REVIEW AND SYNTHESIS

The ecological and evolutionary implications of merging different types of networks

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Abstract

Interactions among species drive the ecological and evolutionary processes in ecological communities. These interactions are effectively key components of biodiversity. Studies that use a network approach to study the structure and dynamics of communities of interacting species have revealed many patterns and associated processes. Historically these studies were restricted to trophic interactions, although network approaches are now used to study a wide range of interactions, including for example the reproductive mutualisms. However, each interaction type remains studied largely in isolation from others. Merging the various interaction types within a single integrative framework is necessary if we want to further our understanding of the ecological and evolutionary dynamics of communities. Dividing the networks up is a methodological convenience as in the field the networks occur together in space and time and will be linked by shared species. Herein, we outline a conceptual framework for studying networks composed of more than one type of interaction, highlighting key questions and research areas that would benefit from their study.

Keywords

Aboveground–belowground, evolutionary dynamic, facilitation, interaction network, mutualistic, parasitic, stability, traits, trophic.

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INTRODUCTION

Ecological communities, whether they are meadows, tropical forests, lakes or coral reefs, consist of a wide range of species that interact with each other in many ways, for example, by predation, parasitism, mutualism, competition or facilitation. These interactions are a key component of biodiversity, since all organisms rely upon interactions with other individuals for feeding, reproducing or for being protected (Thompson 2005). Knowledge of these biotic interactions is essential to improve our understanding of how nature works. Moreover, species interactions are the backbone of key ecosystem services, such as primary production, nutrient cycling, water purification, pest control or pollination. One of the biggest challenges in ecology is to understand how these complex systems of interdependent species assemble, function and evolve. The description of the structure of these systems along with an understanding of the underlying processes can be used to predict how ecological communities will respond to increasing human impacts such as harvesting, land use change, climate change and species introduction. Ultimately, these insights should enhance sustainable management and utilisation of the services provided by natural communities.

Networks provide a systematic way of representing, characterising and comparing the complexity of ecological communities, where species are represented by nodes and interaction by links between nodes (Pimm 1982; van Veen *et al.* 2008). Historically, most network research has focused on food webs (Pimm 1982) and parasitoid webs (Hawkins 1992). Apart from seminal studies by Jordano (1987) and Fonseca & Ganade (1996), it is only in the last decade that network approaches have started to become widely applied to other types of ecological interactions such as mutualistic and parasitic interactions (see Ings *et al.* 2009 for a review). More recently, network approach has also been extended to facilitative interactions among plants, where adult plants species have a positive effect on the seedling establishment of other plants (Brooker *et al.* 2007; Verdú & Valiente-Banuet 2008). These studies reveal that ecological networks generally exhibit well-defined architectures (Pimm *et al.* 1991; Bascompte *et al.* 2003) with some foreseeable consequences for the ecological and evolutionary dynamics of communities, including species coexistence

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(Bastolla *et al.* 2009), community stability (e.g. Neutel *et al.* 2007), coevolutionary dynamics in multispecies interactions (Guimarães *et al.* 2007; Wade 2007) and responses to environmental change (e.g. Memmott *et al.* 2007).

Despite important progresses in our understanding of ecological communities, ecological network research is still highly segmented with studies mostly focusing on one kind of interaction in isolation. The partitioning of ecological networks in categories such as pollination networks, seed dispersal networks or host–parasitoid networks is mainly the result of the different interests of different scientific communities (Memmott 2009). Such partitioning *de facto* assumes that the ecological and evolutionary dynamics of these interactions are largely independent from other ecological interactions. However, the vast majority of species in natural communities establish different kinds of interactions with different species thereby leading to the different networks being interlinked, at least to some extent (Ings *et al.* 2009). For example, a plant could be pollinated by bees, consumed by caterpillars and its seeds dispersed by birds, i.e. it belongs to pollinator, trophic and seed dispersal networks. Below-ground, mycorrhizal, pathogen and decomposer networks interact with each other through shared host plants and shared predators (Wardle *et al.* 2004). These different interactions are involved in both the population dynamics and the fitness definition of the species within communities. Whether or not our understanding of the ecological and evolutionary dynamics of communities can be increased by taking the interlinked nature of these various interaction kinds into account remains unknown.

Although the seminal work of Odum (1953) first introduced the sign matrix to describe the various interactions among species within communities, subsequent theoretical studies mainly focused on systems encompassing a single interaction type (but see May 1973; Allesina & Pascual 2007). From the very few empirical datasets combining networks of different types, such as predation and parasitic networks (Lafferty *et al.* 2008) or pollination and herbivory networks (Melián *et al.* 2009), it appears that merging networks creates important new pathways for direct and indirect interactions. This will have potentially important, but largely unexplored, consequences for the ecological dynamics of these systems. From an evolutionary view point, theoretical studies suggest that considering two interaction types simultaneously, such as mutualistic and antagonistic interactions, influences the evolutionary dynamics of species traits (Nuismer *et al.* 1999; Bronstein *et al.* 2003). In addition to new theoretical perspectives, progress in this direction could greatly benefit applied ecology, for example enabling ecologists to jointly manage pest control and pollination in agroecosystems. Without a better understanding of the structure and function of the sub-networks in a community, wrong or suboptimal decisions could be made when managing or restoring ecosystems. Broadening our views on ecological networks by integrating different interaction types into a single complete network remains a key challenge in community ecology (Olff *et al.* 2009).

Herein we provide the first step in addressing this challenge, by taking advantage of the recent developments in our knowledge of bipartite networks (i.e. network consisting of two interacting guilds, such as plant–pollinator or plant–herbivore networks). First, we review the growing evidence that network architecture and related ecological and evolutionary processes depend on interaction type (i.e. antagonistic vs. mutualistic) and the intimacy of interaction (i.e. the degree of biological association between individuals of interacting species; see Appendix S1 for detailed definition and calculation).

Second, we use these results to speculate about the different ways sub-networks (i.e. networks based on a single kind of interaction) can be assembled into a more complete network hereafter named 'interlinked network'. We discuss how merging different kind of interactions within such interlinked networks affects our understanding of the ecological and evolutionary processes. Third, we highlight the research areas that would benefit from considering interlinked networks, and we identify the questions that need answering if the field is to move forwards.

