Plant Facilitation and Phylogenetics

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Abstract

The relationship between facilitation and evolutionary ecology is poorly understood. We review five issues elucidating how the phylogenetic relatedness of species provides insight into the role of facilitation in community assembly: (*a*) Are the facilitative interactions more common between species that differ in a regeneration niche? (*b*) Are facilitative interactions more common between distantly related species? (*c*) Do communities governed by facilitation (rather than competition) have higher phylogenetic diversity? (*d*) As facilitated juvenile plants mature, do they compete with their nurses more often if they are closely related to them? (*e*) How does the phylogenetic signature in a community reveal ecological processes, such as succession, regeneration dynamics, indirect interactions, and coextinction cascades? The evolutionary history of lineages explains the regeneration niche of species, which ultimately determines the facilitation-competition balance and therefore community assembly and dynamics. We apply this framework to the conservation of biodiversity and propose future research avenues.

> [I]n all these scenes of animal life which passed before my eyes, I saw Mutual Aid and Mutual Support carried on to an extent which made me suspect in it a feature of the greatest importance for the maintenance of life, the preservation of each species, and its further evolution.
>
> –*Mutual Aid: A Factor of Evolution*, Piotr Kropotkin (1902)

1. INTRODUCTION

The most accepted idea having to do with community organization assumed that communities are the result of the confluence of species adapted to a specific environment (Gleason 1926) and the outcome of competitive exclusion (Silvertown 2004). This axiomatic-like paradigm originated from Darwin's ideas connecting natural selection with the universal density-dependent Malthusian population theory (den Boer 1986). Thus competition was believed to affect the numerical processes in both populations and communities, and therefore the view that communities are structured by negative-type interactions has dominated ecology. Although positive interactions are ubiquitous and the first studies were published since the nineteenth century, they were not of interest to ecologists for most of a century (Boucher et al. 1982). Facilitation is a positive interaction between species where at least one participant benefits and no harm is caused to either; it could also be a mutualism when mutual benefit exists (Stachowicz 2001). Despite the fast development of facilitation theory and the accumulation of empirical data in the past few decades (Callaway 2007), it was not until recently that the role of phylogeny in facilitative interactions has begun to be explored by borrowing the principles from community phylogenetics (Valiente-Banuet & Verdú 2007, Brooker et al. 2008, Thorpe et al. 2011). This discipline is rooted in Elton's (1946) idea that communities structured by competition show a low species-to-genus ratio because of competitive exclusion of ecologically similar congeneric species (Webb et al. 2002). Community phylogenetics, thanks to the increasing availability of molecular phylogenies for ecologists (see the sidebar, How to Construct a Plant Community Phylogeny), refined this idea by quantifying the evolutionary relatedness between species instead of using their taxonomic adscription. Community phylogenetics studies started to test whether competition or habitat filtering were the main mechanisms structuring the communities, but such dichotomy has now been superseded (Mayfield & Levine 2010, Pausas & Verdú 2010), and new assembly mechanisms like facilitation are starting to be considered under trait-based (Schöb et al. 2012) and phylogenetic-based approaches (Valiente-Banuet & Verdú 2007; Soliveres et al. 2012a,b).

How facilitation has historically contributed to species richness in local communities through evolutionary time remains poorly understood. Reconciling historical and current ecological processes is necessary to understand global patterns of biodiversity because the composition of communities is constrained by the evolutionary history of the regional species pool (Ricklefs 2004). A number of mechanisms explaining which species from the regional species pool colonize and interact to form a community was proposed and coined with the well-known name assembly rules (Diamond 1975). Thus both regional and local species assemblages are dynamic entities constituted by mixtures of species originated during different geological times, and therefore the historical information provided by phylogenies is needed to obtain a complete picture of community assembly processes.

Facilitation: ecological interaction in which at least one species is benefitted and neither is harmed

Assembly rule: the mechanisms that allow species from the regional pool to colonize and interact to form a community

This review aims to elucidate how the phylogenetic relatedness of co-occurring species provides insight into the role of facilitation in community assembly and discusses the profound implications for the maintenance of biodiversity at local and global scales.

