

## ADVANCES AND CHALLENGES IN THE STUDY OF ECOLOGICAL NETWORKS

# Merging evolutionary history into species interaction networks

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### Summary

1. The occurrence of complex networks of interactions among species not only relies on species co-occurrence, but also on inherited traits and evolutionary events imprinted in species phylogenies. The phylogenetic signal found in ecological networks suggests that evolution plays an important role in determining community assembly and hence could inform about the underpinning mechanisms.
2. The aim of this study was to review the main findings and methodological approaches used for detecting phylogenetic signal in species interaction networks, particularly in different aspects of network structure: conservatism of interactions, modularity, connectivity and nestedness.
3. In general, studies show that species phylogenies determine interacting partners, module composition, species roles and nested patterns, although these influences are not always consistent across different interaction types. The relative importance of phylogeny to network structure, as well as the scale dependence of phylogenetic signal, denotes key areas for future research.
4. Phylogenetically informed network ecology represents a promising field for understanding species interaction patterns, community assembly processes and dynamics. It can also provide important information for predicting community changes and improving management practices.

**Key-words:** antagonistic network, conservatism of interactions, module, mutualistic network, nestedness, network cohesion, phylogenetic signal, phylogeny

### Introduction

In ecosystems, organisms interact with each other in diverse ways, forming complex webs of interactions. These interactions depend not only on species' abundances and their spatiotemporal co-occurrence (Poisot, Stouffer & Gravel 2015), but also on their evolutionary history and traits (Eklöf *et al.* 2013; Dehling *et al.* 2014; González-Castro *et al.* 2015), which are usually inherited from a common ancestor (Felsenstein 1985; Harvey & Pagel 1991). For this reason, ecophylogenetics emerged as a field of study that uses information about the evolutionary history of species (phylogenetics) to answer ecological questions (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012).

Phylogenetic approaches to community ecology have the benefit of combining phenotypic information with past

evolutionary events and thus capture elements of trait matching and evolutionary divergence among species that could be important during community assembly (Cadotte *et al.* 2010; Srivastava *et al.* 2012). The potential of phylogenetics to improve our understanding of community structure (Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012), and the mechanisms driving such structure, has called the attention to network ecologists over the last decade (Gu, Goodale & Chen 2015). Particularly, the presence of a phylogenetic signal in interaction networks, such as antagonistic and mutualistic networks, would suggest that network patterns are influenced by past evolutionary events and not exclusively by current ecological processes (Vázquez *et al.* 2009).

Due to the relevance of phylogeny as one of the factors shaping species interaction patterns (Cattin *et al.* 2004; Rezende *et al.* 2009; Cagnolo, Salvo & Valladares 2011), here I review the main findings and methodological approaches for including phylogenetic information into

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interaction network studies. Specifically, this review covers the effects of phylogeny on different aspects of interaction network structure, methodological approaches for detecting phylogenetic signal and ideas for future research.

### Evolutionary signal in interaction network structure

Do related species interact with similar partners? Are related species clustered in the same modules? Do they have similar roles? Does phylogeny affect network cohesion and nestedness? These are some of the main questions that phylogenetically informed network ecology has focused on. To achieve the answers, studies have analysed different network properties, which show phylogenetic signal, as outlined below.