THE ARCHITECTURE OF BIPARTITE NETWORKS VARIES ACCORDING TO THE TYPE AND INTIMACY OF THE INTERACTION CONSIDERED

The determinants of network architecture

An important body of work has looked for the determinants of network architecture. Most of the studies to date have looked for these in species traits such as body size in food webs (Woodward *et al.* 2005; Petchey *et al.* 2008), morphology and phenology in pollination networks (Stang *et al.* 2006; Olesen *et al.* 2008) or integrative proxies for species traits with the use of the evolutionary history of species (Cattin *et al.* 2004; Rezende *et al.* 2007a,b). It is becoming clear though that interaction characteristics (type and intimacy, Fig. 1A) could also affect the architecture of ecological networks. It has been proposed that antagonistic interactions should be more specific than mutualistic ones because the arms race between hosts and antagonists often leads to adaptation at the expense of the ability to attack alternative hosts (Thompson 1982; Nuismer & Thompson 2006), whereas species in mutualistic interactions are often specialised in traits shared by several species within a community resulting in enhanced generalism (Thompson 2005; Fontaine *et al.* 2009). Similarly, strong interaction intimacy has been suggested to promote specialisation because increasing intimacy, through stronger physiological, and/or physical integration between partners, is often viewed as placing more constraints on the number of partners that may be involved in the interaction (Price 1980; Holmes 1983). However, it is only recently that the effects of the type and the intimacy of interactions on network architecture have started to be properly tested using comparative approaches.

Evidence for the link between interaction characteristics and network architecture

The study by Bascompte *et al.* (2003) was first to suggest the architectural singularity of mutualistic sub-networks compared to antagonistic ones. The authors showed that plant–pollinator and plant–seed disperser sub-networks exhibited higher levels of nestedness than trophic sub-networks. Nestedness occurs when specialist species tend to interact with proper subsets of the species that interact with more generalist ones [Fig. 1B (a,c)]. These findings triggered a number of comparisons of nestedness among various network types such as ant-plant mutualisms vs. food webs (Guimarães *et al.* 2006), plant–pollinator vs. plant–herbivore sub-networks (Thébault & Fontaine 2008, 2010; Fontaine *et al.* 2009), plant–pollinator, plant–seed disperser and host–parasite sub-networks (Joppa *et al.* 2010), or plant–plant sub-networks of host–epiphyte communities that range from commensal to parasitic interactions (Blick & Burns 2009). Although some degree of nestedness can be found in trophic
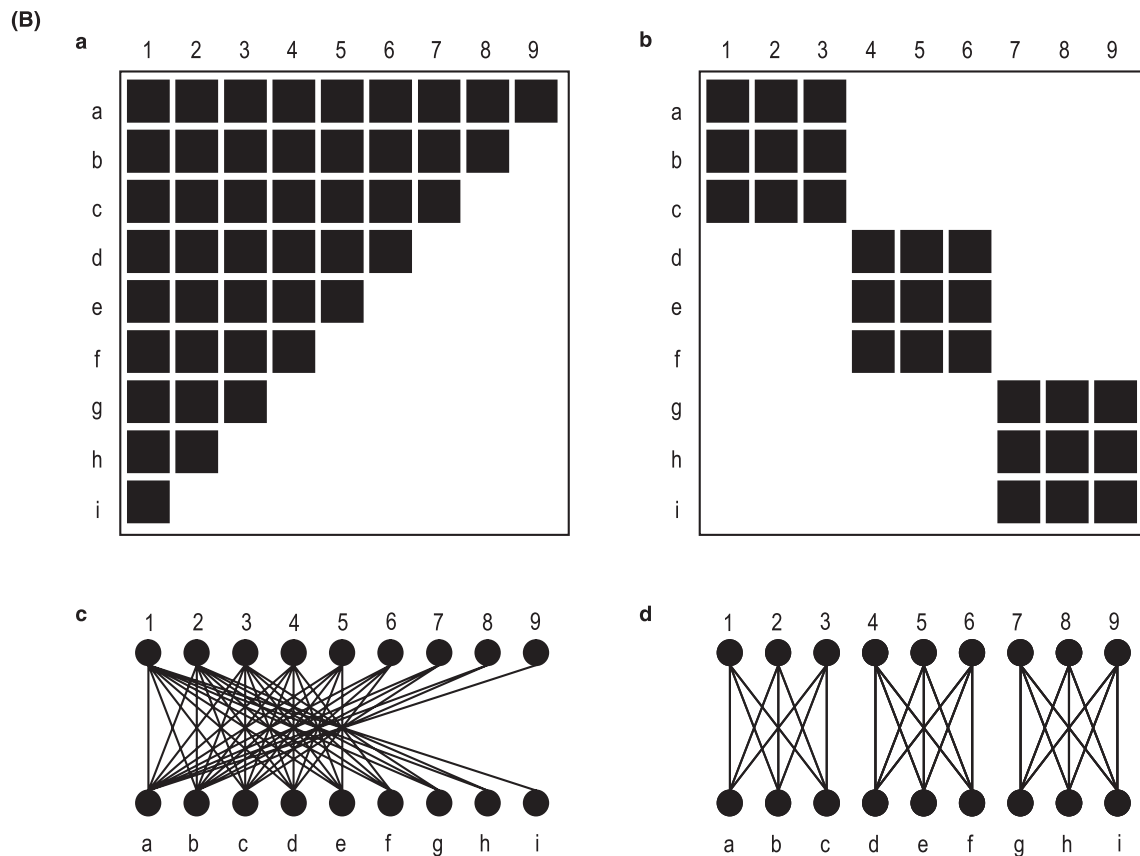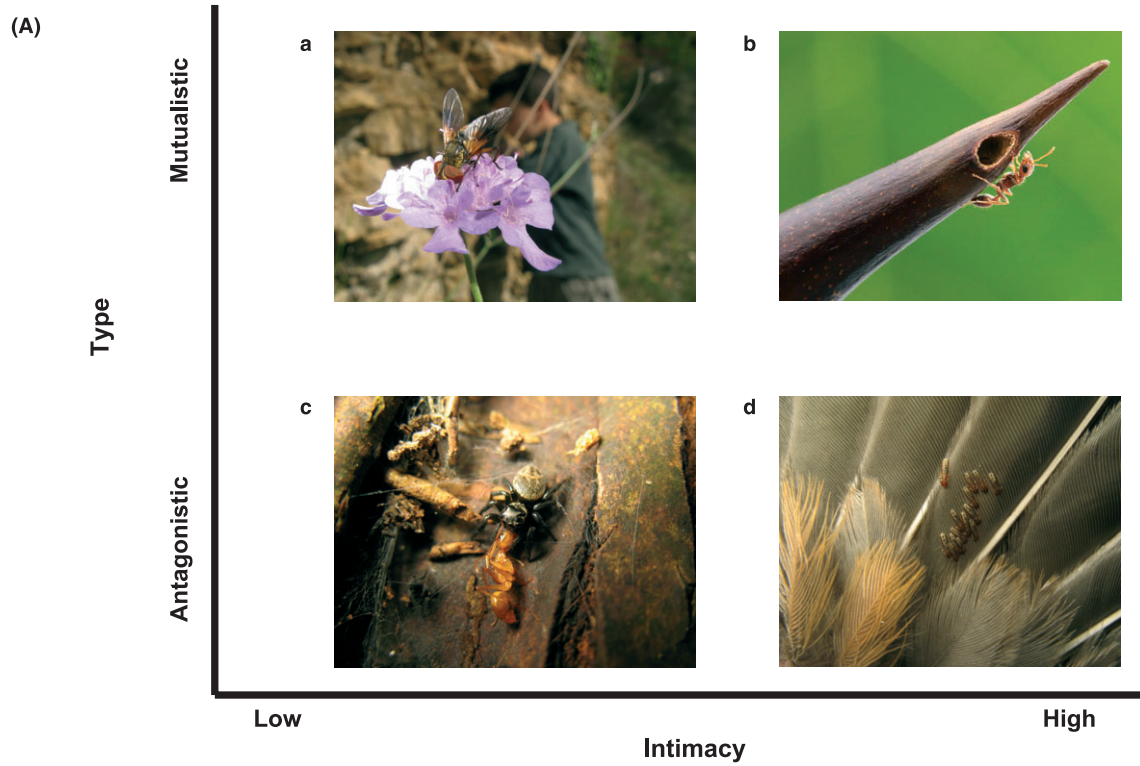
Figure 1 (A) Examples of ecological interactions varying in their type (mutualistic vs. antagonistic) and intimacy (high vs. low) of interactions; (a) plant–pollinator, (b) Acacia–ant, (c), ant–spider, (d) bird–parasite. (B) Schematic representation of nested (a) and (c) and modular (b) and (d) bipartite networks. (a) and (b) Matrix representation, where each row and column represents a species, and the intersections of rows and columns are black when the species interact. (c) and (d) Network representation, where each circle (or node) represents a species, which are connected by edges when the species interact.