HOW TO CONSTRUCT A PLANT COMMUNITY PHYLOGENY

A phylogenetic tree contains information on (*a*) how multiple species are related to each other (topology) and (*b*) when those species diverged (chronology). The tree can be assembled by using published phylogenies or can be constructed de novo by sequencing the DNA of all the species in the community with a barcoding approach. A more detailed procedure of how to make a phylogeny is described by Roquet et al. (2013).

Tree Assembly From Published Phylogenies

Based on the work of the angiosperm phylogeny group (**http://www.mobot.org/mobot/research/APweb/**), a robust phylogeny of the angiosperm families is available for ecologists to assemble the phylogenies of the species coexisting in their study communities. The software Phylomatic (Webb & Donoghue 2005) grafts the species of the community into the angiosperm phylogeny according to the families they belong; then, the families lacking in the community are pruned and the topology of the phylogeny of the community is obtained. New versions of Phylomatic allow one to include within-family resolution.

Chronological information of the tree can be obtained by dating some of the nodes in the tree, ideally with fossil data, and adjusting the dates of the rest of nodes. Two approaches can be applied to such adjustment:

Nonmodel-based approach. Non-model-based approaches, like that used by the branch length adjuster (BLADJ) algorithm in Phylocom (Webb et al. 2008), do not follow an evolutionary model but a simple mathematical rule. The BLADJ algorithm, for example, assigns branch lengths by evenly distributing the undated nodes between the known parent age and the known daughter age.

Model-based approach. Model-based approaches, like that used by the program BEAST (Drummond & Rambaut 2007), follow an evolutionary model, like a birth-death process. This program allows fixing nodes of known age and resolves the undated nodes under a Bayesian approach where a number of evolutionary models can be specified.

Barcoding

DNA barcoding aims to find a few regions of DNA that can be used to identify all the species of the world. Kress et al. (2005) provided the first example of barcoding to identify flowering plants, and they were also the first to construct a plant community phylogeny (Kress et al. 2009). They showed that sequencing a simple three-locus DNA barcode was enough to reconstruct the community phylogeny of a tropical forest in Panama. This approach is becoming more popular owing to the cheaper costs of sequencing. International initiatives, like the Consortium for the Barcode of Life (CBOL) Plant Working Group, are trying to find a robust and effective barcode for plants (Hollingsworth 2011). Advances in barcoding will undoubtedly provide valuable steps forward in the area of community phylogenetics. A review of these advances is provided by Hollingsworth et al. (2011).

2. FACILITATION AND NICHE CONSERVATISM

Hutchinson (1957) made a distinction between fundamental and realized niche; the first referred to abiotic conditions under which a species persists, and the latter to the conditions under which the species persists in the presence of competitors and predators. According to this categorization, the realized niche would always be narrower than the fundamental niche owing to the negative effects of ecological interactions (**Figure 1*a***). This conceptual construct was a major

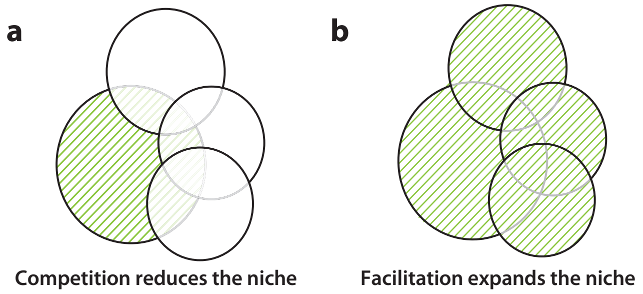

Figure 1

The central circle in each panel represents the fundamental niche of a species. The three peripheral circles represent (*a*) competitive species and (*b*) facilitative species. The realized niche (*green hatched areas*) is always narrower than the fundamental niche in the presence of competitors (*a*) but can be expanded by the effect of facilitators (*b*).

methodological advance for experimental designs to demonstrate the existence and impact of competition in the communities (Fonteyn & Mahall 1981). Grubb (1977) proposed the concept of a regeneration niche, indicating that the diversity of strategies in the species regeneration patterns favors coexistence in plant communities. Facilitation promotes diversity of regeneration niches and may thus maintain species richness in communities (Valiente-Banuet & Verdú 2007). Liancourt & Tielbörger (2011) experimentally demonstrated that nurse species enabled ecotypes of *Brachypodium distachyon* from the Mediterranean extreme of the Dead Sea–Jordan Valley environmental gradient to grow and reproduce in the arid extreme. Thus, the expansion of the regeneration niche that nurses produce for stress-intolerant species also applies to particular ecotypes within a species allowing them to colonize new environments. This parallelism confirms the potential evolutionary consequences of facilitation and opens promising research avenues.