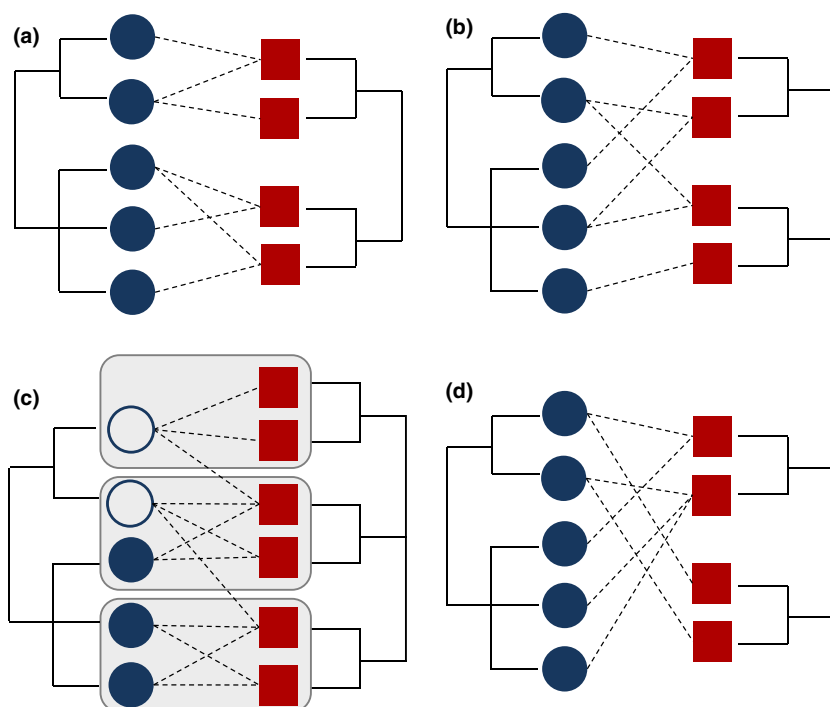
#### CONSERVATISM IN SPECIES INTERACTIONS

The tendency of closely related species to interact with similar partners (Fig. 1a as opposed to 1b), named conservatism of interactions, emerges from the fact that inherited ancestral phenotypic traits determine, at least in part, ecological interactions (Thompson 2005). Several studies have addressed this hypothesis from different perspectives. For example, using a large and diverse group of interactions from different clades, Gómez, Verdú & Perfectti (2010) showed that phylogenetic conservatism occurs across several kingdoms. Among their findings, conservatism of interactions appeared to be equally likely to occur across different interaction types, such as symbiotic and non-symbiotic, as well as antagonistic and mutualistic interactions. However, it has been argued that considering all

interactions per clade might not be the best way to look for associations between species interaction characteristics, phylogeny and network structure (Fontaine & Thébaud 2015), because interactions occur at small taxonomic and local scales, which affect the phylogenetic structure of communities (Cavender-Bares *et al.* 2009). This could explain the number of studies that have found differences in interaction conservatism between distinct network types and depending on whether a resource or consumer perspective was considered.

Particularly, conservatism of interactions has been found to be stronger in antagonistic than in mutualistic networks (Fontaine & Thébaud 2015). In antagonistic networks, it has been repeatedly observed that closely related prey (resource) species tend to share a greater number of predators (consumers) even though closely related predators do not necessarily prey upon the same species (Ives & Godfray 2006; Weiblen *et al.* 2006; Bersier & Kehrlri 2008; Cagnolo, Salvo & Valladares 2011; Naisbit *et al.* 2012; Elias, Fontaine & van Veen 2013; Leppanen *et al.* 2013; Fontaine & Thébaud 2015), potentially due to predators having labile host ranges (Ives & Godfray 2006).

Asymmetry in interaction conservatism among interacting groups has also been observed in mutualistic networks (Rezende *et al.* 2007), although less pronounced (Fontaine & Thébaud 2015). For instance, in plant–pollinator and seed dispersal networks, animals tend to have higher conservatism in their interactions than plants (Rohr & Bascompte 2014; Fontaine & Thébaud 2015; but see Chamberlain *et al.* 2014a), possibly because animals have specialized physiologically to digest certain plant lineages. Other examples of phylogenetic asymmetry include marine goby–shrimp mutualistic networks, where the evolutionary



**Fig. 1.** Schematic representation of bipartite interaction networks and phylogenetic trees of the interacting groups. Species of each interacting group (e.g. hosts–parasites, prey–predators and plants–pollinators) are represented by circles and squares. Dashed lines connecting related species denote interactions. (a) Closely related species interact with similar partners, as opposed to (b) where species interact randomly with respect to their phylogenies. (c) The phylogeny of one of the interacting groups (squares) determines, at least in part, modularity (grey boxes), and species that connect different modules (open circles) are phylogenetically related. (d) Nested interaction pattern and related species having similar number of interactions.

constraints in partner use appear for shrimps (Thompson *et al.* 2013), and myrmecophilic networks, where ants interact with phylogenetically related plant species (Cagnolo & Tavella 2015).