networks (Kondoh *et al.* 2010), comparative studies concluded that nested architecture, or its components (i.e. high generalisation/connectance level and asymmetric specialisation), were more prevalent in mutualistic than in antagonistic sub-networks (Graham *et al.* 2009).

In addition to contrasting levels of nestedness, mutualistic and antagonistic sub-networks also appear to differ with regard to their level of modularity. Modularity occurs when groups of species interact more within groups than among groups [Fig. 1B (b,d)]. Mutualistic sub-networks can exhibit significant levels of modularity (Olesen *et al.* 2008), but they have been shown to be less modular than antagonistic sub-networks such as herbivory networks (Thébault & Fontaine 2010). Such differences in nestedness and modularity have also been found within sub-networks. Pollination sub-networks actually describe interactions between plants and floral visitors that are either true pollinators (mutualists) or cheaters (antagonists). By discriminating cheaters from pollinators, Genini *et al.* (2010) have shown that nestedness tends to be associated with pollination interactions, whereas interaction between plants and cheaters tends to be modular.

The effect of interaction intimacy on sub-network architecture has received less attention than the effect of interaction type, but has been tested in both mutualistic and antagonistic communities. Guimarães *et al.* (2007) compared symbiotic (high intimacy) plant–ant mutualistic networks to non-symbiotic (low intimacy) ones, and found that the former were nested whereas the latter were modular. Similarly, for antagonistic interactions, van Veen *et al.* (2008) compared networks linking aphids to different guilds of natural enemies varying in the intimacy of interaction: predators (low intimacy), pathogens (intermediate intimacy) and parasitoids (high intimacy). They found that from low to high intimacy, network architecture changes from highly connected and weakly modular to weakly connected and highly modular. Although empirical evidence remains scarce, these results strongly support the conclusion that high interaction intimacy leads to compartmentalisation in both mutualistic and antagonistic networks.

From these results both interaction type and intimacy appear to affect sub-network architecture. It is noticeable that until now these two interaction characteristics have been studied separately, thus preventing a comparison of their respective effects or a test for a statistical interaction between them. As studies comparing sub-network architecture among interaction types did not quantify the level of interaction intimacy in their datasets, it could act as a confounding factor. To address these points, we tested the effects of intimacy and type in shaping the architecture of 95 sub-networks available online from the Interaction Web Database, compiled from the literature or kindly provided by researchers (see Appendix S1 for a list of the dataset and the method used). We found a significant interaction between interaction type and intimacy for both network nestedness and modularity (Fig. 2). This finding indicates that the effect of interaction intimacy on sub-network architecture depends on the type of interaction considered (mutualistic vs. antagonistic). The role of interaction intimacy in shaping patterns of mutualistic interactions is particularly clear. Intimate mutualisms often show lower levels of nestedness than non-intimate mutualisms (Fig. 2a). In contrast, antagonisms often show intermediate levels of nestedness, regardless of the level of interaction intimacy (Fig. 2a). Levels of modularity, on the other hand, are higher in intimate mutualisms, whereas non-intimate mutualisms often show low modularity (Fig. 2b). Variation in interaction intimacy, as a result of evolutionary dynamics, will be especially relevant in shaping the structure of mutualisms, whereas antagonisms will show patterns of interaction
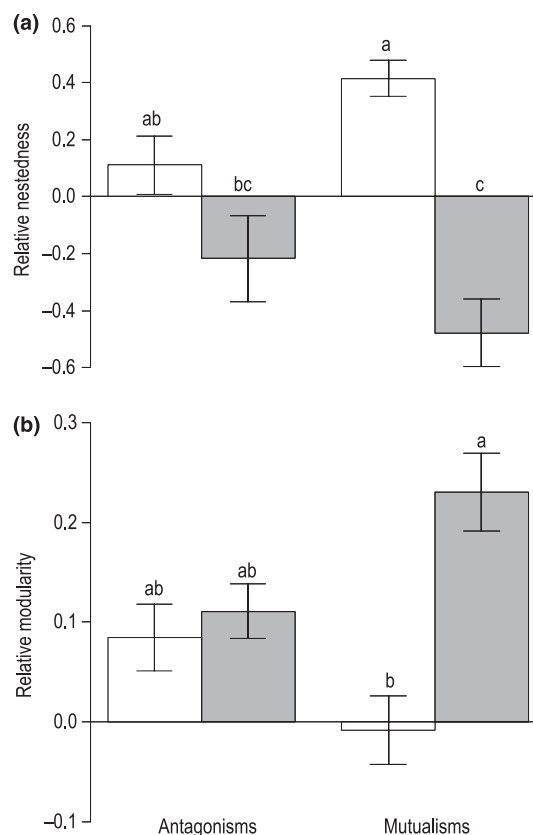
Figure 2 Analysis of the effect of interaction type and intimacy on relative nestedness (a) and modularity (b) of empirical bipartite networks. Columns depict the means and error bars depict standard errors. Grey columns depict sub-networks of intimate interactions, whereas white columns describe non-intimate interactions. Columns not sharing the same lower case letters are significantly different according to *Tukey–Kramer tests*.

similar across different degrees of interaction intimacy. Our analysis suggests a complex interplay between interaction type and intimacy that clearly deserves further attention in future studies.