The growing evidence that closely related species with disjunct distributions have maintained their fundamental niche features through evolutionary time (Wiens & Graham 2005) supports the hypothesis that the niche evolves in a conserved manner. This pattern, known as phylogenetic niche conservatism (**Figure 2*a***), has been a central but highly debated theme for understanding the processes that organize communities (Wiens & Graham 2005). For example, Ricklefs & Latham's (1992) classic work found that herbaceous species that diverged between 10 and 30 Mya show similar distribution patterns in Asia and North America. They interpreted this similarity as the conservation of ecological features that affect the current distribution of the species. The development of comparative biology in a rigorous phylogenetic context has provided a renewed view of the patterns of similarity and divergence of traits defining the niche between related species (Ackerly 2003). Interspecific interactions comprise a substantial part of the niche of species, and interestingly, a general pattern in the organization of biological systems through evolutionary time is mediated by a marked conservatism of ecological interactions across the entire Tree of Life (Gómez et al. 2010).

Nurse species: species that provide the microhabitat for the establishment of other species

Phylogenetic niche conservatism: evolutionary tendency of lineages to maintain their ancestral ecological features, including habitat preferences of juveniles and adults

Current plant communities are the product of historical sorting processes and, therefore, include mixtures of floristic elements originated in different geological times. Paleoenvironmental reconstructions using foliar traits (Wolfe 1995) have shown that many of these floristic elements evolved under different ecological scenarios and have persisted through dramatic changes in global climate. Undoubtedly, one of the most important floristic sorting periods to affect modern plant communities occurred during the shift from the wet Tertiary period to the unusually dry Quaternary when most deserts developed (Valiente-Banuet et al. 2006). The fact that species now inhabit a different environment than that in which they originated and to which they probably

