of λ was tested against the null hypothesis of a null λ (that is, no PS) by comparing the log-likelihood ratio to the χ^2 distribution with 1 *df*.

Thus, λ estimates were inferred for every functional trait in the dataset (trait and functional PS). Taxonomic niche PS was estimated for each interacting taxon. Instead of considering a standard trait, we considered a "trait" value to be either the number of interactions (in the case of the pollination network) or the mass consumed (in the case of the herbivory network). For the insect pollinator phylogeny, we therefore calculated 32 taxonomic niche PS (one for each plant species). For the plant (flowers) phylogeny, we selected the 41 insect taxa for which at least seven individuals were observed (species list in ESM 1). In order to also include rare taxa (<7 individuals), we conducted a separate and complementary analysis where all the insect taxa were grouped into 14 families, super-families or orders (ESM 2). In total, the taxonomic niche PS was estimated for 32 flowers, 41 pollinators, 24 leaves, 26 herbivores (a total of 123 taxa).

Based on the same data, we also estimated whether a multivariate PS could be detected for the entire trait niche, taxonomic niche and functional niche data. To do so, we optimized a multivariate λ index, as implemented in the phylogenetic principal component procedure (Revell 2009). The estimated value of λ was tested against the null hypothesis of a null λ (that is, no PS) by comparing the log-likelihood ratio to the χ^2 distribution with 1 *df*. To ensure that our conclusions relied on robust results and given that the statistical behavior of multivariate λ estimates is unknown, we also tested the significance of a multivariate PS by using the method developed by Jombart et al. (2008), which estimates a global autocorrelation structure based on Moran's eigenvector maps.

Estimation of the cophylogenetic network structure

Interaction networks are jointly shaped by the evolutionary history of both plants and insects. Consequently, the separate estimation of network phylogenetic structure on each guild's phylogeny may obscure important phylogenetic patterns of network structure. In particular, estimating the taxonomic niche PS separately on the plants' and insects' phylogenies does not allow any inference regarding which of the two evolutionary histories most structures the interaction network. Therefore, we also explored the phylogenetic structure of study networks by inferring their so-called cophylogenetic structure. This structure is inferred via a cophylogenetic intercept linear model that includes the phylogeny of both guilds simultaneously in the covariance structure of the error terms (Ives and Godfray 2006). The influence of each phylogeny on the interaction network was characterized by the estimated transformation parameter d (Blomberg et al. 2003), with $d = 1$ corresponding to a Brownian motion and $d = 0$ corresponding to a star phylogeny. Two d parameters per network were estimated, one for each guild. Confidence intervals (CI) for the d parameters were obtained by drawing 1000 bootstrap datasets. Three models were built, namely, a "full" model (each d estimated), a "Brownian" model (both $d = 1$), and a "star" model (both $d = 0$). The goodness-of-fit of each model was compared using mean square errors (MSE) of the predicted versus observed values. In order to compare the results of both networks, the MSE of the three models ($\mathrm{MSE_{full}}$, $\mathrm{MSE_{brownian}}$, $\mathrm{MSE_{star}}$) were standardized by the MSE of the star model, so that $\mathrm{MSE_{star}} = 1$ in both networks. Because this method is computer-intensive, we only included in this analysis those insect species for which at least seven individuals were observed (41 insect species, 31 plants).

Data analyses of both datasets were performed using R version 3.1.1 (R Core Team 2014), with packages geiger (Pennell et al. 2014), phytools (Revell 2012), and picante (Kembel et al. 2010).

Results

Trait PS

In the univariate analysis, all λ values of trait PS were >0.42, with the exception of the width of nectar holders for which λ = 0 (Fig. 2; Table 1). Several traits showed a very strong PS (λ > 0.9), such as flower number, proboscis length, and leaf dry matter content. Of the 14 tested traits, ten had a PS which was significantly different from zero.

