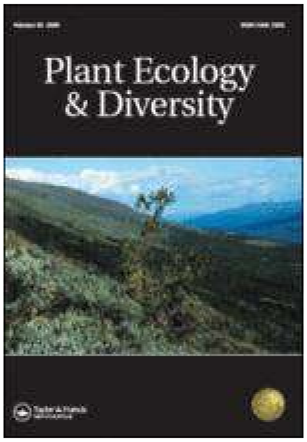

Plant networks and the organisation of biodiversity

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Plant networks and the organisation of biodiversity

Abstract

Plant ecology focuses on how plants interact with each other and with their environment. ~~Plant~~Therefore, plant diversity is more than a list of species, and the multitude and complexity of plant interactions challenges our understanding of plant communities. Recent advances in network theory support the study of biotic interactions among many species within plant communities, unveiling hidden organisation of plant diversity. Here, we review ~~the~~ results and methods to ~~analyse and~~ model plant–plant interaction networks, focusing mainly on natural ecosystems. We highlight how plant networks can help us to: a) assess the balance between facilitation and competition that may result in a wide range of potential outcomes; b) ~~model~~analyse the role of ~~multi-species~~ plant–plant interactions beyond pairwise competition in structuring plant communities, and c) forecast the ecological implications of plant~~–plant interactions~~ interaction networks for biodiversity maintenance across organisational levels. We also discuss the methodological pros and cons of different approaches used for inferring plant interactions, and the limitations and assumptions of network models. Finally, we pave the road for advancing plant ecology by using ecological networks that encompass different levels and spatio-temporal scales, and incorporate more biological information for better understanding the role of plant networks in the organisation and maintenance of biodiversity.

Keywords: biodiversity, commensalism, competition, ecological networks, ecosystem, facilitation, interaction chains, parasitism, plant community, spatial pattern, species interactions

Introduction

'*No plant is an island*' (Nature Plants 2016).

When we look at nature we can appreciate the impressive diversity of life. The biosphere is estimated to host about 450,000 plant species (Pimm and Joppa 2015), which compose highly diverse communities. However, how many different species can ~~occur~~coexist in a given community remains largely unknown. Traditionally, it has been proposed that environmental heterogeneity, competitive ability and niche differences between species ~~pairs~~ are the main ~~drivers maintaining diversity~~ sources of biodiversity in ecological communities (Grubb 1977, Chesson 2000, ~~Adler~~HilleRisLambers et al. ~~2007). However~~2012). In particular, a fundamental mechanism underlying plant diversity is niche differentiation, as highlighted by Grubb (1977). This includes diversification of abiotic requirements, life forms and functional traits, phenology and regeneration through space and time. Each of this process also contributes to and results from differences in species interactions in ecological and evolutionary time scales, respectively. Yet, plant communities harbour a huge variety of complex interactions that we have only recently started to unveil (Callaway 2007, Klein et al. 2016, Mescher and Pearse 2016, Levine et al. 2017~~) and that are~~). Such a complexity is challenging our understanding of plant diversity and the organisation of plant communities. A better understanding of the networks of plant–plant interactions is therefore key to improving our knowledge of plant diversity.

But, *why we should care about plant networks*? Plant diversity is more than a list of species, a collection of herbarium specimens, a summary index, a phylogenetic tree or a multidimensional trait space. Rather, biotic interactions are foundational to plant diversity (Grace and Tilman 1990, Callaway 2007, Levine et al. 2017). That is, the type, intensity, and diversity of interactions and their network structure are all together mechanisms underlying plant diversity and communities. Plant networks can therefore encapsulate emergent properties of plant communities and provide further information that only species richness or phylogenetic similarity cannot. In this sense, plant networks extend knowledge of systematics and functional botany to explain patterns of plant diversity and improve our understanding of processes shaping plant communities (Verdú and Valiente-Banuet 2008, Kefi et al. 2012). This improved knowledge can have important implications to advance our forecasting ability and can benefit practices for conserving single populations and entire communities simultaneously.

We identified three main challenges to be tackled for a better understanding of how networks of plant–plant interactions can influence biodiversity. First, ~~besides~~moving beyond competition and including other widespread interactions between plants ~~such as~~that are crucial for the structure and dynamic of ecological communities. These include facilitation, commensalism, and parasitism ~~are crucial for the structure and dynamics of communities~~ (Callaway 2007, Burns and Zotz 2010). For example, facilitation and competition can potentially balance each other, resulting in a broad range of possible context-dependent outcomes (Callaway and Walker 1997, Levine 1999, Choler et al. 2001, Schöb et al. 2014a,b). Second, ~~although~~moving beyond pairwise interactions and including direct and indirect effects among multiple species. Although research in plant and theoretical ecology has mainly focused on ~~pairwise~~ interactions between pairs of species (Chesson 2000), species do rarely interact in isolation from the rest of species in ~~the~~their community (Bascompte and Jordano 2014, Levine et al. 2017). Pairwise interactions can be affected by other species interactions (Mayfield and Stouffer 2017), as interactions between two species can change depending on the presence of other community members and the interactions among them (Losapio et al. ~~2017~~2019). Third, plant interactions can have implications for ecological processes acting at different levels of organisation, as well temporal~~,~~ and spatial scales~~, including~~. These include effects on plant eco-physiology (Schöb et al. 2014a), demography (Verdú and Valiente-Banuet 2008), structure and diversity of communities (Butterfield et al. 2013; Kikvidze et al. 2015), species biogeography (Cavieres et al. 2014), and even evolutionary diversity at the global scale (Valiente-Banuet et al. 2006). Thus, a proper characterization of interactions in each case will inform us about the ~~implication~~implications of plant interactions in different ecological processes.

The development of new analytical methods has provided valuable tools to approach these mayor challenges. Since the end of the 1990s, ecology has benefited from the ~~application~~development of network theory (Bersier 2007; Fortuna and Bascompte 2008). Originally, network analysis was first applied to predation and second to mutualistic interactions (McCann 2011; Bascompte & Jordano 2014~~), helping to~~). The study of food webs and mutualistic networks substantially helped us to understand ~~their~~the contribution of trophic interactions to ecological and evolutionary processes ~~and~~such as the maintenance of ~~diversity. Nevertheless, despite~~biodiversity. Despite the historical interest for biotic interactions in plant ecology, particularly for competition, plant networks have been largely overlooked in this field (Levine et al. 2017). Only with the development of network analysis based on both graph theory and statistical mechanics (Jordán and Scheuring 2004) along with advances in user-friendly, open source software (e.g. Csardi and Nepusz 2007, Dorman et al. ~~2017), although they~~ 2008), plant ecologists approached to “modern” network theory. Indeed, plant networks are now receiving increasing attention~~.~~

~~A combination of the accumulated knowledge on network theory and plant ecology can help tackling the three challenges mentioned above. Network theory can improve the theoretical models developed to explain plant community structure and dynamics combining different interactions. In addition, networks can help to test novel ecological hypothesis and provide a detailed characterization of the complexity of interactions that can shape plant diversity, potentially improving our forecast for how communities might respond to future changes. Finally, plant networks can be generated at different scales~~ (Verdù and ~~organization levels, identifying the role of plant interactions in specific ecological processes~~Valiente-Banuet 2008, Allesina and ~~therefore contributing to a mechanistic understanding of plant communities~~Levine 2011, Grilli et al. 2017) as models and case studies are rapidly growing in number.

In this review, we synthetize the recent contribution of ~~ecological networks~~the network approach to ~~understanding~~address species interaction in plant ~~community and biodiversity~~communities. In particular, we highlight how ~~plant networks~~studying the organization and dynamics of plant–plant interactions from the network perspective can help us to: a) assess the balance between facilitation and competition that may result in a wide range of potential outcomes; b) model the role of ~~multi-species~~ plant–plant interactions beyond pairwise competition in structuring plant communities, and c) forecast the ecological implications of plant–plant interactions across organisational levels. We further revise classes of indirect interactions among plants (i.e. interactions between two plants mediated by a third plant) and propose how these can be analysed within a plant network framework. Moreover, we discuss assumptions, advantages and weaknesses of different methods ~~used in the analysis of plant networks~~and models and their implications for a better understanding of ecological processes. ~~We finally highlight~~We conclude with highlighting main gaps and unsolved problems, and we design avenues for future research.

Looking at plant networks

Ecological networks are composed by “nodes” (e.g. species) connected by “links” (e.g. biotic interactions) (Fig. 1). Nodes and links are then projected into a matrix, where nodes form rows and columns, and links form matrix entries (Fig. 1). Two types of ecological networks have been mainly used: unipartite and bipartite (Fig. 1). In unipartite networks, there is one set of nodes, and links can connect any node within the network (e.g. predation in food webs). In bipartite networks, there are two distinct sets of nodes, and the links can only connect nodes between sets (e.g. pollinators with plants in pollination networks). A third type of network is the multilayer network, in which nodes are connected across different networks (i.e. layers) which can represent multiple types of interactions, time or space (Fig. 1).