Ecological and evolutionary processes shaping sub-network architecture

Such differences in the architecture of sub-networks raise questions about the ecological, evolutionary and coevolutionary processes that shape these networks. For the nested structure of mutualistic communities, it has been proposed that architecture could result from random interactions among species with different abundances (Krishna *et al.* 2008) or could be a by-product of the higher extinction rates of reciprocal specialists (Ollerton *et al.* 2003). Another possibility involves the effects of nested and compartmented architectural patterns on community dynamics. Nestedness has been shown to have a positive effect on the stability of mutualistic communities (Okuyama & Holland 2008), on their robustness in the face of perturbations (Memmott *et al.* 2004, 2007) and on their ability to support high levels of biodiversity (Bastolla *et al.* 2009). Nestedness has also been shown to have a destabilising effect on antagonistic communities (Thébault & Fontaine 2010). Conversely, compartmented architecture has been highlighted as stabilising in antagonistic networks (Grime *et al.* 1996) and destabilising in mutualistic networks

(Thébault & Fontaine 2010). Such constraints on community stability could therefore be an important driving force shaping the different architectures of interaction networks, with the more stable architecture emerging from the ecological dynamics.

It is important to acknowledge that the argument outlined in the previous paragraph refers to a selection criterion (stability) at the scale of the web as a whole. The relevance of community scale selection has been hotly debated (Dawkins 1994) and a more traditional approach is to base the evolutionary dynamics on differences in individual fitnesses. Individual-based selection has been studied mainly in a multitrophic food web context. Theoretical models based on the evolution of a single or limited number of traits, such as body size (Loeuille & Loreau 2005, 2009), optimal foraging (Petchey *et al.* 2008) or more loosely defined traits such as vulnerability (Ito & Ikegami 2006; Rossberg *et al.* 2006), can generate realistic food web architectures (Loeuille & Loreau 2005; Rossberg *et al.* 2006; Petchey *et al.* 2008). Particularly, results from Loeuille & Loreau (2005) suggest that modularity may emerge from such coevolutionary dynamics depending on the feeding range of the species involved. Coevolutionary models cited above also usually produce stable networks (Loeuille & Loreau 2009; Loeuille 2010). Most of these models use intraspecific differences in phenotypes (usually through mutation process) to get variation of the mean phenotype at the species level (Dieckmann & Law 1996) out of the selection process. Development of similar (co)evolutionary models for mutalistic, competitive and facilitation networks is an important step but no trait has yet been identified as a universal constraint for these other types of networks. This is in contrast to food webs where traits such as body size are known to be important constraints for trophic interactions (Woodward *et al.* 2005).

The role of evolutionary processes in shaping ecological networks has been further highlighted by studies linking network architecture to the evolutionary history of species. Cattin *et al.* (2004) first demonstrated that introducing phylogenetic constraints in a food web model can explain some empirical food web patterns. The reasoning behind introducing such constraints is phylogenetic niche conservatism, i.e. closely related species are more likely to show trophic similarity than unrelated species. In a detailed study of a quantitative leafminer–parasitoid network with species level resolution and phylogenies, Ives & Godfray (2006) found that related hosts tend to share natural enemies but the authors failed to find a significant phylogenetic signal in the parasitoid diet. Such asymmetry in the strength of phylogenetic signal with a stronger signal at the resource than at the consumer level has been highlighted in other types of antagonistic networks (Bersier & Kehrli 2008; Vacher *et al.* 2008). Conversely, Rezende *et al.* (2007b) analysed a large database of plant–animal mutualistic networks and found a phylogenetic signal at both the plant and animal levels with a tendency for a stronger signal at the animal level. Although a proper comparison would be needed, these results hint that the phylogenetic imprint varies between different types of interaction networks (see Jordano 2010 for further discussion).

Finally, evolutionary processes might change the underlying ecological correlates of network architecture, such as interaction type and interaction intimacy. The outcome of ecological interactions is often variable across time and space (Thompson 2005) creating opportunity for evolution to change interaction type. For example, cheating lifestyles might evolve from legitimate mutualistic partners, whereas mutualistic interactions might evolve from antagonistic interactions, e.g. pollination by flower parasites (Thompson 2005) and seed dispersal by scatter-hoarding granivores (Vander Wall 1990). Interaction intimacy is also a product of evolutionary dynamics and selection might increase or reduce the degree of interaction intimacy depending of the ecological scenario (Thompson 1994). Because the effects of interaction intimacy on network structure vary across interaction types (Fig. 2), evolutionary dynamics might shift patterns of interaction in the sub-network by shifting interaction type and intimacy. Moreover, the effects of structural changes might offer feedback in unknown ways leading to an eco-evolutionary dynamics that need further analysis.

In summary, both ecological and evolutionary processes are important in shaping interaction networks, and it seems unlikely that sub-network architecture is the result of a single process but the combination of several ecological, evolutionary and coevolutionary processes (Vázquez *et al.* 2009; Bascompte 2010).

MERGING NETWORKS BASED ON VARIOUS INTERACTION TYPES AND INTIMACY LEVELS

Why do we need to study various interactions and sub-networks simultaneously?