Taxonomic niche PS

For most species, the taxonomic niche PS was weak. Among the 123 taxa analyzed, 95 taxa (77 %) had a λ of <0.3, and the λ of 103 taxa (84 %) was not significant (Fig. 2; ESM 1). For some species, however, their

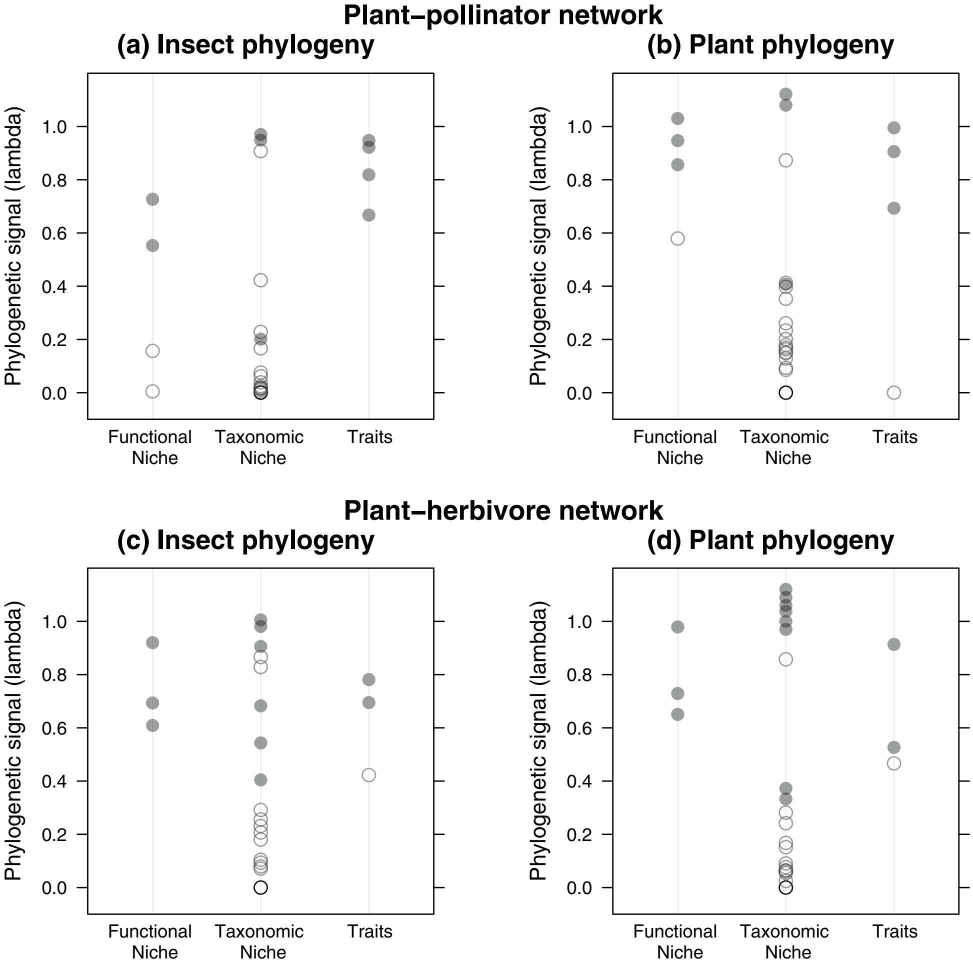

Fig. 2 Values of Pagel's lambda (λ) measuring the strength of the PS in the plant–insect networks. *Each circle* corresponds to a PS in the univariate analysis, measured either on traits, mean trait values of the interactors (functional niche), or interaction strength with each taxon (taxonomic niche). *Filled circles* significant PS ($p < 0.05$), *open circles* non-significant PS ($p > 0.05$)

Table 1 Phylogenetic signals in the plant–pollinator and the plant–herbivore networks

Plant–pollinator network

Plant phylogeny (flowers)	λ	mvλ	Pollinator phylogeny	λ	mvλ
Plant functional traits		0.76***	Insect functional traits		0.72***
Flower number	0.96***		Body mass	0.92***	
Landing zone area	0.55 ns		Functional body length	0.82***	
Width of nectar holder	0 ns		Proboscis length	0.95***	
Depth of nectar holder	0.72***		Proboscis width	0.67***	
Functional niche		0.51*	Functional niche		0.32***
Body mass	0.93**		Flower number	0.55***	
Functional body length	0.89**		landing zone area	0.15 ns	
Proboscis length	0.98*		Width of nectar holder	0 ns	
Proboscis width	0.40 ns		Depth of nectar holder	0.73***	
Taxonomic niche		0.16*	Taxonomic niche		0.13 ns