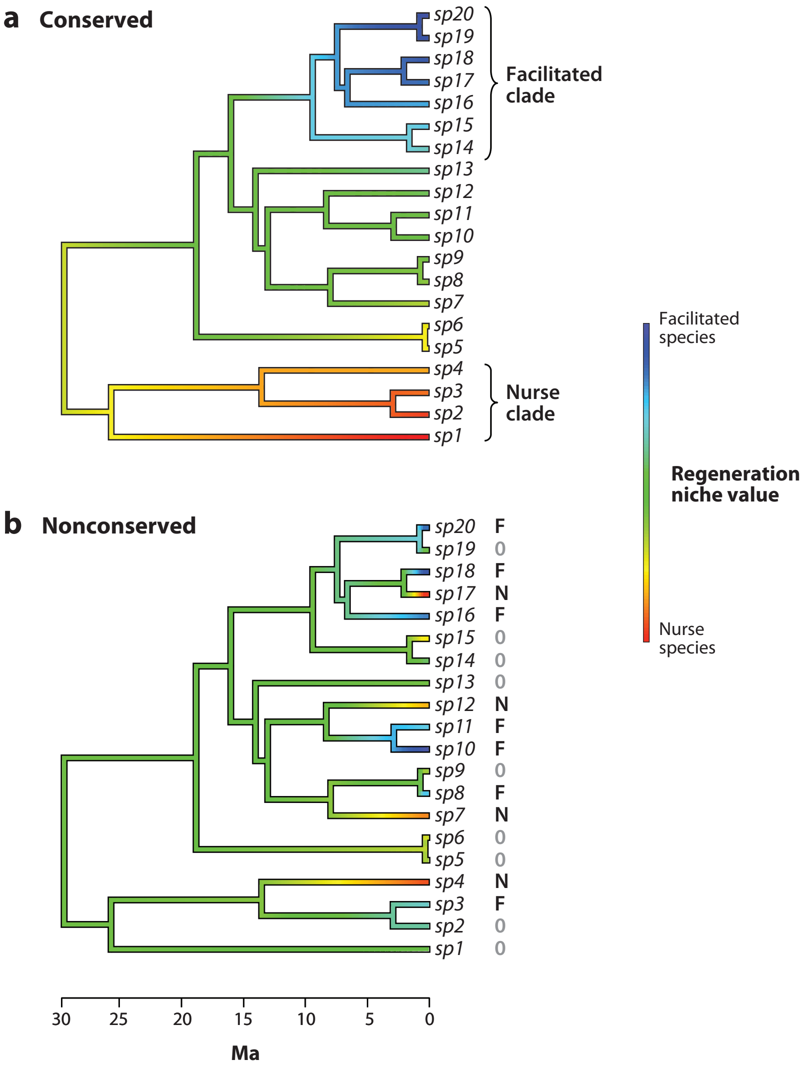

Figure 2

Two scenarios of regeneration niche evolution reconstructed onto a dated (in millions of years, Ma) phylogenetic tree. Niche is scored as a quantitative trait reflecting the habitat where species recruit. The scale shows a gradient ranging from high levels of solar radiation, extreme temperatures, and low moisture levels (*red*) to the opposite environmental conditions (*blue*). Red values are typical of the regeneration niches of nurse species, whereas blue values are indicative of the regeneration niches of facilitated species. (*a*) Closely related species tend to have similar niches under conserved evolution, and therefore the association between a nurse and a facilitated species tends to occur between distantly related species. (*b*) Niche similarity between species cannot be predicted from a phylogeny under nonconserved evolution, and therefore the association between a nurse, N, and a facilitated species, F, does not leave a phylogenetic signature. 0 indicates species that are neither nurse nor facilitated.

were adapted poses a question about the mechanisms that allowed them to persist in a suboptimal environment. Species may commonly exist in suboptimal environments, challenging the largely held idea that species in communities are perfectly adapted to their current habitat and suggesting instead that species cannot do it by themselves but through beneficial interactions. Following this rationale, Valiente-Banuet et al. (2006) hypothesized that there should be a correlation between the characteristics of the environment in which individual taxa evolved and contemporary features of the regeneration niche of these species. They found that most woody taxa present in Mediterranean ecosystems that originated during the Tertiary and evolved in woodlands recruit through facilitation under the canopy of shrubs. Facilitative interactions were particularly critical during the transition from the mesic Tertiary to the arid Quaternary environment. This environmental change promoted the evolution of new taxa that are characterized by stress tolerance and the ability to regenerate in areas devoid of vegetation (Verdú & Pausas 2013). These recently evolved taxa generate more benign microenvironments under their canopy favoring the regeneration of ancient Tertiary species during succession (Valiente-Banuet et al. 2006). These results were consistent with the fact that facilitative interactions increase in intensity and importance as abiotic stress level increases (Hacker & Gaines 1997, Michalet et al. 2006, He et al. 2012). Consequently, facilitation increases biodiversity by ameliorating harsh environments (Valiente-Banuet & Ezcurra 1991, Gómez-Aparicio et al. 2004) through the expansion of the realized niches of the less tolerant species (**Figure 1*b***) (Bruno et al. 2003). Evolutionary conservatism of traits, life histories, and ecological characteristics is a common characteristic across most evolutionary lineages (Webb 2000, Blomberg et al. 2003, Cavender-Bares et al. 2004). Therefore, the evolutionary relatedness across species provides information about the traits they possess and the ecological processes affecting their distribution and abundance (Kraft et al. 2007). According to the widespread conservatism of many ecological traits, the regeneration niche was analyzed in a large worldwide database of species and shown to be strongly conserved (Valiente-Banuet & Verdú 2007). The salient picture of regeneration niche conservatism is that nurse species facilitate distantly related species, suggesting that at the community level, facilitation increases the phylogenetic diversity of the community (**Figures 2*a*** and **3**).

Overall, these findings contrast with the perception that interdependent processes among plant species are insignificant over evolutionary time frames, which is an idea underlying both the concept of communities as a mere coincidence of constituent species (Gleason 1926) as well as the development of neutral model theory on biodiversity (Hubbell 2001). Furthermore, these results have important implications for the prediction of the species response to global change. Particularly, predictions have been made considering only the fundamental niche (Davis et al. 1998); however, the effect of climate change will be determined by interactions with other species. The phylogenetic framework used by Valiente-Banuet et al. (2006) has proved to successfully predict phenological or range shifts attributed to recent climate change. Buckley & Kingsolver (2012) show that both traits and climate change responses tend to be phylogenetically conserved.