As argued in the previous section, the quest for the ecological and evolutionary processes shaping interactions within communities has so far been restricted to sub-networks. Although studying a sub-network in isolation from others brings valuable information on various aspects of biological communities, such as for example the links between species traits, phylogeny and network architecture, a full understanding of the ecological and evolutionary dynamic of biological communities would gain much from considering interlinked sub-networks simultaneously. Herein, we develop the hypothesis that sub-networks are not independent. Species are often involved in different sub-networks either simultaneously or at different life stages (e.g. Gilbert 1980). This increases the number of indirect pathways from one species to another, with different types of interactions producing different types of direct and indirect feedbacks (negative for antagonist interactions and positive for mutualistic interactions). The ecological dynamics of a given sub-network should thus not only depend on its own architecture, but also on the architecture of the other sub-networks it is connected to, as well as on the way they are interlinked. For example, mutualistic interactions between ants and aphids can affect the associated aphid–parasitoid network with ants causing a shift from generalist to specialist dominated secondary parasitoid communities (Sanders & van Veen 2010). Moreover, species traits that are important for one interaction are often directly or indirectly affected by another interaction. For example, herbivory can decrease pollen production and lower the attractiveness to pollinators (Strauss 1997) and while the induction of secondary chemicals in plants by herbivores decreases herbivory, it also decreases visitation by pollinators (Strauss 1997). Therefore, the evolutionary dynamics of such traits could be under the influence of the selection processes arising from a variety of ecological interactions. Thus, to understand the ecological and evolutionary processes shaping ecological communities, ecologists should ideally study interconnected interactions and sub-networks rather than restrict their analysis to a single interaction type or sub-network.

Developing approaches to evaluate how the various sub-networks combine into a single interlinked network is highly relevant for applied ecology. Recently restoration ecology has begun to shift in emphasis from restoring species to restoring the interactions between species,

and thereby ecosystem functions and services (Henson *et al.* 2009; Heleno *et al.* 2010). However, ecosystem services are currently treated as separate entities by ecologists. For example pest control ecologists work on pests and their networks of natural enemies, and pollination ecologists work on crop pollination. However, many parasitoids visit flowers for nectar, these nectar supplies being essential for egg laying (Heimpel & Jervis 2005). Viewing the sub-networks that form particular ecosystem services in isolation is a convenient simplification. In reality agro-ecosystems are very unlikely to consist of a series of neat separate networks and a greater understanding of the linkages between the networks may improve our management and use of them. In agro-environmental schemes, management options that consider optimising a number of ecosystem services rather than on maximising a few of them is obviously attractive, an ecological 'two or three for the price of one'. For example a field margin could provide flowers for pollinators as well as seeds for endangered farmland birds. Currently though pollen and nectar margins and bird seed margins are different options (Natural England 2008) designed by different groups of ecologists (entomologists vs. ornithologists) with relatively little knowledge or appreciation for each other's agendas. Management options that consider the whole network could provide forage for both groups in the same margins, effectively increasing the area available for each.

Characterisation and ecological insights of interlinked sub-networks

In this section, we focus on how to describe interlinked bipartite sub-networks and on the potential ecological implications of merging networks in terms of perturbation spread. We define perturbation as any change in the biological attributes of one or more species, such as species abundance, that may cascade through the network. For the sake of simplicity, we will restrict ourselves to binary sub-networks, which do not include information on interaction strength. To study two interlinked bipartite sub-networks we need to focus on the species that link the different sub-networks. Indeed, because they are involved in the two sub-networks, these species should be the ones channelling the effects from one sub-network to the other. In the example illustrated in Fig. 3, plants are central because they are interacting directly with both pollinators and herbivores. The involvement of the linking species in each of the two sub-networks will provide some insights into the strength of the potential effects of one sub-network on the other. In Fig. 3, these effects might be strong because plants are highly connected to both networks with 75% of plants from the pollination network taking part in the herbivory network and 100% from plants of the herbivory network taking part in the pollination network.

We can extend this approach further focusing on six schematic examples of interlinked networks composed of mutualistic and nested sub-networks, and antagonistic and compartmented sub-networks (Fig. 4). In case of two nested mutualistic sub-networks such as plant–pollinator and plant–seed disperser networks, the linking species, here the plants, can have a similar, an opposite or an unrelated generalism degree in the two sub-networks (Fig. 4a,b). The correlation between the generalism degrees of the linking species in the two sub-networks can then provide a first easy metric to describe the merging of two nested networks. If the correlation is positive (Fig. 4a), species from the two ecosystem services guilds (pollinators and seed dispersers) are linked together by the same generalist species from the linking guild. This implies that any two species from this interlinked network are
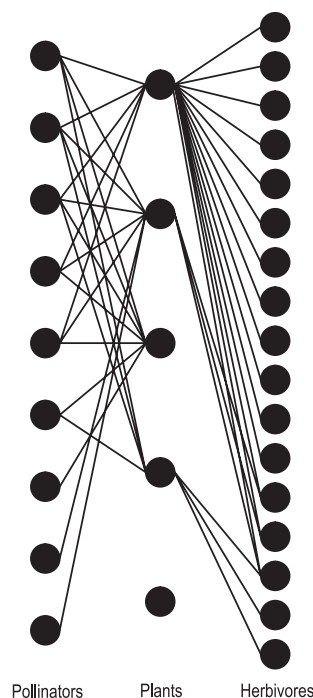

Figure 3 Interlinked network of the heathand community linking plant–pollinator and plant–herbivores sub-networks. Each circle represents a species, which are linked by edges when the species interact. This dataset has been assembled from two separate studies performed at the same field site (from Henson *et al.* 2009 and J. Memmott, unpublished).

linked either directly or indirectly through only one other species. Such proximity among species suggests that perturbations should easily cascade through the complete web. Moreover, in this configuration, the same generalist plant species is sustaining both ecosystem services guilds and should be a priority for a conservation programme. On the other hand, if the correlation in generalism degree of the linking species is negative (Fig. 4b), any two species from this interlinked network are linked either directly or indirectly through one or two other species. Perturbations should thus be less likely to spread from one ecosystem service sub-network to the other. Moreover, the identity of the linking species, and thereby the conservation priorities, differs between the two sub-networks. Conserving both ecosystem services will involve protecting more species than in the previous example and considering only one of sub-networks while ignoring the other could lead to wrong conclusions in terms of the conservation of the whole network.

In case of two antagonistic compartmented networks, such as a plant–above-ground herbivores network and a plant–root parasite network, the linking species, here the plants, can be part of similar (Fig. 4c) or different (Fig. 4d) compartments in the two sub-webs. Overlap in compartments composition between the two networks can thus quantify the extent to which both sub-networks share similar compartment composition. If the compositions of the compartments are similar (Fig. 4c), perturbations should be contained within these compartments. However, if they differ (Fig. 4d), perturbations could spread throughout the whole interlinked network as compartments of one sub-network are linked together by the compartments of the other sub-network.