Plant–herbivore network

Plant phylogeny (leaves)	λ	mvλ	Herbivore phylogeny	λ	mvλ
Plant functional traits		0.51**	Insect functional traits		0.8 ***
Leaf dry matter content	0.91***		Body length	0.4 ns	
Punch toughness	0.53**		Body mass	0.78***	
Leaf thickness	0.47 ns		Mandible incisive strength	0.69***	
Functional niche		0.7 ***	Functional niche		0.56**
Body length	0.73***		Leaf dry matter content	0.69***	
Body mass	0.98***		Punch toughness	0.61**	
Mandible incisive strength	0.65***		Leaf thickness	0.92***	
Taxonomic niche		0 ns	Taxonomic niche		0^{ns}

The table lists the estimated values of the univariate PS, i.e., Paget's lambda (λ), and of the multivariate PS (mvλ) on the plants' and insects' phylogenies for plant and insect traits, their functional niche (mean functional traits of interacting insect and plant species, respectively), and the taxonomic niche (frequency of interaction with each insect and plant species, respectively). λ estimates are tested against the null hypothesis ($\lambda = 0$) with a χ^2 test-with 1 *df*. The results of the univariate analysis for the taxonomic niche PS of the 123 plant and insect taxa are presented in ESM 1

Significance levels are: ns, non-significant; * $p < 0.05$; ** $p < 0.01$; *** p value < 0.001. For more details on the statistics of the phylogenetic signal (PS), see "Materials and methods" section

interactors were highly clustered in the phylogeny. For example, in the herbivory network this was the case of four katydids (*Astragalus alpinus*, *Decticus verrucivorus*, *Tettigonia cantans* and *T. viridissima*) out of seven. Interestingly, the plant *Heracleum sphondylium* was simultaneously visited and eaten by phylogenetically related pollinators and herbivores, respectively.

According to the cophylogenetic method (Ives and Godfray 2006), the phylogenetic signal of the pollination network was weak for both guilds, as the confidence

Table 2 Results of the cophylogenetic intercept linear model for the plant–pollinator and the plant–herbivore networks

Network	d_{insect} [a]	d_{plant} [a]	MSE_{full} [b]	MSE_{star} [b]	$\text{MSE}_{\text{Brownian}}$ [b]
Pollination network	0.20 (0.00–0.65)	0.00 (0.00–0.52)	0.98	1.00	2.21
Herbivory network	0.12 (0.04–0.22)	0.00 (0.00–0.01)	0.92	1.00	4.48

The dependent variable was the interaction strength between plants and insect pollinators (or herbivore insects)

[a] *d* parameters measure the influence of each phylogeny on the interaction networks. The values between parenthesis are 95 % confidence intervals obtained by bootstrap analysis

[b] Mean square errors (MSE) correspond either to the full model (each *d* estimated), a "Brownian" model (both $d = 1$), and a "star" model (both $d = 0$). All MSE were standardized by the MSE of the star model, so that $\text{MSE}_{\text{star}} = 1$ in both networks

intervals of both *d* parameters included zero (Table 2). The standardized MSE of the full model (where both *d* are estimated) was very close to that of the star phylogeny model (Table 2), indicating a weak cophylogenetic signal. Similar results were obtained for cophylogenetic analysis of the herbivory network (Table 2), except that the PS for the insect phylogeny was small (0.12) although still significant (95 % CI 0.04–0.22). However, the standardized MSE indicated that the overall cophylogenetic signal was weak (Table 2).