Differences in the conservatism of interactions between interacting groups could also greatly influence the evolution of the network, with the higher conservatism group potentially driving the evolution of the system (Jordano 2010). Therefore, in antagonistic networks, it could be expected that traits determining foraging strategies and capabilities of predators evolve faster than traits determining the vulnerability (i.e. defences) of prey species, which should be more conserved and hence have a higher contribution to the network evolution (Rossberg *et al.* 2006; Fontaine & Thébault 2015). Furthermore, according to the competition relatedness hypothesis (Cahill *et al.* 2008), if traits responsible for ecological similarity are conserved in the phylogeny, this would increase the competition for resources between closely related species, which could explain why closely related predators do not necessarily prey on the same species.

Conversely, in mutualistic networks, where complementarity and convergence have been identified as potential factors shaping these networks (Thompson 2005; Rezende *et al.* 2007; Santamaria & Rodriguez-Girones 2007; Vázquez *et al.* 2009; Guimarães, Jordano & Thompson 2011), evolution should be influenced by the phylogeny of both interacting groups. Specifically, convergence of traits among distantly related species, emerging as a response to similar selective pressures, should facilitate their persistence through positive indirect interactions (Jordano 2010; Guimarães, Jordano & Thompson 2011). Meanwhile, complementarity between interacting partners should facilitate efficient use of the mutualistic services provided by the partners (Jordano 2010).

#### MODULARITY AND SPECIES ROLES

Modules (compartments) are subsets of a network formed by species that tend to interact more between each other than with species from other modules (Krause *et al.* 2003). Modularity of mutualistic networks has been found to be lower compared to that of antagonistic networks (Thébault & Fontaine 2010; Fontaine *et al.* 2011), although, in both network types, there is evidence that module composition is characterized by groups of closely related species (Dupont & Olesen 2009; Mello *et al.* 2011) and species converging to certain sets of traits (Corbet 2000; Montoya, Yallop & Memmott 2015).

In antagonistic webs, the hypothesis that phylogeny determines module composition has been tested in several systems. For instance, in plant–herbivore and herbivore–parasitoid food webs, it has been observed that the interaction range boundaries that determine modules are imposed by resource and host phylogenies (Cagnolo, Salvo & Valladares 2011). Similarly, in host–parasite networks,

closely related hosts tend to cluster in the same modules, while the distribution of parasite lineages across modules did not seem to follow a specific pattern (Vacher, Piou & Desprez-Loustau 2008; Krasnov *et al.* 2012; Lima *et al.* 2012). In addition, in marine food webs, closely related top predators tend to occupy different modules of the food web, potentially to reduce competition and enhance coexistence of those species in the community (Rezende *et al.* 2009). In summary, the shared evolutionary history of hosts, but not that of predators, seems to constrain the modular structure observed in antagonistic webs (Fig. 1c). However, other factors such as host switching behaviour between unrelated host lineages (Johnson *et al.* 2011) and trait convergence in unrelated predator species (Perez-Lozada, Hoeg & Crandall 2009) may also contribute to shape modularity in antagonistic networks (Krasnov *et al.* 2012).

Fewer studies have analysed the influence of phylogeny on modularity of mutualistic networks. For example, in seed dispersal networks, shared evolutionary history of both interacting groups partially explained the modular structure observed (Donatti *et al.* 2011; Mello *et al.* 2011). In these cases, modularity seems to emerge from a combination of phylogeny and trait convergence of phylogenetically unrelated species. Similarly, the convergence of floral characters towards pollination syndromes has been identified as determinant of the pattern of interactions and the modules detected in a plant–pollinator network (Danieli-Silva *et al.* 2012). Also, modularity of plant–pollinator and seed dispersal networks has been found to correlate with phylogenetic tree balance, that is the variation in evolutionary rates among clades within a phylogeny (Chamberlain *et al.* 2014b). This suggests that evenness in the distribution of diversification events among clades also promotes modularity. Despite the positive relationship between modularity and phylogenetic signal found in these studies, Schleuning *et al.* (Schleuning *et al.* 2014) found that modular structure in avian seed dispersal networks was more related to factors depending on species abundance rather than phylogenetic conserved traits.