We can consider plant–plant interactions as unipartite networks or bipartite networks. In unipartite networks, plants belong to a single set, while in bipartite networks there are two different sets. In ~~this~~the former case, plants are ecologically equivalent, while in the latter case~~,~~ we ~~would~~ recognize a priori structural and functional differences between plants. For instance, two different sets of plants can be arranged on the basis of growth form (e.g. tree and liana), functional role (e.g. competitor and subordinate species) or life-history stage (e.g. seedling and adult). These groups will represent the two distinct sets of nodes in a bipartite plant–plant network. This type of bipartite network model assumes no direct interactions among members of each set of nodes (e.g. among trees in tree–liana networks).

Links in plant networks can be ~~characterized~~established either by directly measuring a selected type of interaction or by measuring species associations and then inferring interactions on the basis of spatial distribution. In the first case, the strength and sign of plant interactions is determined by any proxy for fitness (i.e. survival, reproductive success or growth rate) and quantified in the presence and absence of other plants (Connell 1961, Verdú and Valiente-Banuet 2008, 2011, Alcantara et al. 2012, Delalandre and Montesinos 2018). In the second case, positive (or negative) species associations are based on spatial co-occurrence data that are used as a proxy for positive (or negative) interactions between species (Burns and Zotz 2010, Saiz and Alados 2011a, Losapio et al. 2018a, Montesinos-Navarro et al. 2018). Contrary to plant networks based on fitness measurements, co-occurrence networks describe the spatial organization of communities~~.~~ and can be expressed at different spatial scales. It is important to keep in mind that ~~this~~the spatial distribution of species is potentially influenced by ~~plant~~biotic interactions together with other fundamental ecological processes such as colonization, dispersion, habitat filtering and species turnover (Connell 1961, Kikvidze et al. 2015), so the interpretation of these spatial networks is different from the first case. Finally, links in plant networks usually represent interspecific interactions, which ~~are often~~can be classified ~~based on~~as qualitative ~~rather than~~or quantitative net effects of ~~the~~biotic interaction on the fitness or spatial distribution of species (Kefi et al. 2012). ~~In this way, links~~Links are often depicted as categorical variables including '-1' or '-' for negative effects and '1' or '+' for positive effects, which can represent the outcome of interactions as well as reciprocal effects between species (Fig 1).

Methodological pros and cons

The application of network approaches to characterize ecological systems presents several features that make this methodology convenient. Networks enable to explore any system of interacting components at different levels, including single individuals, species (nodes), groups of species (blocks) or the community as a whole network across multiple spatial and temporal scales (Olesen et al. 2010). In addition, ecological networks can be able to unveil complex effects that methods traditionally used in community ecology cannot, such as indirect biotic interactions or emergent properties of ecological communities (e.g. extinction cascades, Bascompte and Jordano 2014). However, the use of networks is not exempt of problems, particularly because measuring or inferring plant interactions is not always an easy task.

Measuring biotic interactions at the community level can be challenging as the potential number of interactions increases exponentially with species richness (Scutari et al. 2014), so that the quantification of these interactions in the field or using experimental designs might be unfeasible. Fine-scale spatial distribution patterns can help to overcome this limitation if combined with measures of environmental heterogeneity plus independent proxies for growth rate and fitness. Surely, spatial patterns alone might not exclusively unveil biotic interactions even at the appropriate spatial scale (Connell 1961). This can therefore blur or bias our understanding of other ecologically-relevant processes that may play a role, such as dispersal or microhabitat conditions. This is the case of co-occurrence networks, which although useful to synthetize processes where spatial or environmental effects operate synergistically with biotic interactions and might reveal overall net effects, might not unveil properly the mechanisms underlying plant interactions (Delalandre 2018, Freilich et al. 2018). In addition, studies on ecological networks have demonstrated that ecological drivers behind network structure can be obscured by neutral factors such as abundance distribution or the number of interactions observed (Dorman 2007).

The use of interaction networks in plant ecology implicitly assumes that the network reasonably reflects the ecological process it is representing. Building networks using experiments where biotic interactions are explicitly measured can establish a clear connection between network links and biotic interactions. On the other hand, limitations associated to co-occurrence networks can be partially overcome by controlling environmental heterogeneity, plants dispersal patterns and survey scale (Saiz et al. 2018, Losapio 2018a). Methodologically, the application of null models to estimate the significance of observed patterns must be included in any analysis (Bascompte and Jordano 2014), and the use of networks should be encouraged to study emergent properties that cannot be addressed otherwise. In this way, networks will become a promising tool to better understand the role of direct and indirect biotic interactions in plant communities.

Plant–plant interactions in ecological networks

Competitive networks

Competitive networks represent competition among plants (Fig. 2). Competitive interactions are often represented as direct links, resembling the net outcome of negative interactions. Laird and Schamp (2006) proposed a theoretical model of competitive network based on species dominance, in which species are organised according to their direct net effects on other species, such as A > B, B > C and C > A. These competitive outcomes were therefore organised in square matrices with varying levels of species richness. Results indicate that intransitivity increased potential for promoting species coexistence. The competitive network model of Allesina and Levine (2011) considered different competitive abilities of species in relation to environmental limiting factors. This model assumed species competing in numerous patches, each of which is limited by a combination of up to five limiting factors. Results show that coexistence via intransitive competition (e.g. species A outcompetes species B, B outcompetes C, and C outcompetes A) is a stabilizing niche mechanism, and that heterogeneous environmental conditions interact with network structure to favour diversity. Since then, accumulated evidence has shown that intransitivity might play an important role in maintaining biodiversity. Along the same line, the theoretical model proposed by Grilli et al.

(2017) assumes species competing for gap colonization in forest ecosystems and is built on competitive exclusion principle. Interestingly, results showed that intransitive competition in forests may maintain biodiversity by increasing the stability of the community.

Godoy et al. (2017) tested the contribution of intransitive competition to explain stability in annual plant community. They found that intransitive competition was not common and coexistence was driven by niche differences when species richness is relatively low. These results therefore contradict the foregoing theoretical expectation given by random matrix theory. Similarly, Nakagawa et al. (2015) explored whether intraspecific competition was evenly distributed in the community. Building a competitive network between trees in a fir plantation, where links were the effect of neighbours on tree size, they show that competition was stronger between similar trees of similar age and that this effect may drive the spatial distribution of age classes. Using co-occurrence data, Soliveres et al. (2015) found a positive correlation between degree of intransitivity of competitive networks and species richness, suggesting a positive effect of intransitive competition on biodiversity.

Facilitation networks

The pioneering study of Verdú and Valiente-Banuet (2008) described facilitation patterns using seedling recruitment, seed-set and occurrence patterns of plants associated to nurse plants. Results show that facilitation networks across desert ecosystems exhibited a nested structure, which was similar to other mutualistic networks (Bascompte and Jordano 2014). This nested pattern implies that the establishment and survival of facilitated specialist species was enhanced by generalist foundation species, which are plants with important structural and functional role in the ecosystem and that interact with a broad range of other species. The arrangement of facilitative interactions in a nested way resulted in plant communities less vulnerable to biodiversity loss (Verdú and Valiente-Banuet 2008). Several subsequent studies have explored factors that can explain nestedness in plant facilitation networks. Nestedness can be explained by a combination of species abundance and their phylogenetic relationships (Verdú and Valiente-Banuet 2011, Marcilio-Silva et al. 2015). This pattern was consistent across different habitats such as drylands and forest-grassland ecotones. Phylogenetic relationships can be used as a proxy for functional dissimilarity, as closely related species are assumed to be more ecologically similar. Verdú et al. (2010) found different phylogenetic patterns when considering facilitation networks based on seedling or adult facilitated plants, suggesting an ontogenetic shift from facilitation to competition across species and highlighting potential consequences for the organisation and evolution of the whole community.

Ecological networks can also help to understand dynamical properties of plant communities, in particular the process of ecological succession. Replacement networks have been used for this purpose, in which plant–plant interactions are modelled as a flow of resources across the ecosystem (Alcantara and Rey 2012). In food webs, resources can be light or nutrients that flow across species. In replacement networks, available space and gaps within vegetation can be seen as resources. In these gaps, plant species recruit and facilitate the establishment of other species, and these facilitated species can eventually replace the former over time. This approach allows identifying species associated in strongly connected components (i.e. tight groups of species that facilitate each other), where species are likely to persist over time, or other network components in which species are more likely to disappear (Alcantara and Rey 2012). In addition, authors showed that replacement networks can project realistic ecological succession using forest communities as a case of study (Alcantara et al. 2015).

Finally, plant network can explain variation in facilitation patterns across successional gradients. Losapio et al. (2018b) considered a multilayer network with facilitation by nurse plants at different ages and associated species in seed and adult stages. Results showed that life history stages and ontogeny drive the organisation of plant networks, suggesting that different processes are operating within the same community. For example, seed bank development was mainly due to random events while the establishment of adult plants was better supported by mature communities. Understanding plant networks over the course of an organism's lifetime is therefore crucial for predicting the dynamics of communities across spatial and temporal scales.