Functional niche PS

In contrast to patterns of taxonomic niche PS, the estimated functional niche PS was generally much stronger. In the univariate analysis, all λ values of trait PS were >0.40, with the exception of the width of nectar holders ($\lambda = 0$) and the landing zone area ($\lambda = 0.15$) (Fig. 2; Table 1). Several functional niche components showed a very strong PS ($\lambda > 0.9$), including proboscis length, body volume, and leaf thickness. Of the 14 tested functional niche components, 11 had a significant PS. We also ran the three PS analyses of the plant–pollinator network for both study sites separately in order to test if the phylogenetic patterns depended on the study site; the results remained qualitatively unchanged from those of the analysis of the network for both study sites together (ESM 3).

Multivariate PS

The multivariate analysis gave qualitatively similar results (Fig. 2; Table 1). For the trait PS all multivariate λ were >0.51, and all were significant. For the taxonomic niche PS, the λ from the multivariate analysis ranged from 0 to 0.16; all λ were very low estimates and thus not significant, with the exception of the multivariate λ of insect taxa on the plant phylogeny ($\lambda = 0.16$). In contrast, and in accordance with the results of the univariate PS, for the functional niche PS the multivariate analysis gave qualitatively similar results. All multivariate λ were >0.33, and all were significant. For trait PS, taxonomic niche PS or functional niche PS, the multivariate Moran's eigenvector maps led to the same conclusions as the multivariate λ (ESM 4).

Discussion

Very few studies have jointly analyzed the phylogenetic structure of interaction networks from both a taxonomic and functional standpoint (Rezende et al. 2007a, 2009; Rafferty and Ives 2013; Schleuning et al. 2014). Integrated datasets combining network structure, functional traits, and phylogenetic trees are scarce, but they have the potential to provide novel insights into unexplored mechanisms underlying the assembly and functioning of interaction networks. Most datasets only include networks and phylogenies, but not traits (Rezende et al. 2007b; Gómez et al. 2010; Krasnov et al. 2012; Rohr and Bascompte 2014; Minoarivelo et al. 2014). As such, the results of our study provide novel data relating to the complex interplay between taxonomic niche and functional niche—i.e., how species specialize with specific interacting species depending on their taxonomy or on the match between their functional traits.

A primary result of our study is that we found a strong trait PS in both guilds within both networks. The finding is in accordance with existing evidence that functional traits show a significant PS (Ives and Godfray 2006; Cornwell et al. 2014; Rohr and Bascompte 2014; Zanne et al. 2014; Chalmandrier et al. 2015). In a second step in our analysis, we found that not only functional traits of individual species, but also traits of their interacting species showed consistently a high PS. However, the PS in taxonomic niche was consistently low, and most of the time it was not significantly different from the value expected under conditions of no PS (i.e. star-like phylogeny). The pattern was clear-cut and observed in both networks, and in both plant and insect communities (Fig. 2; Table 1).

Weak taxonomic niche PS is a common feature of interaction networks. For example, closely related pollinators were found not to be more likely to visit the same plant species in a pollination network in a tallgrass temperate prairie (Rafferty and Ives 2013), and the taxonomic niche PS was found to be weak in *Orchis*–fungus interactions in Europe (Jacquemyn et al. 2011). In a meta-analysis of 53 plant–pollinator and plant–frugivore mutualistic networks, Minoarivelo et al. (2014) detected a significant taxonomic niche PS in only about 20 % of the networks. Taken together, these findings highlight the weak potential of phylogenetic data alone for predicting the structure of ecological networks. To the contrary, the functional niche PS may provide more insight into the structure of interaction networks.

The interplay between trait convergence and interactor sampling

We believe that the pattern of a weak taxonomic niche PS combined with a strong functional niche PS is the result of the interaction between two processes, namely, trait convergence and interactor sampling. Trait convergence is when two phylogenetically distant clades share similar traits values. For example, Krasnov et al. (2012) found that convergence disrupted the taxonomic niche PS in mammal–flea networks. Trait convergence might be particularly common in interaction networks, as a simulation study conducted by Guimaraes Jr et al. (2011) showed that co-evolutionary cascades in networks favored trait convergence. Interactor sampling occurs when species interact only with a random subset of the set of potential interactors determined by their functional traits. In other words, a species has a potential taxonomic niche corresponding to the set of species sharing the traits of its potential interactors (Junker et al. 2013) and a realized taxonomic niche corresponding to the few species that were sampled in this larger set. The potential set of interactors is determined by functional traits, whereas the realized set is sampled according to neutral theory (Hubbell 2001; Chave 2004).