Another approach to clustering species within a network has been to break interaction webs into subsets of few species representing important types or arrangements of ecological interactions, that is motifs (Milo *et al.* 2002). Using this approach, the role of individual species within a network can be described by their participation in different motifs (Stouffer *et al.* 2012) allowing a species-centric perspective of the interaction network. Species' roles have been found to be influenced by phylogeny and to contribute differently to network persistence (Stouffer *et al.* 2012), which suggests that species roles could be an inherited characteristic, shaped by the evolutionary history of species. This hypothesis is strengthened by observations that numerous ecological and life-history traits vary according to their phylogenetic history (Peterson, Soberón & Sánchez-Cordero 1999; Blomberg, Garland & Ives 2003)

and that species roles are shaped by those traits (Stouffer, Rezende & Amaral 2011).

#### NETWORK CONNECTIVITY

Apart from the phylogenetic signal found within modules, species evolutionary history can also influence the among-module connectivity, that is cohesion, of the interaction network (Fig. 1c). Specifically, in host–parasite networks, it has been observed that the extent to which species (parasites) connect different modules depends on their phylogeny (Poulin *et al.* 2013). In addition, Krasnov *et al.* (2012) found that the among-module connectivity of another host–parasite network was constrained to a certain extent by species phylogeny, but also affected by local factors such that connectivity may also vary geographically. Similarly, in seed dispersal networks, species that connect different modules are phylogenetically related regardless of being plants (Nogales *et al.* 2015) or animals (Schleuning *et al.* 2014). This evidence of species relatedness contributing to network cohesion reinforces the idea that phylogenetically related species may have similar roles across different interaction networks (Stouffer *et al.* 2012; Poulin *et al.* 2013; Baker *et al.* 2015).

The presence of a strong phylogenetic signal in module connectivity embraces great importance for network cohesion and stability. For example, the extinction of a lineage with high-module connectivity could cause the fragmentation of a network into isolated modules (Krasnov *et al.* 2012), which could enhance stability in trophic networks, but diminish it in mutualistic networks (Thébault & Fontaine 2010).

From a species-level perspective, connectivity could be measured as the number of species with which a given species interacts (degree). In mutualistic networks, degree has been found to depend on phylogeny (Rezende *et al.* 2007), suggesting that phylogenetically related species have a similar number of interaction partners (Fig. 1d). However, interaction strength (an estimate of the ecological impact of one species on another) does not seem to be affected by the evolutionary history of species, potentially due to variability in species abundance, changes in phenology and sampling errors (Rezende *et al.* 2007), which tend to decrease phylogenetic signal (Blomberg, Garland & Ives 2003).

#### NESTEDNESS

Interaction networks are said to be nested when specialist species interact with a proper subset of the species that generalists interact with (Bascompte *et al.* 2003) (Fig. 1d). Nested patterns suggest that reciprocal specialization should occur rarely among interacting species, although there is controversy on whether relationships between specialist species are rare in nested networks (Bascompte *et al.* 2003; Bluthgen *et al.* 2007). Nestedness has been mostly reported for mutualistic networks and has also been found

to be influenced by phylogenetic relationships and trait matching (Rezende, Jordano & Bascompte 2007).

For example, in an orchid mycorrhizal system, the nested structure of the network was correlated to the phylogeny of orchid species but only weakly with the phylogeny of the fungi (Jacquemyn *et al.* 2011). This suggests that the orchid species associated with few fungi rely on the most common fungi, while orchid species associated with many fungi are also associated with sporadically observed fungi. Even though the exact mechanisms explaining the relationship between phylogeny and nestedness remain unclear (Jacquemyn *et al.* 2011), it has been suggested that nested patterns in mutualistic networks arise from a combination of complementarity and convergence of traits among species (Thompson 2006). Conversely, for antagonistic networks, it has been shown that nested diets are a consequence of phylogenetic constraints and adaptation (Cattin *et al.* 2004). Nonetheless, it has been recently argued that although phylogenetic proximity is compatible with nestedness, it cannot be claimed to determine it, that is a network assembly model that favours phylogenetic proximity of each guild cannot give rise to a nested pattern (Perazzo *et al.* 2014). Instead, nestedness could be attributed to a general rule by which species tend to behave as generalists, holding contacts with counterparts that already have a large number of contacts.

#### Methodological approaches to interaction network phylogenetics

To perform phylogenetic network studies, three elements are essential: species interaction data, the phylogenies of the interacting groups and appropriate analytical methods.