3. FACILITATION AS A COMMUNITY ASSEMBLY RULE

The search for general community assembly rules explaining patterns of species co-occurrence and morphology has been a traditional research avenue in community ecology. Proposed assembly rules included constant body-size ratios, favored states, guild proportionality, species nestedness, competitive interactions, and trait-environment associations (Gotelli & McCabe 2002).

The rationale of facilitation as an assembling mechanism relied on the previous finding described above that facilitation among plants is affected by the evolutionary relationships of species within communities. These results showed that (*a*) the regeneration niche is evolutionarily

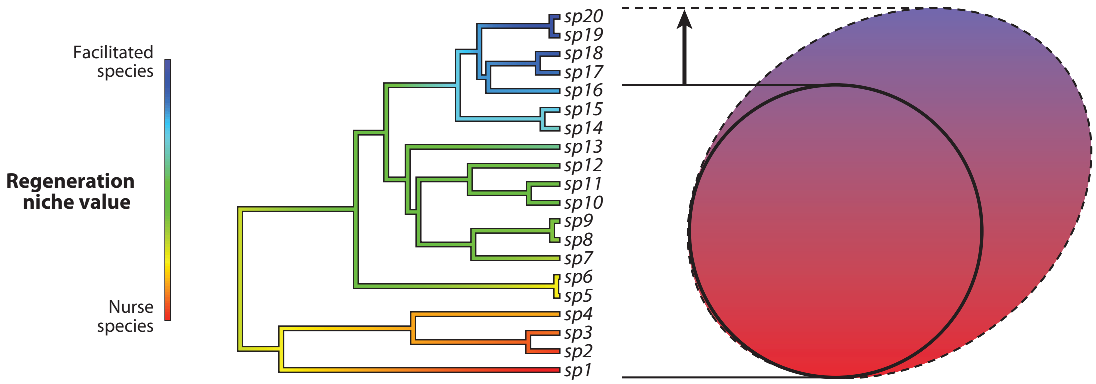

Figure 3

Colors in the phylogeny represent the regeneration niche values as in **Figure 2**. The red color of the circle represents the predominant environmental conditions in the community (e.g., high levels of solar radiation, extreme temperatures, and low moisture levels). Under these conditions, blue-colored species are not able to enter the community. The oval represents the modification of environmental conditions produced by nurse plants. Under these newly modified environmental conditions, blue-colored species may enter the community through facilitation. When the regeneration niche is conserved (as similarly depicted in the phylogeny in **Figure 2*a***), the new species entering the community tend to be distantly related to their nurses, and therefore facilitation increases the phylogenetic diversity of the community.

conserved and (*b*) lineages originated during the Quaternary facilitated those lineages evolved in the Tertiary (Valiente-Banuet et al. 2006), and therefore it was hypothesized that positive interactions should tend to occur between phylogenetically distant species and ultimately lead to phylogenetic overdispersion of the community (**Figures 2*a*** and **3**).

This hypothesis was first tested in Mexican desert plant communities (Valiente-Banuet & Verdú 2007) and later on Mediterranean shrublands (Verdú et al. 2009) and semiarid Mediterranean perennial grasslands (Soliveres et al. 2012a). In the Mexican desert communities, the mean phylogenetic distance between nurses and facilitated species was 240 Ma, which was significantly higher than the 226 Ma expected between two randomly selected species in the community. Similarly, in Mediterranean shrublands, the mean phylogenetic distance between nurses and facilitated plants was 314.3 Ma; this distance was higher than the null expectation (279.3 Ma). In semiarid perennial grasslands, phylogenetic distances higher than 273 Ma to the nurse *Quercus coccifera* led to facilitation, whereas values between 207 and 273 Ma resulted in competition. Interestingly, this range of mean phylogenetic distances between nurses and facilitated plants occurring in natural communities (240–314.3 Ma) contains the minimum phylogenetic distance ensuring maximum benefits of facilitation. Verdú et al. (2012) performed a meta-analysis of nurse-based restoration experiments worldwide and found that the minimum phylogenetic distance between nurse and facilitated species to enhance early survival of the latter was around 100 Ma, but much longer distances were required (260 Ma) to minimize later competitive effects on density. The fact that facilitation could be promoted between species as closely related as 100 Ma through early survival but requires longer distances to minimize competition in later stages is a clear indication that a balance between facilitation and competition exists and that such balance leaves a phylogenetic signature.