Competition-facilitation networks

Competition and facilitation usually concur within the same plant community (Callaway and Walker 1997, Brooker et al. 2008), although they are often considered separately (Maestre et al. 2009). Thus, competitive networks neglect facilitative effects such as recruitment and reduced physiological stress, while facilitation networks overlook competitive interactions among subordinate species (Schöb et al. 2013) or negative feedbacks to foundation species

(Schöb et al. 2014). However, competition-facilitation networks can describe both competitive and facilitative interactions within the same community or ecosystem (Fig. 2a).

Interestingly, the first plant network we found in literature included both putative competition and facilitation (De Vries et al. 1954). Based on rank correlation between species abundances, it depicts a network – so called ‘constellation of plants’ – of both positive and negative co-occurrence links among 45 grassland species. Further studies used transplant experiments (Turkington and Harper 1979) together with community matrix theory (Roxburgh and Wilson 2000, Dormann 2007~~).~~), which is the matrix that includes the direct effects between species in a population dynamic model. These studies substantially contributed to understanding the consequences of species interactions, mainly competition, for the diversity and stability of plant communities. Nevertheless, ~~only with the development of modern network analysis based on both graph theory and statistical mechanics (Jordán and Scheuring 2004), along with advances in user-friendly open source softwares (e.g.~~ knowledge of~~Csardi and Nepusz 2007, Dorman et al. 2008), ecologists approached to “modern”~~ ecological networks comprising both competition and facilitation is still very poor.

Recent advances for inferring ~~plan~~plant–plant interactions based on spatial patterns ~~considers~~can consider both competition and facilitation simultaneously. Here, positive spatial association can indicate putative facilitation, while negative spatial association can indicate putative competition (Callaway 2007). Using this approach, several authors have explored different factors affecting the spatial structure of plant communities. For instance, Fuller et al. (2008) showed that tree size can drive the spatial organization of tropical-forest networks, and Losapio et al. (2018) found that few stress-tolerant species were responsible for the cohesiveness of an alpine-tundra network, ultimately increasing the connectivity among plants. The consideration of both positive and negative links simultaneously can be relevant, considering that a right balance between positive and negative associations can have stabilizing effects for network structure (Saiz et al. 2017).

Analytical proposals to combine facilitation and competition within a given ~~networks~~network resulted in the seminal theoretical framework of Kefi et al. (2012), in which authors organized interactions in functional types and provided pathways to incorporate non-trophic interactions into ecological networks. They considered both direct and indirect effects of foundation species on biomass density of associated species, showing that including facilitation in the network can increase species persistence and consequently plant diversity.

Overall, including both competition and facilitation within the same plant network is not a trivial detail but it is a more realistic assumption that can have relevant consequences for modelling plant communities~~.~~ (Box 1).

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~~From a different perspective, Godoy and colleagues (Godoy et al. 2017) tested the contribution of intransitive competition to explain community stability. In an experiment with annual grasses, they found that intransitive competition was not common and community coexistence was driven by niche differences when species richness is relatively low. Similarly, Nakagawa and colleagues (Nakagawa et al. 2015) explored whether intra-specific competition was evenly distributed in the community. Building a competitive network between trees in a fir plantation, where links were the effect of neighbours on tree size, they show that competition was stronger between similar trees of similar age.~~

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Parasitic and commensalistic networks

Apart from competition and facilitation, interactions among plants can also be parasitic and commensalistic (i.e. when species need their partners to growth and reproduce as for obligate symbiosis). However, parasitism and commensalism at plant community level have been largely overlooked. Parasitic and commensalistic plant networks describe host–parasite interactions and host–guest interactions between plants, respectively. Given the asymmetrical nature of these interactions and the clear functional differences between the two distinct sets of partners, both parasitic and commensalistic interactions are better represented by bipartite networks. Studies have mainly focused on epiphyte–tree interactions in tropical forests and often measured interactions by integrating natural history of species and spatial patterns, but less often using fitness components.

The pioneering study of Burns (2007) in New Zealand forests found that interactions between epiphyte plants and host trees were organized in a nested way, in which generalist epiphytes were the first to colonize host trees while specialist epiphytes grew only in a subset of trees hosting diverse species. A similar result was obtained for Amazonian-forest networks (Sfair et al. 2010) and for Chilean-forest networks (Taylor et al. 2016). Nestedness in commensalistic networks suggested that facilitation by soil accumulation on host ~~tress~~trees may be the mechanism responsible for epiphyte succession (Burns 2007). According to this model, early-generalist colonists ameliorate environmental conditions within host trees for later recruiting species that are more specialised and less stress tolerant. The distribution of epiphytes was clustered at both fine and large spatial scales (Burns and Zotz 2010), indicating that positive feedbacks may operate to drive the establishment of epiphyte communities over trees. Strikingly, all these plant–epiphyte networks were structurally similar to those of facilitation networks in desert ecosystems discussed above (Verdú and Valiente-Banuet 2008) and to pollination networks (Bascompte and Jordano 2014~~).~~), as they all showed a nested structure of species interactions. This suggests that ~~general rules~~common processes may underlie the formation ~~and stability~~ of ecological networks regardless of study systems. Either pollination or plant commensalism, mutualistic networks tend to show a nested pattern, so that specialist species tend to avoid interacting with small sets of specialist partners maximizing the interaction overlap between generalist and specialist species (Bascompte and Jordano 2014).

~~A few~~Further studies looked at possible determinants of nestedness in plant commensalistic networks~~.~~ using phylogenetic and traits tools. The nested structure of commensalistic networks ~~seem~~seems independent from the phylogeny of epiphytes and trees (Silva et al. 2010). A possible explanation is that the huge taxonomic and phylogenetic diversity harboured in tropical forests may blur the signal of phylogenetic filtering. On the other hand, phenotypic traits showed stronger ~~predictive~~predicting power. Analysing bromeliad communities in tropical forests, Sayago et al. (2013) found that tree size, wood density and bark texture were important factors contributing to the nested assembly of commensalistic networks. Overall, commensalistic networks change with forest age~~, being~~ as the distribution of commensalistic interactions was more nested in old than young forests (Piazzon et al. 2011). The importance of mature forests as well as of tree abundance, tree size and bark texture was further confirmed by a later study in montane forests (Ceballos et al. 2016). As for previously mentioned plant facilitation networks (Losapio et al. 2018b), ~~this result suggests~~these results suggest that ecological networks can change over organism's lifetime with fundamental biological characteristics ~~of the organisms~~ such as ontogenetic stage and plant size.

Beside plant commensalistic networks, there is little consideration of parasitic interactions in plant networks. Plant parasitic networks seem to be composed by species-specific interactions organised in a modular way. For instance, generalist mistletoes did not share host trees but colonized distinct groups of specific hosts (Genini et al. 2012). Studies looking at the organisation of interactions between ~~epiphyte, mistletoe~~epiphytes, mistletoes and ~~liana~~lianas with their host trees have found that coevolutionary dynamics can shape the spatial distribution of parasitic interactions (Blick and Burns 2009). They found evidence for competition among lianas for access to host trees, while host specificity limited species associations (Blick and Burns 2011). Moreover, a functional perspective has been also considered in plant parasitic networks but we cannot draw any clear pattern at the moment. Blick et al. (2012) explored whether the structure of plant parasitic networks can be predicted based on plants traits. Results show that phenotypic similarity between mistletoes and host ~~tress was not responsible for the particular network structure~~trees was not responsible for the particular network structure. This result contradicts with results in plant–insect mutualistic networks, where interaction intimacy, the degree of biological association between partners, leads to differences in specialization patterns and might affect network organization (Bascompte and Jordano 2014). However, the intensity of interaction intimacy in plant community can substantially vary among individuals and communities, depending on life history traits and interaction types. In mistletoe–tree parasitic networks we propose that interaction intimacy can be an important factor of coevolution. On the other hand, in transient or unstable plant competition networks in disturbed environments we expect lower interaction intimacy than other plant networks.

Plant interactions: more than direct and pairwise

Plants in nature are confronted with a variety of neighbours belonging to the same and many different species. Nevertheless, interspecific biotic interactions are often described at the pairwise level, considering direct net effects between species pairs. However, it is increasingly recognized that interactions between two species change depending on other species in the community (Levine 1999, Callaway 2007, Levine et al. 2017, Losapio et al. ~~2017~~2019; Mayfield and Stouffer 2017). In other words, a third species can change the effects of one species on another. In the following paragraphs, we review the main classes of ~~indirect~~non-pairwise effects among plants: diffuse interactions, indirect interactions and intransitive interactions (Fig. 3). During the last few years, excellent reviews on indirect interactions have been published (Sotomayor and Lortie 2015; Levine et al. 2017, Godoy et al. 2018, Soliveres et al. 2018). Thus, our next paragraph focuses on how plant networks have helped to assess the relevance of the different non-pairwise and indirect effects among plants for plant ~~communities~~diversity.