Interactor sampling can be due to individual specialization (Bolnick et al. 2002). In this case, the lack of taxonomic niche PS could be an artefact due to insufficient sampling effort (Martinez et al. 1999; Blüthgen et al. 2008). This is a possible limitation of our study as the mean sampling completeness of the plant–pollination dataset equals 60 %. Alternatively, partner sampling can apply at the species level in which case the potential taxonomic niche is larger than the realized taxonomic niche at the species level. In that case, the lack of taxonomic niche PS becomes permanent, whatever the sampling effort.

Here, we provide examples from both networks to illustrate how the interplay between trait convergence and interactor sampling can explain the pattern observed in our study and disrupt the relationships between traits, species interactions and phylogenies. In the pollination network, trait convergence was frequent (Fig. 1). Consider the species *Bombus mesomelas*, for which only four individuals were observed but all plant species visited were from different families (Dipsacaceae, Orobanchaceae, Boraginaceae and Fabaceae). The traits of these plant species converge as they all have relatively deep nectar holders. The four *B. mesomelas* individuals visited unrelated plant species having similar trait values, which weakens the taxonomic niche PS. The three Fabaceae of our study plant community, however, are all visited by insects having relatively long proboscis, which strengthens the functional niche PS, although some insects are unrelated but have convergent traits (e.g. *Empistes selata* and *B. mesomelas*). From the perspective of the nectar holder depth, the *B. mesomelas* individuals could have visited a larger set of potential interactors. Instead, four plant species were sampled, and *B. mesomelas* visited unrelated species having similar traits. Interactor sampling is therefore combined with trait convergence, which disrupts the taxonomic niche PS and at the same time preserves the functional niche PS.

In the plant–herbivore network, trait convergence was less frequent (Fig. 1), although as an example the case of *Trifolium alpinum* is striking. The leaf toughness of *T. alpinum* is similar to the toughness of many grasses, such as *Dactylis glomerata*, and *T. alpinum* is mainly consumed by Gomphocerinae grasshoppers, which is the clade having the highest incisive strength. Patterns of convergence of trait matching on several portions of plant and insect phylogenies suggest that the evolution of a plant–insect interaction network can be conceived as a macro-evolutionary adaptive landscape, where different lineages evolve along different adaptive peaks that are determined by matching traits with the interacting clades. This concept suggests that Ornstein–Ulhenbeck models, which have been widely used for studying the evolution of species environmental niches (Mahler et al. 2013), could potentially be used for models considering network phylogenies taken together (Nuismer and Harmon 2015).

Implications of weak taxonomic niche PS and strong functional niche PS

Interaction networks are highly variable in space and time (Dupont et al. 2009; Díaz-Castelazo et al. 2010; Lázaro et al. 2010). For example, in two separate 4-year studies of plant–pollinator networks, only 5 % (Greece; Petanidou et al. 2008) and 30 % (California; Alarcón et al. 2008) of the pairwise interactions were observed each year. In the light of our finding that functional niche PS is more frequent than taxonomic niche PS, we predict that networks should be more stable from a functional point of view than from a taxonomic one. In other words, when the set of potential interactors is large, interactor sampling should lead to highly variable networks; if, however, the potential interactors have similar traits, then the functional properties of the networks should be more stable. This hypothesis was partly validated at the functional group-level for a pollination network studied during a 3-year period in China (Gong and Huang 2011), but more data are required at the species level allow more robust conclusions to be drawn.

Our finding of weak taxonomic niche PS combined with strong functional niche PS can also have important consequences on the stability of interaction networks. Co-extinction cascades of related species may occur in networks showing a strong taxonomic niche PS (Rezende et al. 2007b), along with a rapid decline of phylogenetic diversity (Srivastava et al. 2012). If the taxonomic niche PS is weak and the functional niche PS is strong, co-extinction cascades may affect functionally similar but phylogenetically distant species. This mechanism is likely to limit the loss of phylogenetic diversity when such networks experience species extinction.

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