Finally, in the case of a mutualistic nested network merged to an antagonistic compartmented network, the most generalist species from
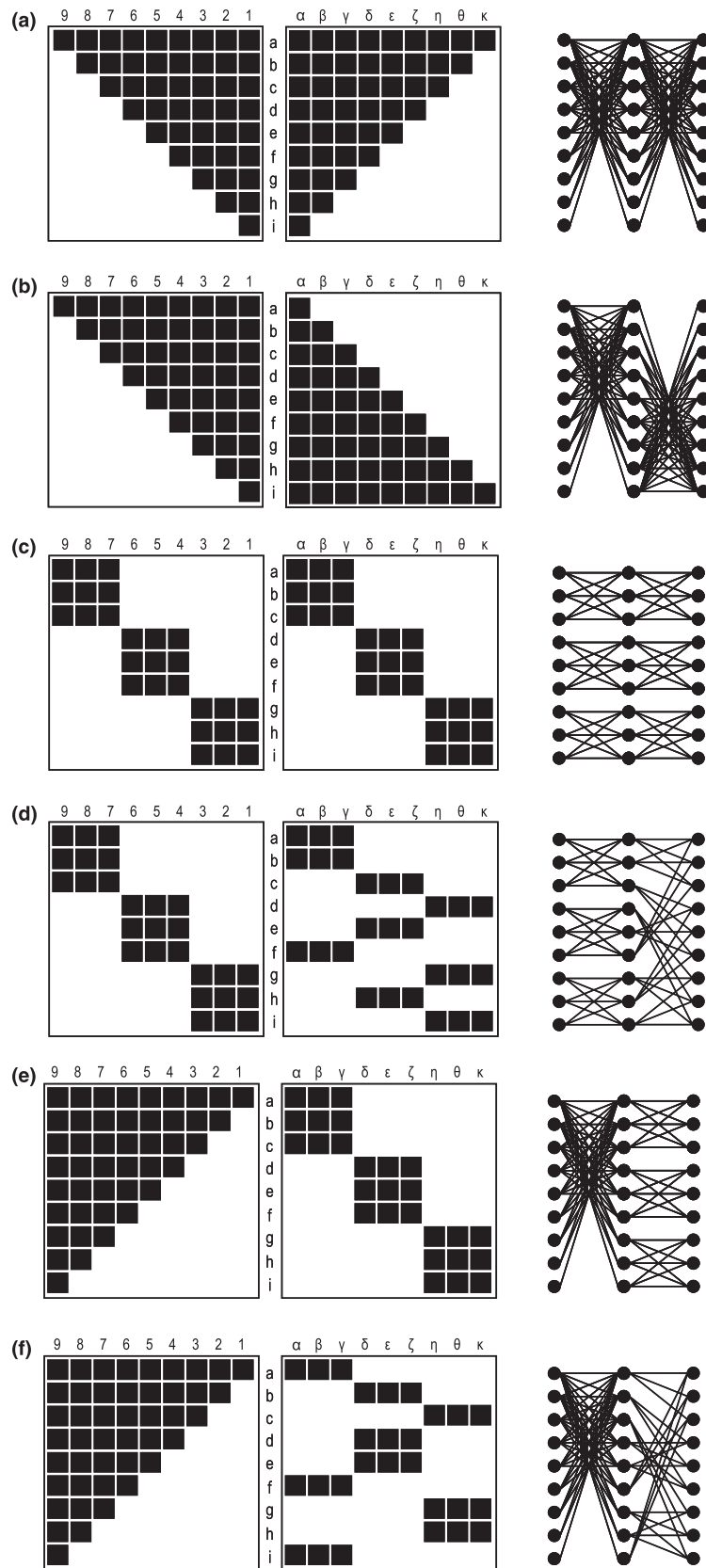
Figure 4 Matrix (left) and network (right) representation of various scenarios of interlinked networks based on: (a) and (b) two-nested sub-networks; (c) and (d) two-compartmented sub-networks; (e) and (f) one-nested and one-compartmented sub-networks.

the nested network can be part of the same (Fig. 4e) or of different compartments (Fig. 4f). The fact that one of the sub-networks is nested links the different compartments of the other sub-networks. These last configurations (Fig. 4d–f) challenge the assumption that compartments contain the spread of perturbations: taking other types of interactions into account, compartments might actually be connected with each other through other sub-networks, leading to cascading effects of perturbations throughout the complete network.

Of course, the outcome of a perturbation will not only depend on the structure of the sub-networks and on the way these sub-networks are linked but also on the type of interaction. As a first approximation, we can speculate that when two mutualistic networks are linked to each other, a perturbation might be amplified during its propagation through the network because of the presence of positive feedbacks. On the contrary, when the two antagonistic networks are linked to each other, the perturbation could be dampened by negative feedbacks as it propagates through the web. Interestingly, when a mutualistic network is associated with an antagonistic one, the antagonistic network may act as a stabilising entity dampening the perturbation, while this same perturbation would have been amplified when only the mutualistic sub-network would have been considered.

The structure of interlinked networks might also affect other stability measures such as diversity persistence. Current results found in single sub-networks (Bastolla *et al.* 2009; Thébault & Fontaine 2010) can easily be transferred to interlinked networks when a single interaction type is considered. Interlinked networks made of two mutualistic sub-networks can be expected to sustain higher number of coexisting species when both sub-networks are nested and when the generalism degree of the linking species are positively correlated, making that their overall structure nested (Fig. 4a). Similarly when two antagonistic sub-networks are interlinked, a globally compartmented structure should promote diversity (Fig. 4c). However, when a mutualistic sub-network is interlinked with an antagonistic one, the current theoretical results are insufficient to predict diversity persistence.

Obviously this is simply speculative at this stage and requires further analysis, especially since complex, unexpected dynamics might emerge in interlinked networks (Buldyrev *et al.* 2010). This very simple framework needs to be further refined, for example by taking weighted interactions into account, or extending it to more than two sub-networks. Other metrics and associated null models (e.g. Melián *et al.* 2009) may also be needed to better characterise how sub-networks are interlinked and which processes can explain the observed patterns.

Evolutionary insights of merged networks

To study the evolutionary processes taking place within interlinked networks, we believe that focusing on key phenotypic traits, which act as important constraints for the different interactions types, may be an interesting starting point. In this section, we first identify such traits, and then speculate on the implications of interlinked networks for the evolutionary dynamics of these traits. Assuming intraspecific variability in these phenotypic traits and assuming that they are heritable, it is possible to speculate on how merging networks will affect their dynamics, by discussing how it alters the selective pressures acting on them.

Interactions between organisms, allies or enemies, depend crucially on the ability of the two organisms to detect each other. We propose that traits used for signals and detection may provide the ecological glue that merges several networks together. An intuitive example is

flower's corolla. Increasing the size of the corolla will make the flower more detectable not only to pollinators, but also to herbivores (Strauss *et al.* 2002). A similar argument can be made with plant volatile compounds, whose perfume may be an efficient defence as well as a cue for pollinators (Courtois *et al.* 2009). These types of interaction while observed infrequently (we would argue because they are not often looked for) should not be seen as exceptions. Moreover, virtually any trait (body size, colour, birdsong, scent) affecting detection of the individual by other organisms can modify simultaneously negative and positive interactions, thereby bridging the different networks.