Diffuse interactions

Diffuse interactions take place when several species compete with or facilitate more than one species ~~with~~within the community (Pianka 1974; Moen 1989, Vandermeer 1990; Callaway and Pennings 2000) (Fig. ~~3a-b).~~3a-b). The overall effect of diffuse interactions on a focal species is equal to additive net effects of pairwise interactions. Theory shows that competitive inhibition by many species in diffuse competition can be equivalent to strong competitive inhibition by fewer competing species (Pianka 1974). Diffuse competition among three plant species has been reported in field experiments in salt marshes (Callaway and Pennings 2000), indicating that diffuse interactions can cancel direct competitive effects between plant species.

There is also evidence that a single species may facilitate many other subordinate species at the time, leading to diffuse facilitation (Chacòn-Labella et al. 2016, Losapio et al. 2018a).

Indirect interactions

Indirect interactions occur when many interaction pathways can take place between the same ~~two (or more)~~ species, so that the effects of one plant on another can be mediated by a third ~~plant~~species (Grace and Tilman 1990; Callaway 2007) (Fig. 3c-j~~) or~~). The intermediary species can also ~~by~~be other ~~organisms such as herbivores (Saiz and Alados 2014). These~~organism than plants, like pollinators or mycorrhizal fungi, but here we focus only on interactions among plants, avoiding for instance insect-mediated indirect interactions (Sauve et al. 2014). Indirect interactions can buffer net effects, reversing the outcome of direct interactions (Levine 1999), and have the potential to result in profound effects on community dynamics (Levine 1976). Indirect interactions can occur through interaction chains and higher-order interactions~~.~~ (Wootton 1994). Interaction chains are sequences of direct species interactions resulting in indirect effects that are mediated by changes in population size, density or growth rate of intermediary species (~~Grace and Tilman 1990;~~ Sotomayor and Lortie 2015; Levine et al. 2017). On the other hand, for higher-order interactions the effects of interactions between two species on a third species are mediated by changes in species phenotypes or functional traits (Vandermeer 1990, Ohgushi et al. 2015; Levine et al. 2017).

Examples of indirect interactions are depicted in Figure 3 (c-j). One species can indirectly decrease the abundance of a second species by directly increasing the abundance of its competitor (Fig. 3c). This apparent competition often involves enemies like herbivores and pathogens associated to the third species (Burger and Louda 1994). Negative indirect effects can also raise when a species suppresses a facilitator of another species, a case of exploitation competition (Fig. 3d), like in the case reported by Llambi et al. (2018) where an invasive plant is suppressing a native plant by outcompeting its facilitator. One species can also indirectly increase the abundance of a second species by facilitating its facilitator as in the case of facilitation cascade (Altieri et al. 2007) (Fig. 3e). ~~The intermediary species can also be other organism than plants, like pollinator or mycorrhizal fungi.~~ Conversely, one species can indirectly increase the abundance of a second species by suppressing its competitor, as in apparent facilitation (Fig. ~~3f). This indirect facilitation~~3f) (Levine 1999~~) is the example in which ‘the enemy of my enemy is my friend’.~~). A separate case is facilitation-induced competition (Fig. 3g), in which one species is facilitating two other species that are therefore indirectly competing against each other. This can particularly be the case of facilitation-driven systems like arid environments, where it has been found that foundation species had positive effects on annual plant species that thereby go into competition (Schöb et al. 2013). On the other way around, two species can indirectly facilitate each other by outcompeting a common competitor. This type of competition-mediated facilitation (Fig. ~~3h) can occur for instance~~3h) resembles the case when "the enemy of my enemy is my friend". Evidence for this interaction type has been found among animals rather than among plants in coral reefs, where parrotfish and corals are mutually facilitating each other by competitively excluding macroalgae (Bozec et al. ~~2013).~~2013). We hypothesise that indirect interactions with positive outcomes would increase spatial aggregation and network nestedness, while negative outcomes would promote the development of modular structure.

Both diffuse and indirect interactions may be explored using Bayesian network inference. By looking at all potential direct and indirect relationships among species in the community (i.e. by assessing the conditional dependencies among species abundance) it might be possible to identify interactions that significantly affect a given focal species (Scutari et al. 2014, Staniczenko et al. 2017). This technique overcomes the challenge of estimating an unfeasible number of parameters by applying a heuristic search for optimal solutions. A network is proposed by different algorithms and sequentially compared to co-occurrence relationships observed though ~~a~~ goodness-of-fit statistics. Then, the network is modified and the process iterated until maximum fitness is reached, and the network that best matches the data can be selected. This tool has been widely used to study interaction patterns in disciplines such as molecular biology and medical bioinformatics (Chai et a. 2014), but its application to study ecological interactions has been much less ~~extended~~explored (but see Staniczenko et al. 2017, Delalandre et al. 2018, Montesinos-Navarro et al. 2018).

Intransitive interactions

When interactions between species are non-hierarchical, as net direct effects cannot be linearly ranked, intransitive loops can emerge (Fig. 3i-j). In intransitive competition, like in a 'rock-paper-~~scissor~~scissors game', competitive dominance of species is even so that A outcompetes (>) B, B > C and C > A (Fig. 3i). Despite plant communities are often envisioned as characterized by hierarchical, competitive dominance ~~(i.e. transitive competition) was~~

~~considered the rule in plant communities~~ (Grace and Tilman 1990, Keddy 2017), the list of studies reporting intransitivity is rapidly growing during last few years (see e.g. Grilli et al. 2017, Soliveres et al. 2015~~), yet~~). Yet, its ~~widespread~~spread and importance ~~remains~~remain highly controversial (Levine et al. 2017).

The swap from interaction hierarchies to intransitive loops is likely to emerge in spatially or temporally heterogeneous systems, when there is more than one limiting resource or when species differ in their traits trade-offs related with growth rates and resource acquisition (Allesina and Levine 2011). Intransitivity may also occur in facilitative interactions (Fig. 3j), due to indirect reciprocity 'I help you, somebody helps me' (Boyd et al. 2003) but its relevance remains still unveiled in natural communities. Although intransitive facilitation is a well-established factor in evolutionary biology, the ecological implications of this type of interactions are still unexplored also under the theoretical point of view.

Theory shows that intransitive competition in complex ecological networks can enhance community persistence (Laird and Schamps 2006, Allesina and Levine 2011, Grilli et al. 2017). Network properties such as species connectance (Alcantara et al~~-~~. 2015), relationships between the subnetworks within the network (Alcantara et al. 2012) and the competitive ranking among species (Laird and Schamp 2006) can significantly influence the persistence of species within communities. Moreover, compartmentalization and high number of species participating in these intransitive loops can increase the robustness of plant communities to species loss (Alcantara et al. 2012~~)~~). These modelling studies indicate how intransitive interactions can support plant diversity by enhancing community stability. Yet, its importance and empirical evidence is controversial (Godoy et al. 2017) as intransitive competition alone might be not strong enough to determine species persistence within a community.

Taken together, these studies suggest that ~~indirect~~non-pairwise interactions ~~may~~ occur at the whole-network level and can be relevant for community dynamics. This implies that indirect effects of plant interactions are more complex than previously thought and can substantially depend on network organisation. These diffuse, indirect and intransitive interactions 'spread' across the networks and have the potential to reverse negative effects of direct pairwise interactions, with fundamental consequences for species persistence and biodiversity maintenance. However, we still do not know enough to draw causal relationships between these interactions and the biodiversity we observe in nature. Indirect interactions in plant networks may be hard to unveil but this is a crucial challenge as these network-level interactions may improve our understanding about the stability and functioning of ecological communities.

Ecological implications of plant interactions across organisational levels

A combination of the accumulated knowledge on network theory and plant ecology is tackling the three challenges mentioned above. Network theory improves models of plant community structure and dynamics (Kefi et al. 2012, Grilli et al. 2017), particularly by combining different interaction types within and across trophic levels (Sauve et al. 2014, Losapio et al. 2019). Ecological networks have been ~~applied~~used to answer relevant questions in plant ecology at different scales, from populations to ecosystems (Box 1).

Box 1. Effects of livestock grazing on a spatial plant network.

Sustaining livestock grazing is one of the most important services provided by plants. In turn, grazing has important effects on plant communities, such as reducing biomass, altering regeneration niches and modulating interspecies competition (Olff and Ritchie 1998). Here, we present a case study of how grazing influences the structure of spatial networks in Mediterranean plant communities (South East Spain, data from Saiz and Alados 2012).

We selected two communities: one natural (i.e. absence of livestock grazing) and another overgrazed (i.e. livestock grazing intensity higher than sustainable levels). For each community, we created a network with positive and negative links based on the spatial aggregation and segregation between each species pair, respectively. These were assessed on the basis of abundance data correlation. Then, for each network, we calculated the proportion of non-connected species (*NC* = species with no links divided by total number of species), link density ($D = I/SR$, where I is the total number of links over total number of species), link ratio ($R = (I^+ - I^-)/I$, where I^+ and I^- are the total number of positive and negative links, respectively), and the occurrence of highly connected modules ($M = \sum_{S=1}^{N_M}\left(\frac{I_S}{I} - \left(\frac{k_S}{2I}\right)^2\right)$, where N_M is the number of modules in the network, I_S is the number of links within module S, and k_S is the sum of links of all species in S). Observed network properties were then compared with null models.