As expected from these patterns, facilitation between closely related species is rare in nature. Only 1% of more than 2,000 cases of facilitation reviewed in the literature (Bonanomi et al. 2010, 2011) occurred between congeneric species. This percentage is even lower than that occurring between conspecifics (5%); this type of interaction is considered rare in terrestrial plants (Bonanomi et al. 2010, 2011). Soliveres et al. (2012a) found that not only high (>273 Ma) but also

Phylogenetic distance: the time since divergence from the most recent common ancestor of two species

Facilitated species: species that benefit from the nurse habitat modification for their establishment low (<207 Ma) phylogenetic distances lead to facilitation. Two mechanisms have been proposed to explain the exceptional pattern of facilitation between closely related species: (*a*) trait-divergence and (*b*) indirect interactions (Beltrán et al. 2012). Trait divergence between congeneric species may arise because of rapid speciation events occurring after adaptive radiation, such as that occurring in the genus *Lupinus* after the uplift on the Andes (Hughes & Eastwood 2006), or because of long divergence times between congeneric species (Beltrán et al. 2012). When congeneric species have nonconserved, divergent traits (**Figure 2*b***), competition is relaxed and coexistence allowed. For example, *Juniperus sabina* is a prostrate shrub that facilitates its congeneric *Juniperus communis*, which is an erect shrub. Similarly, *Euphorbia balsamifera* is a dendroid shrub that facilitates the congeneric *E. canariensis* that is a cactoid shrub. These simple morphological differences between congeneric species are indicative of profound physiological differences that reduce niche overlap and minimize competition (Beltrán et al. 2012). Indirect interactions involving third interplayers (mycorrhizal fungi, seed dispersers, pollinators, or pathogens) can also alleviate competition, allowing the coexistence of species that could not coexist in their absence (Callaway 2007). This point will be treated in depth below (see the section titled Multispecific Associations and Indirect Effects).

The consequence of facilitation occurring between distantly related species is that communities governed by this positive interaction are phylogenetically overdispersed, or in other words, have high values of phylogenetic diversity (Valiente-Banuet & Verdú 2007). The phylogenetic overdispersion pattern produced by plant facilitation can be masked by other assembly mechanisms pulling toward phylogenetic clustering. For example, most of the semiarid grassland communities along a climatic gradient in Spain showed a random phylogenetic structure (Soliveres et al. 2012b). However, phylogenetic randomness was not the result of a lack of effect of facilitation on the phylogenetic structure of these communities; instead, facilitation increased phylogenetic overdispersion, whereas higher rainfall increased phylogenetic clustering. Similarly, Butterfield et al. (2013) found an apparent lack of relationship between phylogenetic alpine community structure and environmental severity as a result of nurse plants producing phylogenetic overdispersion in more abiotically stressful environments and open microsites pushing toward phylogenetic clustering. These results underscore the importance of moving beyond simple dichotomies (clustering versus overdispersion; facilitation or competition versus habitat filtering) and suggest that inclusion of multiple determinants should be considered in the study of assembly mechanisms in ecological communities. Several statistical methods are now available to separate the opposing phylogenetic effects of mechanisms occurring simultaneously, like phylogenetic clustering driven by environmental filtering and phylogenetic overdispersion caused by facilitation or competition (Helmus et al. 2007, Ives & Helmus 2011).