In addition to the traits used by one organism to detect another, the phenotypic traits that affect the transmission of energy through networks will influence whether or not networks merge. Evolution of plant defences again provides a useful example. Some of these defences involve the production of digestibility reducing compounds, some others, toxicity (Müller-Schärer *et al.* 2004). In both cases, the trait affects the transmission of energy up the food web by reducing the total consumption of plants by above-ground herbivores. They also inhibit the activity of decomposers so that energy available for the below-ground food web is reduced (e.g. Grimm 1996). Such plant defence-related traits should affect the merging of above-ground and below-ground food webs by reducing resource availability and/or vulnerability in both habitats simultaneously. Again, the argument is not restricted to defences and extends to any trait that redistributes the energy among webs, for example, shoot-root ratio, nectar quantity or stoichiometric ratios.

If phenotypic traits are simultaneously involved in different networks, their evolution depends on selective pressures coming from both the merged webs. It is intriguing to consider the implications of this idea. Going back to the evolution of plant volatile compounds, the diversity of these compounds is very high, with hundreds of molecules identified (Courtois *et al.* 2009). Such a diversity is also reported in the defence strategies of plants (Strauss *et al.* 2002). The maintenance of such a high diversity of strategies is counter-intuitive as the defence strategy that has the highest benefit for the least cost should be selected and exclude the other strategies (Müller-Schärer *et al.* 2004). Maintaining this diversity implies very strong disruptive selection. It is possible that this disruptive selection arises from the presence of several webs, with a benefit in one web (e.g. attracting more pollinators) being counteracted by costs in another web (e.g. attracting more predators). Frequency dependence may arise because a given rare phenotype may be favoured by one of the two interaction type network, and the alternative phenotype favoured by the other network when rare. Analyses that focus on only one type of interaction would therefore likely miss this kind of frequency dependence. At this stage, this should only be considered as an intriguing possibility for the emergence and maintenance of diverse phenotypes. The selection regime depends on many details related to genetic background of the phenotypic traits and trade-offs that are associated to them and much theoretical work is needed to understand the implication of merging networks (see part 3). Pairwise coevolutionary models in which the interaction is a mutualism on one site and an antagonism on the other, have demonstrated the potential of merging interactions in maintaining trait variation (e.g. Nuismer *et al.* 1999).

Because of conflicting pressures on a given trait from different webs, the consequences for evolutionary dynamics are hard to predict. The first section of this article demonstrated that mutualistic and trophic networks differ in their nestedness and compartmentation.

Both these characteristics emerge, at least partially, from the evolution of specialisation. Evolution of specialisation has been most studied in models using only one interaction type (e.g. predation and mutualism, respectively: Egas *et al.* 2004; Ferrière *et al.* 2007). Results are diverse, but to illustrate the argument, let us focus on direct feedbacks associated to each interaction. In trophic interactions, specialised predators might deplete their prey, decreasing their frequency, thereby creating selective pressures for less specialisation. In mutualistic interactions, a specialised mutualist might increase the frequency of its partner, thereby creating selective pressures that may favour further specialisation. Now consider the two interlinked networks: once the mutualist increases the frequency of its partner, this increased frequency may well attract predators from the other web, so that the outcome of evolution depends on the relative weight of the two networks, in terms of total density and/or interaction strength. This means that the complete understanding of evolution of specialisation, as well as its structural consequences (nestedness and compartmentation) may require both types of interaction to be considered simultaneously.

THE CHALLENGES AHEAD

In the preceding sections, we highlighted how the interlinked nature of the different sub-networks that constitute communities can affect ecological and evolutionary processes. In what follows, we identify some important challenges that need to be addressed to move the field forward.

Getting the data

First, ecologists have very little data on the links between sub-networks. Very few studies have investigated how mutualistic and antagonistic sub-networks combine into interlinked networks, and to date, examples are restricted to aboveground communities (Henson *et al.* 2009; Melián *et al.* 2009). More data and analysis are clearly needed to look for the general patterns if they exist. Datasets on interlinked networks coupling different habitats could be particularly interesting. Studies such as those of Knight *et al.* (2005) showing the relationship between fish predators in ponds and the pollinators of waterside plants, or Poveda *et al.* (2003) demonstrating the effects of below- and above-ground herbivores on plant pollination remain very rare. This is unfortunate as they are probably not uncommon; rather they are rarely studied because few ecologists have the ability to work on such divergent systems.

One way forwards in making ecosystem webs is to locate a site with a history of use by a part of the scientific community which can provide an initial start up quantity of data (see Fig. 2). For example in the UK Sourhope experiment sampled soil bacteria under a variety of experimental regimes over 13 years. It would be relatively straightforward to augment these data with other members of the soil fauna along with plant–pollinator, seed dispersal and plant–herbivore–parasitoid networks. Similarly, the French 'zones atteliers' or the Jena experiment in Germany could offer opportunities to unravel the relative impact of the various sub-networks on the causes of the patterns commonly observed in the natural world. Pollinators, mychorrhizae and herbivores have all been attributed with being important in patterns in plant community ecology. Are they equally important, important at different stages, do they interact and how can they all be restored in restoration programmes?

It is important to notice that some real challenges remain to construct interlinked networks. One is to accurately estimate the costs and/or benefits of each interaction. For example flower–visitor networks often implicitly assume mutualistic interactions among species; however, we know that pollinator efficiency greatly varies among species and can involve cheating (e.g. Genini *et al.* 2010). For the interlinked network to be an effective framework, in addition to good estimates of interaction costs and benefits, one needs to get the different sub-networks expressed in common units which is not a trivial task.