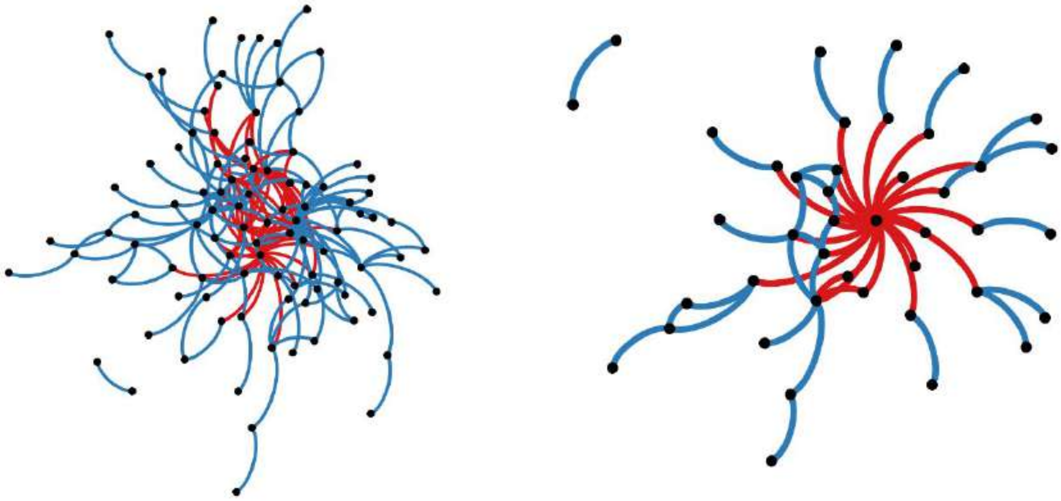

Figure B1. Plant spatial networks for the natural (left) and overgrazed (right) communities in Mediterranean ecosystems (South East Spain). Nodes (dots) represent plant species, blue links represent positive links (aggregation) and red links represent negative links (segregation).

We found that overgrazing had a strong impact on the structure of plant networks (Table 1, Figure 1). Overgrazing substantially simplified the community and caused the loss of many positive associations between species. In particular, overgrazing breaks the patchy structure of the vegetation, precluding the persistence of species that require the presence of plant patches to survive. Interestingly, both communities show highly connected modules, but for different reasons. In natural communities, modules represent the many patches with different species composition. Whereas, in overgrazed communities, modules organize around one highly segregate species, that is poorly consumed by livestock and dominate the community (Fig. 1). These results shed new light on the profound consequences of overgrazing on the structure and functioning of plant communities.

	NC	*D*	*R*	*M*
natural	0.18	3.18	0.38	0.49***
Overgrazed	0.42	1.44	0.12	0.49**

Table B1. Structure of spatial networks in two communities with different livestock grazing intensity. NC is proportion of non-connected species; D is the link density; R is the link ratio; M is the modularity. ** and *** indicate that modularity is significantly higher than expected by 1000 random networks.

Plant network structure has been linked to community robustness and stability. Some properties of plant facilitation networks such as nestedness or scale-free degree distributions can maximize the number of species occurring in the community (Verdú and Valiente-Banuet 2008; Saiz and Alados 2011a; Kefi et al. 2012). On the other hand, replacement networks have been shown to be structured in strongly connected components (Alcantara 2012). Saiz and Alados (2014) found that grazing simplifies the structure of the plant community, with livestock disturbance increasing the number of species isolated from the rest of the community. Using a modelling approach, Losapio and Schöb (2017) also proposed a framework for assessing the response of plant networks to climate change. This model integrates functional traits as biology-informed criteria of species sensitivities into facilitation networks, showing that the resistance of plant communities ~~. Specifically, some~~and inherent biodiversity depend on the driver of environmental change. Plant networks can therefore contribute to conservation by gaining a better understanding of how plant network structure can be altered by extrinsic factors (e.g. global change drivers) and can limit local population extinction. These areas constitute a potential framework to assess how plant interactions contribute to species persistence and community robustness against species loss, with important implication for conservation strategies. Future studies shall empirically test how different aspects of plant networks, such as the distribution of plants in modular patches, may increase the conservation of local populations. Future studies shall also improve forecasting of interaction-mediated community response to environmental change by including different layers of plant fitness information as well as addressing direct and indirect antagonistic and mutualistic interactions (Sauve et al. 2016). In sum, plant networks seem a promising tool to improve management strategies by considering how the whole organisation of plant communities can be affected by changes driven by both extrinsic and intrinsic factors.

Other applications of plant networks have been oriented to ~~assess~~studies of spatio-temporal dynamics~~ of plant communities (succession), predict spatial distribution of species from local to broad geographical scale, explore mechanisms maintaining plant diversity, improve the design of management strategies, and evaluate the potential responses of plant communities to climate change.~~

~~The temporal dynamics of successional~~. In particular, processes ~~has~~involved in ecological successions have been ~~approached using plant networks~~examined by both focusing on foundation-species effects and other components such as replacement and turnover. Overall, the role of foundation species in plant communities is~~-~~ comparable to that of keystone species in food webs (Jordán 2009). Foundation species play a key role for structuring plant facilitation networks, especially in stressful environments such as arid ecosystems (Verdú and Valiente-Banuet 2008, 2011, Saiz and Alados 2011b, Losapio et al. 2018b) and alpine ecosystems (Losapio et al. 2018a). For instance, the tussock grass *Stipa tenacissima* increased the spatial aggregation of subordinate species (Saiz and Alados 2011a). These plant networks show a scale-free degree distribution (Jordán and Scheuring 2004), meaning that the majority of plant species is loosely associated to other species while only few species have a large number of neighbours (Saiz and Alados 2011b).

~~A deeper understanding of succession processes in plant communities can arise from predicting networks' dynamical properties based on their topologies. Alcantara et al. (2012) proposed that the theoretical concept of strongly connected components can be a useful property to consider for this aim.~~ Nestedness of plant facilitation networks has been proposed to be also responsible for driving ecological succession as networks become more nested with increasing successional age (Losapio et al. 2018a). This suggests that the stability of ecological networks increases throughout ecological successions, as also evidenced by plant–insect network dynamics (Losapio et al. 2015). Results from tropical forests (Marcilio-Silva et al. 2015) also highlight the importance of species turnover over the influence of some species traits related to dispersal and canopy size. Alcantara et al. (2012) proposed the concept of strongly connected components for predicting dynamical properties of networks based on network topology. These network components are groups of nodes where resources flow either directly or indirectly, from one to the other and in both directions, and they can represent successional dynamics among species that can persistent over time. ~~Nestedness of plant facilitation networks has been proposed to be also responsible for driving ecological succession, in this~~

~~case in tropical forests (Marcilio-Silva et al. 2015), highlighting the importance of species turnover over the influence of other traits related with dispersal and canopy size.~~

~~Plant networks have~~Ecological network theory has been also succinctly used to ~~assess~~model species distribution at different spatial scales, but its application to study plant interactions and plant communities has been much less extended. From a biogeographical perspective, species distribution models have usually considered macroecological abiotic factors to predict species distribution~~, although the~~. However, recent interest in including ~~biotic interactions~~ plant interaction networks into species distribution models has increased recently (Staniczenko et al. 2017). Results of Bayesian network of annual plant community showed that considering plant interactions substantially altered assessments of species range changes under future environmental change. Indeed, Bayesian network inference ~~has been showed to improve~~improves the prediction of plant species distribution models ~~by providing~~and provides a feasible way of including information about the co-occurrence patterns among all the species in the community (Montesinos-~~Navavro~~Navarro et al. 2018). At a local scale, it has been also tested whether this technique can precisely infer plant–plant interactions, showing that networks could reflect different processes at different spatial scales, and its sensitivity to the sampling spatial scale requires caution in the interpretation of the inferred links (Delalandre and Montesinos-Navarro 2018). Potential future applications include integrating individual-based networks models (Olesen et al. 2010) with species distribution models, then testing these predictions in the field. Particularly relevant to future directions is understanding how current network structure may drive local adaptation to microhabitat conditions as well as to novel interacting partners and extinct partners.