#### INTERACTION NETWORK DATA

Observing and collecting species interaction data require greater effort than sampling only species. In addition, biases towards studying interaction types that are easy to record (e.g. plant–herbivore, plant–pollinator, etc.) represent a challenge that we need to overcome. Nonetheless, with the increasing availability and decreasing cost of new techniques, the field and laboratory effort needed for sampling interactions is declining (Poole, Stouffer & Tylianakis 2012; Garcia-Robledo *et al.* 2013), making it easier to improve the resolution of interaction networks and explore other interaction types. Furthermore, publicly available data bases (Table 1a) are increasingly incorporating interaction network data, allowing larger scale analyses to be performed using numerous networks.

Several authors have questioned the validity of ecological network data, emphasizing problems of sampling effort (Polis 1991; Martinez *et al.* 1999). However, network structure appears to be less sensitive to sampling effort, even though the number of species and links within a network tend to increase with it (Nielsen & Bascompte 2007).

Moreover, the use of quantitative (incorporating the interaction strength) instead of qualitative interaction data (presence–absence) can, to some extent, minimize the effects of sampling biases (Banasek-Richter, Cattin & Bersier 2004).

#### PHYLOGENETIC VS. TAXONOMIC TREES

Due to the difficulties associated with constructing phylogenetic trees, the use of taxonomic trees has been a common alternative, particularly in interaction network studies (Bersier & Kehrlí 2008; Cagnolo, Salvo & Valladares 2011;

Stouffer, Rezende & Amaral 2011; Lima *et al.* 2012). For constructing taxonomic trees, taxa are organized into hierarchical nodes where each node represents a taxonomic rank (e.g. species, genus and family). Then, the taxonomic distance between species pairs is determined by counting the number of nodes necessary to reach a common node. Hence, two species within the same genus have a distance of one, while if they pertain to the same family but to different genera, their distance equals two, etc. Because, for example, steps from species to species have the same values as jumping from order to order, taxonomic trees underestimate evolutionary differences compared with real

**Table 1.** Elements to perform phylogenetic network analyses (a–c), examples of tools for obtaining a–b and tests (c) used in published studies.

Elements	Tools	Description	References
a) Interaction network data	Sampling	Methods depend on the study system; all present challenges and constraints.	Jordano (2015)
	Data bases	Published data on species interaction networks.	Dryad ( <a href="http://datadryad.org/">http://datadryad.org/</a> ), Interaction Web Database ( <a href="https://www.nceas.ucsb.edu/interactionweb/index.html">https://www.nceas.ucsb.edu/interactionweb/index.html</a> ), Web of Life ( <a href="http://www.web-of-life.es/">http://www.web-of-life.es/</a> )
b) Phylogenies	Tree of Life	Information on phylogenetic branching patterns between groups of organisms. Useful for constructing backbone trees.	Maddison & Schulz (2007)
	Sequence data bases	Gene sequences that can be used to reconstruct phylogenies, e.g. in BEAST.	Benson <i>et al.</i> (2013), European Bioinformatics Institute Database ( <a href="http://www.ebi.ac.uk/genomes/">http://www.ebi.ac.uk/genomes/</a> )
	Phylomatic	Plant phylogenetic data base provides phylogenetic trees by inputting plant species lists.	Webb & Donoghue (2005)
	Phylocom	Software for estimating branch lengths of phylogenetic trees produced by phylomatic.	Webb, Ackerly & Kembel (2008)
	Bayesian Evolutionary Analysis Sampling Trees (BEAST)	Software for reconstructing ultrametric phylogenies from molecular sequences.	Drummond & Rambaut (2007)
c) Analytical methods	Mantel test	To correlate phylogenetic distance and interacting partners overlap matrices for determining <i>conservatism of interactions</i> .	Mantel (1967), Cattin <i>et al.</i> (2004), Rezende <i>et al.</i> (2007)
	Generalized least-square model	For testing the influence of both phylogenies on the interaction matrix, with species interaction strength described by a linear model, to determine <i>conservatism of interactions</i> .	Ives & Godfray (2006)
	Correlation	To assess the relationship between species phylogenetic distance and the degree of co-occurrence within <i>modules</i> .	Cavender-Bares <i>et al.</i> (2004), Krasnov <i>et al.</i> (2012)
	Multiresponse permutation procedure	Used to test whether phylogenetic distance between species is lower within than between <i>modules</i> .	Mielke & Berry (2001), Vacher, Piou & Desprez-Loustau (2008), Cagnolo, Salvo & Valladares (2011)
	Generalized linear mixed model	To assess the influence of phylogeny on <i>network connectivity</i> by calculating the proportion of variance accounted by a random factor (phylogeny) in a GLMM with PC (participation coefficient: degree to which interactions of each species are distributed among modules) as the response variable.	Poulin <i>et al.</i> (2013), Guimera & Amaral (2005)
	K-statistic	Compares the observed phylogenetic signal in PC to the signal under a Brownian motion model of trait evolution on a phylogeny. $K > 1$ indicates strong phylogenetic signal.	Blomberg, Garland & Ives (2003), Jacquemyn <i>et al.</i> (2011), Krasnov <i>et al.</i> (2012)
	phyloNODF	Measure of <i>nestedness</i> that takes into account species relatedness by incorporating the phylogenetic structure.	Melo, Cianciaruso & Almeida-Neto (2014)