4. BALANCE BETWEEN FACILITATION AND COMPETITION

In some cases, the initial spatial association between seedlings of facilitated plants and their nurses disappears when seedlings become adults, suggesting that facilitation may turn into competition along the ontogeny of the nurse and the facilitated species (Callaway & Walker 1997, Schiffers & Tielbörger 2006). In contrast, in some other cases, adult plants remain spatially associated, suggesting that facilitation does not turn into competition with time (Pugnaire et al. 1996, Armas & Pugnaire 2005). Multiple shifts between facilitation and competition may occur not only depending on the life stage of the facilitated species but also owing to spatiotemporal fluctuations in the environment (Tielborger & Kadmon 2000, Soliveres et al. 2010). For example, the effect of the nurses on facilitated plants can be positive in some years but negative in other years depending on the annual rainfall. Ultimately all this variability must be integrated across the life of the interaction to determine whether the net balance between competition and facilitation is positive (and then adults will remain associated) or negative (and then the spatial association between adults will disappear). The balance tends to be positive if the adult niche of the facilitated plant overlaps with that of its nurse and negative if both niches tend to differentiate. Although the niche is a complex trait to measure, it has been shown that a simple measure, like life form, suffices to explain niche overlap between species in plant facilitation experiments (Verdú et al. 2012). This is because life form encapsulates a complex array of phenotypic characters that are crucial in the outcome of the plant-plant interactions (Valiente-Banuet et al. 2006, Gómez-Aparicio 2009).

Based on the concept of limiting similarity determining the balance between facilitation and competition, Valiente-Banuet & Verdú (2008) proposed that the net outcome of the balance can be studied by inspecting the phylogenetic signature left by the facilitation and competition processes. Their proposal was based on the observation that closely related species tend to be phenotypically similar, and therefore they are expected to have great niche overlap and high competition. In this scenario, the phylogenetic distance between nurse and facilitated plant species should be a good proxy to detect competition. By recording which of the interactions between nurses and seedlings of facilitated species persisted later in time (i.e., when seedlings of the facilitated plants became adults) and which disappeared, they quantified that the net balance between facilitation and competition was positive for 53% and negative for 47% of the paired interactions occurring between 102 woody species in three Mexican semiarid communities. Consistent with the phylogenetic prediction, the balance was negative (i.e., early facilitative associations disappeared with time) for those interactions involving nurse and facilitated species more related than expected by chance (those averaging a distance of 235 Ma). In contrast, the balance was positive (i.e., early facilitative associations persisted in time) for interactions involving nurses and distantly related facilitated plants (those averaging a distance of 244 Ma).

Such a phylogenetic signature in the switch from facilitation to competition may not occur if the traits determining the niche are not phylogenetically conserved. In that case, phylogenetic distance is not a good proxy of niche overlap (**Figure 2*b***), and then the outcome of the interaction cannot be correctly predicted with phylogenetic information. For example, He et al. (2012) have shown that two congeners (*Suaeda salsa* and *Suaeda glauca*) differ in competitive response to the same nurse (*Tamarix chinensis*) despite the fact that both *Suaeda* species are at the same phylogenetic distance to *T. chinensis*. This is a clear example of trait divergence between congeneric species, with *S. salsa* being stress tolerant and competitively inferior and *S. glauca* being stress intolerant and competitively superior. Under a scenario of rapid trait divergence, as explained in the section above, phylogenetic information is of limited value because it is not informative for niche overlap. The importance of trait divergence for the outcome of the interaction is revealed even at the intraspecific level. Suzuki & Suzuki (2012) show how trait divergence following morphological adaptation of the palatable plant *Persicaria longiseta* to long-term grazing can shift interactions with the unpalatable plant *Urtica thunbergiana* from facilitative to competitive.

The fact that the balance between facilitation and competition was positive in more cases than negative supports the idea that positive interactions, like facilitation, and not only negative interactions, like competition, are structuring communities (Valiente-Banuet & Verdú 2008). Spatial vegetation models in semiarid plant communities now conceive facilitation as a more general driver of vegetation dynamics than previously thought (Rietkerk et al. 2004).

5. FACILITATION AND COMMUNITY DYNAMICS

The recognition of facilitation as a mechanism of succession was originally proposed by Connell & Slatyer (1977). Successional assembling processes might initiate through positive interactions such as facilitation, whereas negative interactions start to operate later in time. Facilitation and competition operate via the same mechanisms in studies of facilitation in nonsuccessional dynamics (Brooker et al. 2008), and therefore a similar phylogenetic signature would be expected to occur in both successional and nonsuccessional communities. Based on the available successional studies in Mediterranean ecosystems, Valiente-Banuet et al. (2006) found that species evolved under Quaternary arid conditions are early colonizers of open areas, which in turn facilitate the establishment of late colonizers (i.e., Tertiary elements). Through time, Tertiary species outcompete Quaternary species and become the dominant elements of the community, opening then the possibility of Tertiary species to facilitate other Tertiary species.