~~In addition, plant networks have also contributed to a better understanding of the mechanisms that can maintain biodiversity. Thus, network structure has been linked to community robustness and stability. For example, some properties of plant facilitation networks such as nestedness or scale-free degree distributions can maximize the number of species occurring in community (Verdú and Valiente-Banuet 2008; Saiz and Alados 2011a; Kefi et al. 2012). On the other hand, replacement networks have been shown to be structured in strongly connected components, constituting a potential tool to assess which plant-plant interactions are more likely to contribute to species persistence and community robustness to species loss (Alcantara 2012).~~

~~Finally, plant networks can also contribute to design management strategies if we gain a better understanding of how their structure can be altered by extrinsic factors. Saiz and Alados (2014) found that grazing simplifies the structure of the plant community, with livestock disturbance increasing the number of species isolated from the rest of the community. Using a modelling approach, Losapio and Schöb (2017) also proposed a framework for assessing the response of plant networks to climate change. This model integrates functional traits as biology-informed criteria of species sensitivities into facilitation networks, showing that the resistance of plant communities depends on the driver of environmental change (Losapio and Schöb 2017). Thus, plant networks seem a promising tool to improve management strategies by considering how the whole structure of plant communities can be affected by changes driven by both extrinsic and intrinsic factors.~~

~~**Methodological pros and cons**~~

~~The application of network approaches to characterize ecological systems presents several features that make this methodology convenient. Networks enable to explore any system of interacting components at different levels, including single species (nodes), groups of species (blocks) or the community as a whole (network, Bocaletti et al. 2006). Interaction networks can be able to unveil complex effects that methods traditionally used in community ecology cannot, such as indirect biotic interactions or emergent properties of ecological communities (e.g. extinction cascades, Bascompte and Jordano 2014). Finally, network theory can be particularly convenient in plant community ecology, as there is a considerable amount of existing data of plant species co-occurrences, which can be easily used to elucidate plant interactions patterns in plant communities.~~

~~However, the use of networks is not exempt of problems. Measuring biotic interactions at community level can be challenging as the potential number of interactions increases exponentially with species richness (Scutari et al. 2014), so that the quantification of these interactions in the field or using experimental designs might be unfeasible. An approach to overcome this limitation is using spatial distribution patterns as proxies for biotic interactions, but with the caveat that they might not exclusively unveil biotic interactions. This can therefore blur or bias our understanding of other ecologically-relevant processes such as dispersal. This is the case of co-occurrence networks, which although useful to synthetize processes where spatial or environmental effects operate synergistically with biotic interactions, might not~~

~~represent properly pairwise plant interactions (Delalandre 2018, Freilich et al. 2018). In addition, studies on ecological networks have demonstrated that ecological reasons behind network structure can be obscured by neutral factors such as species richness or abundance distribution, or the number of interactions observed (Dorman 2007).~~

~~The use of interaction networks in plant ecology implicitly assumes that the network reasonably reflects the ecological process it is representing. Building networks using experiments where biotic interactions are explicitly measured can establish a clear connection between network links and biotic interactions. On the other hand, limitations associated to co-occurrence networks can be partially overcome by controlling environmental heterogeneity, plants dispersal patterns and survey scale (Saiz et al. 2018, Losapio 2018a).~~ Methodologically, the application of null models to control neutral factors ~~must be included in any analysis (Bascompte and Jordano 2014), and the use of networks should be encouraged to study emergent properties that cannot be addressed otherwise. In this way, networks will become a promising tool to better understand the role of direct and indirect biotic interactions in plant communities.~~

Conclusion ~~and future directions~~

The combination of network theory and plant ecology has provided new avenues to study the role of biotic interactions for the structure and dynamic of plant communities. ~~The study of plant networks~~Research along this line has indicated how the hierarchy of plant competition can influence species persistence and community stability. ~~We~~By highlighting how species are connected, what makes some species more connected than others, and how they influence each other's persistence through the community network we have gained a deeper understanding of the effects of plant~~–plant interactions~~ facilitation on the maintenance of ~~species diversity. In addition, plant networks show structural properties common to other classes of ecological and complex networks. Indeed, plant facilitation networks and plant commensalistic networks have similar architecture (nestedness and modularity) to other types of networks such as pollination networks. Finally, plant networks may help quantifying the effects of indirect interactions on species persistence.~~biodiversity at the community level. Overall, plant networks ~~are revealing general processes underlying the organisation of biodiversity across systems as patterns seem~~reveal properties that are consistent over many different species and environments, from tropical forests to alpine tundra, and are common to other classes of ecological and complex networks.

~~But *why we should care about plant networks?* Plant diversity is more than a list of species, a collection of herbarium specimens, a summary index of diversity, a phylogenetic tree or a multidimensional trait space. Rather, biotic interactions are fundamentals for plant communities and the *diversity of interactions* as well as the *structure of plant networks* may ultimately contribute to biodiversity maintenance. Plant networks can therefore help to capture some emergent properties of plant communities and provide further information that only species richness or relative abundance cannot. In this sense, plant networks can complement knowledge of systematics and functional botany to better explain patterns of plant diversity and improve our understanding of processes shaping plant communities. For instance, considering positive, neutral and negative interactions at the same time will substantially help moving the field of plant ecology forward. Dynamic plant networks can play a fundamental role for the persistence of plant populations, species and communities in natural ecosystems under climate change. Characterizing plant networks under different environmental conditions and interaction regimes can therefore improve the accuracy of our predictions to how single species and entire communities can respond to global warming.~~

~~Our understanding of processes shaping plant networks as well as their consequences for biodiversity is still limited by scarce theoretical and experimental understanding.~~Yet, our understanding of processes shaping plant networks as well as their mechanisms underlying biodiversity maintenance is still limited, particularly in natural ecosystems. Questions like how robust are specialised and generalised plant interactions, the combined effects of facilitation and competitive networks on community stability, or the role of ~~network structure~~interaction diversity for biodiversity maintenance are still largely unanswered under both theoretical and empirical point of view. ~~Some of the future~~Future directions where research on plant networks may move forward ~~involve considering~~can considers plant multilayer networks that include different interaction types and trophic levels responsible for plant fitness, such as mutualistic and antagonistic organisms~~.~~ (Sauve et al. 2016). Plant network modelling in a context of ecological succession and environmental gradients can reveal mechanisms linking biotic interactions, community dynamics and ecosystem ~~functioning such as plant productivity.~~processes. Finally, we still have a very limited knowledge of the ~~effects~~role of plant interactions and their networks ~~on~~in eco-evolutionary dynamics~~. A plant~~ (Schöb et al. 2018). In this area, relevant questions such as how indirect interactions and network ~~understanding~~ ~~can~~structure contribute to ~~assess the role of multiple biotic interactions on~~ micro-evolutionary processes and local adaptation in plant communities are still unanswered. To do so, it seems important moving from the description of local plant networks to formalise mathematical models associated with experimental assessment in the lab and in the field. Plant network studies ~~at different levels of organisation embracing~~that embrace the peculiarity of plant kingdom across different organisation levels have a great potential for advancing plant ecology and ~~diversity~~biodiversity science.

Disclosure statement

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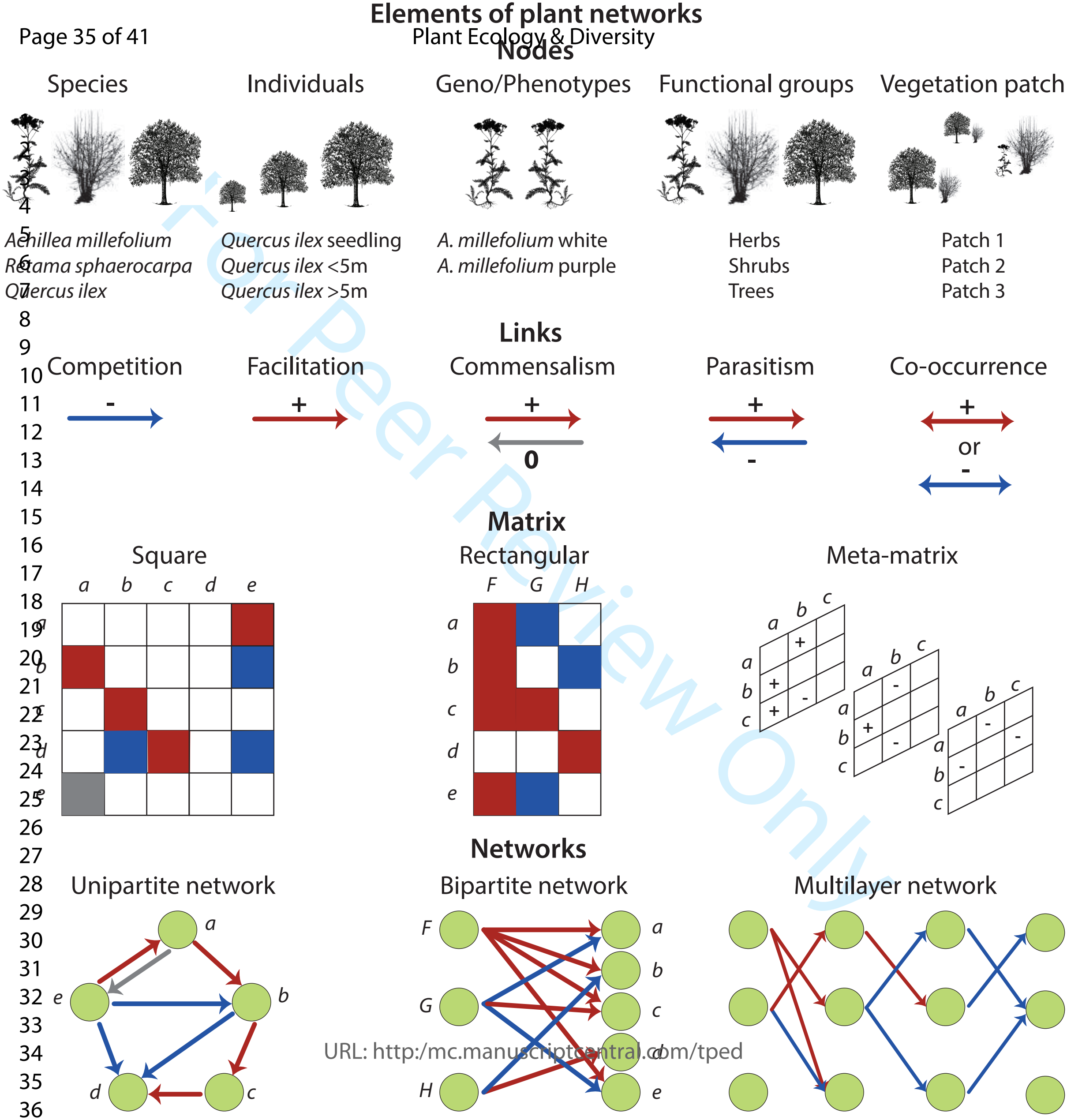
Figure captions