phylogenies (Weiblen *et al.* 2006). Also, phylogenies inferred from taxonomy often result in numerous soft polytomies (many branches descend from a single node), where all species within a genus are equally related, and the same for genera, families, etc. Therefore, even though lineages could have diverged at different times, the lack of phylogenetic information misleadingly makes all taxa equally related to each other. These topological uncertainties as well as the arbitrary assignment of branch lengths can be particularly inconvenient for phylogenetic tests that strongly rely on topology.

Although many groups of organisms lack sufficient phylogenetic information, public resources often provide information that can be used to obtain better-resolved phylogenies (Table 1b). For example, it is possible to construct backbone trees for the members of higher clades, for example families, which can be even scaled by known dates for some of the nodes. Even though such phylogenies would not be perfect (e.g. branch lengths would probably be inaccurate), they would be more resolved than phylogenies based on taxonomy alone. Also, special tools are being designed for easily obtaining phylogenies based on supertrees (Webb & Donoghue 2005; Webb, Ackerly & Kembel 2008) and based on molecular sequences (Drummond & Rambaut 2007) (Table 1b). Therefore, in many cases, it is possible to get better-resolved phylogenies than those based on taxonomy alone.

#### ANALYTICAL METHODS

Multiple analyses can be performed to detect phylogenetic signal on interaction network structure. For instance, if the interest is in knowing whether interactions are conserved, we could perform a Mantel test (Mantel 1967) with the species relatedness and interaction-partner overlap matrices (Cattin *et al.* 2004; Rezende *et al.* 2007; Bersier & Kehrl 2008; Jacquemyn *et al.* 2011; Naisbit *et al.* 2012; Fontaine & Thébault 2015). Another method for detecting whether related species interact with similar partners is the generalized least-square (GLS) model (Ives & Godfray 2006) (Table 1c). With this method, it is possible to estimate the independent signals of the phylogenies of the interacting groups (e.g. plants and animals separately) as well as the strength of the signal of both phylogenies combined.

To determine whether phylogenetic signal underlies modularity, we first need to find the modules, for which several methods are available (Guimera & Amaral 2005; Guimera, Sales-Pardo & Amaral 2007; Leger, Daudin & Vacher 2015). Then, it is possible to assess whether phylogenetic distance between species is related with the degree of co-occurrence within modules (Cavender-Bares *et al.* 2004; Krasnov *et al.* 2012) and/or whether phylogenetic distance is lower within than between modules (Vacher, Piou & Desprez-Loustau 2008; Cagnolo, Salvo & Valldares 2011) (Table 1c). Meanwhile, to estimate whether

species relatedness affects network among-module connectivity, we can relate a measure of how a species is connected to species in other modules (e.g. by the participation coefficient, Guimera & Amaral 2005) with its phylogeny (Poulin *et al.* 2013) or use Blomberg, Garland & Ives (2003) K-statistic (Table 1c).

Finally, although there are a variety of metrics for estimating the degree of nestedness (Almeida-Neto *et al.* 2008; Ulrich, Almeida-Neto & Gotelli 2009), they do not consider ecological and evolutionary differences among species associations. However, a new index, which allows determining whether phylogeny underlies nested patterns (Table 1c), has been recently developed (Melo, Cianciaruso & Almeida-Neto 2014).