Second, there is not usually equitable data on the various networks that make up communities and ecosystems. The 'easy' networks such as pollination or aboveground herbivory are well documented, but other networks such as those from the soil are far less understood. Although research on soil systems is considering various interactions, both mutualistic (between plant and mycorrhizal fungi, or symbiotic nitrogen fixing microbes) and antagonistic (predation or root feeding) with various degrees of interaction intimacy (van der Heijden *et al.* 2008), network approaches have focused on food webs where trophically equivalent species are lumped together into feeding guilds (e.g. de Ruiter *et al.* 1995). This difference in comparison to aboveground systems can be explained by the difficulty in identifying both soil species and their feeding preferences, difficulties which can only be solved using complex molecular or isotope-based techniques (Ruess *et al.* 2002). Traditionally, interactions among soil organisms, as well as between soil biota and plants, have been considered as relatively unspecialised. However, studies over the past decade have shown that these interactions are more specific than previously assumed (Bardgett & Wardle 2010). For example, a detailed analysis pointed out that the composition of the soil food web underneath a plant depends on the plant identity as well as on the composition of the surrounding plant community (Bezemer *et al.* 2010). How the level of specificity depends on interaction characteristics and what are the architectures of the corresponding interaction networks is unknown for below-ground systems. A recent study reported nested patterns in a plant-mycorrhiza network (Jacquemyn *et al.* 2010), a result which is in keeping with the mutualistic networks found aboveground. Another recent study related orchid speciation to shift in pollinators but found no evidence for change in the mycorrhizal associations (Waterman *et al.* 2011). Transferring the highly resolved approach used to study of aboveground networks to soil communities is clearly a very promising research avenue, which should give new insights on the organisation and functioning of belowground communities. Moreover, it would ease their fusion with aboveground communities leading to a single integrative framework.

Looking at ecological processes through the lens of interlinked networks

In addition to the data which characterises the links between different sub-networks, theoretical developments coupled with experiments that manipulate the sub-networks are also needed. These would enable ecologists to elucidate the processes underlying the observed patterns. Our understanding of species coexistence or perturbation spread mainly comes from work considering one interaction at a time, most frequently predation and/or competition (De Angelis 1975; McCann *et al.* 1998; Kondoh 2003). Integrating the different interaction types in experimental and theoretical approaches is likely to change our current understanding of these processes. For example, species coexistence is usually predicted using competition models (inter-

mediate disturbance hypothesis; R^* rule; storage effect; competition-colonisation trade-off) and classical theory predicts that the species that is the most efficient at getting the resource will eventually outcompete all the others. By including facilitation between species as well as competition, the number of species capable of surviving on a single resource is increased (Gross 2008; Díaz-Sierra et al. 2010), a theoretical result in agreement with field observations (Hacker & Gaines 1997; Verdú & Valiente-Banuet 2008). Similarly, the propagation of disturbances within an ecosystem is usually studied using trophic models (resilience constraints; trophic cascade). However, trophic interactions alone provide a restricted view of how disturbances may propagate within complex networks of interactions. Mutualistic or facilitative interactions, by adding positive feedback loops, may change the pathway of this propagation and thus the consequences of perturbations at the system's scale. Whether extra interactions types will enhance or buffer perturbations will depend on their sign, abundance, intensity, location within the network, and the architecture of the network itself. More generally, the inclusion of positive interactions in ecological theory may change our understanding of other general ecological patterns, such as the species range distributions and the diversity-productivity relationship (Bruno 2003; Michalet et al. 2006).

Our understanding of the dynamics of such interlinked ecological networks could also benefit from theoretical advances in research fields outside ecology. The importance of linking networks has been highlighted recently in internet communication webs and metabolic networks through the development of new concepts such as 'network of networks' or 'interdependent networks' (Ideker et al. 2001; Buldyrev et al. 2010). The interlinked networks defined here have the particularity of linking sub-networks based on different kind of interactions. Multidisciplinary crossing among these different fields and concepts should provide exciting insights.

Looking at evolutionary processes through the lens of interlinked networks

Our perception of evolutionary dynamics will also be affected by considering positive and negative interactions jointly. Most theoretical models currently use pairwise coevolution (e.g. Nuismer et al. 1999). Even diffuse coevolution models mostly focus on one interaction type (competition: e.g. Rummel & Roughgarden 1983; predation: e.g. Kondoh 2003). However, fitness benefits in relation to a given interaction may involve a cost to another interaction (ecological cost: Strauss et al. 2002). Coupling the different interaction types is required to define the fitness associated to the phenotypic trait as one interaction sub-network cannot provide sufficient information. The ensuing evolutionary dynamics of the trait will depend on the frequencies of the species of the various interlinked webs, with unknown consequences for the ecosystem functioning and for the resilience of the system as a whole. Both these ecological and evolutionary challenges need the description of interactions among interlinked networks, as well as the careful identification of traits that are key for the different interactions. The section 'Evolutionary insights of merged networks' lists different traits that could be considered as links between antagonistic and mutualistic networks, but it is unlikely that only one trait will be involved in isolation of others. It is therefore necessary to develop diffuse coevolution models that will be able to account for several important traits, simultaneously affected by the merging of the two networks.

It is also necessary to go beyond the phenotypic-based selection arguments described in 'Evolutionary insights of merged networks', to include a better understanding of genetic aspects of the eco-evolutionary dynamics of traits involved in merged networks (Wade 2007). Evolution of such traits may be affected by reaction norms ($G \times E$ components), epistasis ($G \times G$ components). Higher order interaction terms may even matter ($G \times G \times E$, cf Thompson 2005). In the section 'Evolutionary insights of merged networks', we propose a first set of phenotypic traits likely selected simultaneously in antagonistic networks and mutualistic networks, and whose evolution affects the structure of such networks. It is necessary to confirm the identification of these key phenotypic traits through empirical observation or experimental works to then assess genetic components associated to them. Although some important challenges clearly remain, understanding the genetic aspects of interlinked networks may be possible in the near future: works on community genetics (Whitham et al. 2003), though not focused on merged network structures, show that carefully identified genes may indeed be linked to community characteristics through $G \times E$ components. We suggest similar work should be undertaken for phenotypic traits that are involved in the merging of different networks.

Finally, if understanding of genetic and phenotypic intraspecific variation is needed to understand fully the evolutionary dynamics, other aspects of intraspecific variations are also important (Bolnick et al. 2011). For instance, consider a species whose role (mutualistic or antagonistic) is dependent on the life stage (e.g. caterpillar–butterfly), then the life-stage structure of the population will directly couple the two networks and the strength of the coupling will be directly dependent on the transition between these life-stages.

CONCLUDING REMARKS

Our understanding of the patterns and processes taking place in biological communities has been greatly improved by the use of network approaches. Merging the various ecological interactions into a single framework is the next challenge in network ecology, offering considerable opportunity for unravelling the ecological and evolutionary processes that shape biological communities. Progress towards this goal, by gathering quality data and developing experimental and theoretical approaches, is essential if we are to understand, conserve and sustainably exploit the natural world.

AUTHORSHIP

CF and ET initiated the project; CF led the writing, PRG did the analysis; all authors contributed to the writing.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Analysis of the effect of interaction type and intimacy on the architecture of interaction networks.

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