Figure 1 Elements of plant networks. Plant networks are composed by nodes (e.g. species, individuals, genotypes, phenotypes, functional groups, vegetation patches) connected by links (e.g. competition, facilitation, commensalism, parasitism, co-occurrence). Nodes and links are represented in matrices and therefore network objects.

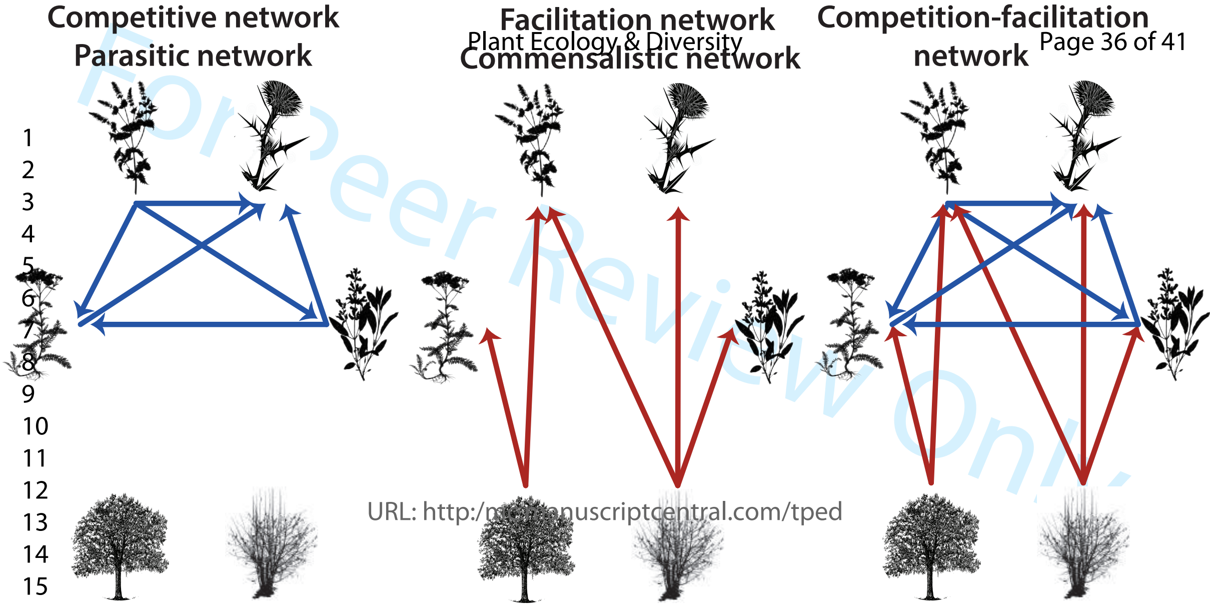
Figure 2 Types of plant networks. Competition-facilitation networks are composed by both competitive (blue) and facilitative (red) interactions. Competitive or parasitic networks are composed only by negative interactions, while facilitation and commensalistic networks are composed only by positive interactions.

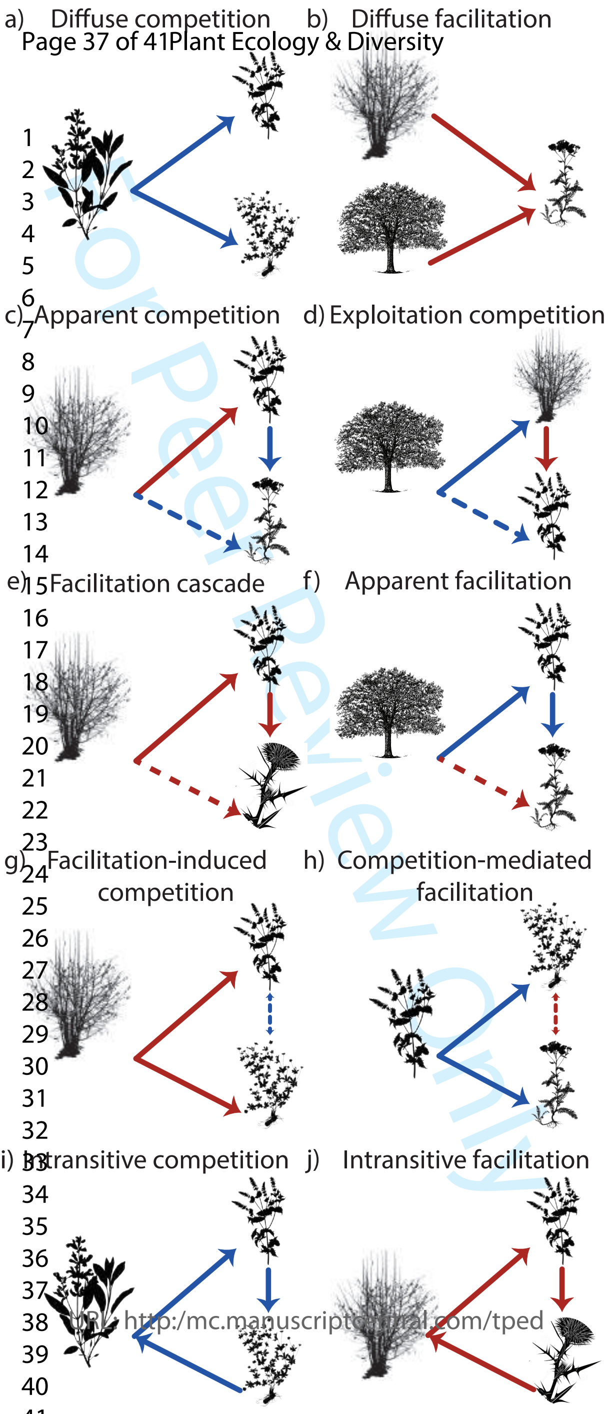
Figure 3. Indirect effects among plants. Diffuse interactions (a-b), interaction chains and higher-order interactions (c-h), intransitive interactions (i-j).



	a	*b*	*c*	*d*	*e*
a					🟥
b	🟥				🟦
c		🟥			
d		🟦	🟥		🟦
e	▨				

	F	*G*	*H*
a	🟥	🟦	
b	🟥		🟦
c	🟥	🟥	
d			🟥
e	🟥	🟦	


Competitive network
Parasitic network
Facilitation network
Commensalistic network
Competition-facilitation network


a) Diffuse competition
b) Diffuse facilitation
c) Apparent competition
d) Exploitation competition
e) Facilitation cascade
f) Apparent facilitation
g) Facilitation-induced competition
h) Competition-mediated facilitation
i) Intransitive competition
j) Intransitive facilitation

Plant networks and the organisation of biodiversity

Gianalberto Losapio, Alicia Montesinos-Navarro, Hugo Saiz

Supporting Information

Tab. 1 Summary of literature analysis about plant networks.