#### Future perspectives

Despite the recent advances in phylogenetic network ecology, there are still many open questions before we can fully understand the mechanisms underlying observed relationships and their effects on community dynamics. Moreover, the relative importance of phylogeny for network structure, compared with environmental and demographic factors, and whether phylogenetic signal scales with the level of organization and space, are key aspects that remain unknown. From an applied perspective, available information on the phylogeny interaction network relationship could be used to improve conservation and management strategies.

#### PHYLOGENETIC SIGNAL DETECTION AND RELATIVE IMPORTANCE

Several factors can potentially mask the phylogenetic signal found on network structure, such as the lack of well-resolved phylogenies and poor sampling of interactions. Also, environmental conditions of the interacting partners can blurred the true pattern of specificity (Krasnov *et al.* 2004), confounding the effects of phylogenies.

Establishing the relative importance of phylogeny on network structure compared with demographic and environmental factors, such as species abundance and environmental change, represents also a relevant point for clarifying the mechanisms driving community assembly and dynamics. Furthermore, recent studies show that phylogenetic congruence can be altered by abiotic conditions, such as habitat modification (Peralta *et al.* 2015; Aizen *et al.* 2016) and temperature (Lavandero & Tylianakis 2013), suggesting that phylogenetic signal could also be affected by environmental changes.

#### SCALE DEPENDENCE IN PHYLOGENETIC SIGNAL

Although geographical structure is an important component in the evolution of interactions (Brodie, Ridenhour & Iii 2002), it is still unknown the extent to which phylogenetic signal scales with space in interaction networks

(Mouquet *et al.* 2012). Even more, incorporating species interaction networks and phylogenetics into spatial distribution models could help in understanding and predicting how communities will occur in the landscape (Lavergne *et al.* 2010) and potentially inform us about community responses to human-induced changes. Incorporating spatial and evolutionary dynamics into ecological network models could also improve our understanding on the functional dynamics of species interactions (Proulx, Promislow & Phillips 2005).

Other than the geographical scale, the organizational scale at which interaction networks are constructed, for example nodes representing species vs. nodes representing phenotypes or genotypes, should also be considered. The network organizational scale we use could generate differences in the phylogenetic signal found, which in turn could help in understanding evolutionary processes, which occur within species. In addition, most agricultural management practices select for particular genotypes (Robinson *et al.* 2015), making this organizational scale widely spread and hence important to understand.

#### PREDICTING THE FATE OF SPECIES INTERACTIONS

Phylogenetic interaction network methods can highlight species roles in communities and hence their dynamic importance and benefits for the wider community (Stouffer *et al.* 2012). However, we still know little about whether the phylogenetic imprint of species roles holds across different network types and across different environments.

Additionally, determining the role of a species in a community based on its phylogeny could help in predicting the fate of novel interactions, such as those produced by introduced species (Ives & Godfray 2006). The phylogenetic relatedness of a community with an introduced species could affect the probability of establishment and invasion (Thuiller *et al.* 2010). For example, when a foreign organism is introduced into a new region, comparing its phylogenetic position with that of the species that form the local interaction network could help in assessing the risk of it becoming invasive (Ives & Godfray 2006), due to its similar requirements and/or likelihood of being attacked by the natural enemies already present (Mooney & Drake 1986). Even more, evaluation of biological control agents on non-target species (Howarth 1991; Henneman & Memmott 2001) as well as the impact assessment of infectious disease spread (Galvani 2003; Poisot, Thrall & Hochberg 2012) could potentially be improved by incorporating these techniques (Ives & Godfray 2006).

#### Conclusions

Phylogenetic signal underlying network architecture suggests that interaction networks follow deterministic associations underpinned by species evolutionary history. In general, related species tend to interact with similar partners, cluster in the same modules and present similar roles

(e.g. connecting modules). However, the phylogenetic signal found varies from weak to strong depending on the interaction type and the study system considered, potentially due to different underlying mechanisms. Although there is still a lot of ground to cover, the field of phylogenetic network ecology holds promise for enhancing our understanding and predicting changes in community structure and dynamics.

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#### Data accessibility

This manuscript does not use data.

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