Plant	Interaction	Link	Network type	System	Property	Method	Output	Reference	Type of study
Model	Facilitation, competition	Spatial occurrence	Bayesian network inference	Machair vegetation	Inference of the interaction pattern	Bayesan network inference	There is an imbalance between positive and negative interactions, dominating the positive interactions	Aderhold et al. 2012	Data from other sources
Tree, sapling	Replacement	Spatial occurrence + recruitment	Unipartite	Forest	Components, modularity, robustness	Observation, null model	Modularity decreases network robustness	Alcantara & Rey 2012	Observational
Nurse, sapling	Replacement	Spatial occurrence	Bipartite	Forest	Cover	Observation, simulation	Disturbance decreases forest recovery	Alcantara et al. 2015	Theoretical
Model	Competition	Competitive outcome	Complete unipartite	Random tournaments	Species richness	Simulation	Core of intransitive competition supports networks	Alcantara et al. 2017	Theoretical
Model	Competition	Competitive outcome	Complete unipartite	Random tournaments	Species richness	Simulation	Intransitive competition increases species richness	Allesina & Levine 2011	Theoretical
Mistletoe/liana/epiphyte, tree	Parasitic, commensalistic	Spatial occurrence	Bipartite	Forest	Nestedness	Observation, null model	Coevolutionary dynamics shape network structure	Blick & Burns 2009	Observational
Liana, tree	Commensalistic	Spatial occurrence	Bipartite	Forest	Species association	Observation, null model	Host specificity limits species associations	Blick & Burns 2011	Observational
Mistletoe, tree	Parasitic	Spatial occurrence	Bipartite	Woodland	Specialization, interaction strength	Observation, null model	Phenotypic-trait similarity predicts network structure	Blick et al. 2012	Observational
Epiphyte, tree	Commensalistic	Spatial occurrence	Bipartite	Forest	Species association, meta-community	Observation, null model	Species distribution clumped at fine and large scales	Burns & Zotz 2010	Observational
Epiphyte, tree	Commensalistic	Spatial occurrence	Bipartite	Forest	Species and community organisation	Observation, null model	Species randomly distributed within nested community	Burns 2007	Observational
Epiphyte, tree	Commensalistic	Spatial occurrence	Bipartite	Forest	Connectance, nestedness, specialisation	Observation, null model	Tree size and species abundance explain network structure	Ceballos et al. 2016	Observational

Adult	Facilitation, competition	Clustering and segregation	Unipartite	Grassland	connectance	observation	first plant-plant spatial association network I found	de Vries et al. 1954	Observational
Nurse, seedling/sapling	Facilitation, competition	Spatial occurrence + fitness	Unipartite	Steppe	Species association	Observation, null model	Multiple indirect interactions structure plant communities	Delalandre & Montesinos-Navarro 2018	Observational
Model	Inter-guild mutualism and intra-guild competition	temporal overlap between species phenology	Bipartite	Annual plants	Community stability	Simulation	The distribution of phenologies influences the stability and coexistence of species.	Encinas-Viso et al. 2012	Theoretical
Tree	Association	Clustering and segregation	Unipartite	Forest	Clustering, path length	Observation, null model	The effect of plant traits on network structure depends on stem size	Fuller et al. 2008	Observational
Mistletoe, tree	Parasitic	Spatial occurrence	Bipartite	Forest	Nestedness, modularity	Observation, null model	Parasitic networks are modular	Genini et al. 2012	Observational
Annual grasses	Competition	Fitness	Unipartite	Mediterranean vegetation	Triplets	Experiment	Competitive networks for annual grasses are not intransitive	Godoy et al. 2017	Experimental
Model	Facilitation	Facilitation strength	Food web	Food web	Species richness	Simulation	Facilitation increases species richness	Kefi et al. 2012	Theoretical
Whole community	Facilitation, competition	Real interaction	Unipartite	Rocky shore	Connectance, compartmentalization	Observed	Network combining different types of interactions (including plants)	Kefi et al. 2015	Observational
Model	Competition	Competitive outcome	Complete unipartite	Random tournaments	Relative intransitivity	Simulation	Intransitive competition increases species coexistence	Laird & Schamp 2006	Theoretical
Model	Competition	Competitive outcome	Complete unipartite	Random tournaments	Relative intransitivity	Simulation	Global intransitive competition increases with species richness	Laird & Schamp 2008	Theoretical
Model	Competition	Competitive outcome	Complete unipartite	Random tournaments	Species richness	Simulation	Network structure mediates species coexistence	Laird & Schamp 2009	Theoretical
Nurse, adult	Facilitation	Spatial occurrence	Bipartite	Grassland	Species richness	Observation, simulation	The importance of facilitation depends on environmental change	Losapio & Schöb 2017	Observational
Adult	Facilitation, competition	Clustering and segregation	Unipartite	Scrubland	Species association, clustering	Observation	Network structure changes across spatial scales	Losapio et al. 2017	Observational
Adult	Facilitation, competition	Spatial association	Unipartite	Grassland	Degree, clustering	Observation, null model	Abundance, LMA and height explain the assembly of plant networks	Losapio et al. 2018	Observational

Nurse, adult, seed	Facilitation	Spatial occurrence	Tripartite	Desert	Nestedness, specialisation	Observation, null model	Nurse age affects neste structure of adult networks but not seed banks	Losapio et al. 2018	Observational
Nurse, seedling	Facilitation	Spatial occurrence	Bipartite	Forest, grassland	Connectance, nestedness, specialisation	Observation, null model	Woody plants drive expansion of forest facilitation networks	Marcilio-Silva et al. 2015	Observational
Community co-occurence	Facilitation, competition, habitat filtering	Spatial occurrence	Bayesian network inference	Mediterranean vegetation	Inference of the interaction pattern	Bayesan network inference	Functional dissimilarities between species linked based on coexistence networks can dissentangle mechanisms underlying speices coexistence (i.e. habitat filtering and biotic interactions)	Montesinos-Navarro et al. 2018	Data from other sources
Seedlings	Competition	Mortality	Unipartite	Forest	Species interaction	Experiment	Bigger and older plants support competitive networks	Nakagawa et al. 2016	Experimental
Epiphyte, tree	Comensalistic	Spatial occurrence	Bipartite	Forest	Nestedness	Observation, null model	Commensalistic networks are highly nested and was modulated by forest age	Piazzon et al. 2011	Observational
Adult	Facilitation, competition	Spatial occurrence	Unipartite	Steppe	Species association	Observation	Nurse plants increases network complexity	Saiz & Alados 2011a	Observational
Adult	Facilitation, competition	Spatial occurrence	Unipartite	Steppe	Species association	Observation	Scale-free network and preferential species association	Saiz & Alados 2011b	Observational
Adult	Facilitation, competition	Clustering and segregation	Unipartite	Steppe	Partition, species association	Observation, null model	Grazing increases network fragmentation	Saiz & Alados 2014	Observational
Adult	Facilitation, competition	Clustering and segregation	Unipartite	Steppe	Partition, species association	Observation, null model	Gypsicole plants presnet diferent network roles	Saiz & Alados 2014	Observational
Adult	Facilitation, competition	Clustering and segregation	Unipartite	Steppe, forest	Structural balance	Observation	Positive and negative associations stabilise network structure	Saiz et al. 2017	Observational
Adult	Facilitation, competition	Clustering and segregation	Unipartite	Dryland	Species association, structural balance	Observation, null model	Tight associations and structural balance increase with species richness	Saiz et al. 2018	Observational
Epiphyte, tree	Commensalistic	Spatial occurrence	Bipartite	Forest	Connectance, nestedness, specialisation	Observation, null model	Plant traits explain network structure	Sayago et al. 2013	Observational
Liana, tree	Commensalistic	Spatial occurrence	Bipartite	Forest	Modularity, nestedness	Observation, null model	Nested and non-modular networks	Sfair et al. 2010	Observational
Liana, tree	Antagonistic	Spatial occurrence	Bipartite	Forest savanna	Nestedness	Observation, null model	Abundance and tree height determines species contribution to nestedness	Sfair et al. 2017	Observational
Epiphyte, tree	Commensalistic	Spatial occurrence	Bipartite	Forest	Nestedness, phylogeny	Observation, null model	Nested networks indepent of phylogeny	Silva et al. 2010	Observational

Adult	Facilitation, competition	Bayesian dependencies	Unipartite	Grassland	Species distribution	Observation, experiment, simulation	Interaction network improve predicting species dynamics	Staniczenko et al. 2018	Observational
Adult	Facilitation, competition	Clustering and segregation	Unipartite	grassland	conectance	observation	Spatial associations at community level	Stowe 1979	Observational
Epiphyte, tree	Commensalistic	Spatial occurrence	Bipartite	Temperate forest	Nestedness, co-occurrences	Observation, null model	Epipthyte-tree networks are highly nested	Taylor et al. 2016	Observational
Flowers	Facilitation, competition	Pollen transfer	Unipartite	Scrubland	Species interaction	Observation	Facilitation for pollination increases with altitude	Tur et al. 2016	Observational
Adult	Facilitation, competition	Clustering and segregation	Unipartite	grassland	Conectance	observation	Spatial associations at community level	Turkington 1979	Observational
Nurse, seedling/sapling	Facilitation	Spatial occurrence + fitness	Bipartite	Desert	Nestedness, specialisation, robustness	Observation, null model	Generalist nurses and nested communities increases network robustness	Vardu & Valiente-Banuet 2008	Observational
Nurse, seedling	Facilitation	Spatial occurrence + fitness	Bipartite	Desert	Nestedness, resistant to extinction cascades	Observation, null model	Facilitation communities are assembled as networks with significant nested structure	Verdú & Valiente-Banuet 2008	Observational
Nurse, seedling	Facilitation	Spatial occurrence + fitness	Bipartite	Desert	Nestedness, connectance	Observation, null model	Phylogeny and species abundance explain network structure	Verdu & Valiente-Banuet 2011	Observational
Nurse, seedling, adult	Facilitation	Spatial occurrence + fitness	Bipartite	Desert	Phylogeny, nestedness, connectance	Observation, null model	Phylogenetic signal changes between seedling and adult networks	Verdu et al. 2010	Observational