Based on this work, Verdú et al. (2009) assessed the phylogenetic signatures of competition and facilitation in Mediterranean successional communities by sampling over a chronosequence of postfire succession. They reported a phylogenetic overdispersed pattern when Quaternary early-colonizer species started to facilitate late-colonizer Tertiary species. This phylogenetic pattern disappeared with time, when early colonizers were competitively excluded by the Tertiary species. Similar results have been reported in studies like that by Allan et al. (2012), who show that facilitation and competition led to an increase of the phylogenetic overdispersion of a community. Raevel et al. (2012) also found, by using a multidimensional functional trait analysis, that facilitation at early stages and competition at late stages influence niche differentiation of resource acquisition. Thus during succession, there is a loss of phylogenetic diversity produced by competitive exclusion of early colonizers by late colonizer species. Afterward, late colonizers may facilitate other late colonizer species in a cyclical manner (McAuliffe 1988, Callaway & Davis 1993).

Similar processes to those found in successional communities have been reported in nonsuccessional communities, such as North American deserts, although in these communities early colonizers do not disappear from the community (McAuliffe 1988, Verdú et al. 2009). In these communities, cycles of interspecific patterns of replacement result in sequential changes in the occupancy of a small area by individual plants and not a shifting mosaic of communities (Callaway & Davis 1993). Early colonizers, such as *Ambrosia dumosa* and *Ambrosia deltoidea* (McAuliffe 1988) in the Sonoran Desert and *Mimosa luisana* in the Tehuacán Valley (Valiente-Banuet & Ezcurra 1991), initiate the dynamics by facilitating a high percentage of species of the community. Later, all the species replace each other without disappearing from the community, and therefore there is not a reduction in the phylogenetic diversity as in Mediterranean successional communities (Verdú et al. 2009). This would be an example in which the same process (competition) may lead to a different phylogenetic community structure. However, both successional and nonsuccessional dynamics would be exactly the same when the competitive exclusion of early colonizers by late colonizer species does not occur. This may happen when late colonizers do not crowd the space and leave open spaces available for the recruitment of early colonizer species. Future efforts need to clarify this aspect in order to disentangle the trajectories and the phylogenetic signatures of facilitation and competition during dynamics.

In the extreme, there are communities in which all the species only recruit through facilitation (Valiente-Banuet & Verdú 2007). This means that there are no species able to recruit in open space, and consequently dynamics follow a cycle in which species X facilitates Y, which in turn facilitates Z and in turn facilitates X. These cyclical dynamics may reflect the historical inertia of past vegetation living in more humid conditions where all the species recruited associated to other species. Aridity in these areas has increased very recently (M. Canul, E. Ramírez, E. Martínez, J. Ortega, J. Medina, & A. Valiente-Banuet, unpublished data), and therefore the absence of species able to recruit in open space triggering succession may reflect a time lag for species to evolve a stress-tolerant strategy.

6. MULTISPECIFIC ASSOCIATIONS AND INDIRECT EFFECTS

Most of the studies previously described are based on pairwise species interactions despite the well-known fact that species in nature are immersed in a complex network of interactions involving a large number of species (Bascompte & Jordano 2007). To get a better understanding of how plant facilitation preserves biodiversity in complex ecological communities, we clearly need to move away from the study of pairwise interactions and begin to study the real world of multispecific systems, where many species are interacting simultaneously (Stanton 2003).

Multispecific patches are the arena in which coexistence develops among different phylogenetic groups within communities. Phylogenetic relationships among co-occurring species within the patch have been shown to be useful to predict individual performance and species coexistence. Castillo et al. (2010) experimentally demonstrated that survival and growth of the cactus *Neobuxbaumia mezcalaensis* inhabiting multispecific patches sequentially depended on the phylogenetic distances to its nurse, to its nearest relative, or to all its neighbors. Seedling establishment of *N. mezcalaensis* increased under distantly related nurses, especially as a result of the low number of seedlings emerging under conspecific nurses. This fact is consistent with the rareness of self-facilitation in nature (Bonanomi et al. 2010). When facilitated seedlings grew up, the phylogenetic distance to the nurse became irrelevant, and it was the distance to the neighbors in the multispecific patch that was driving the performance of the seedlings. In the three first years, the growth of the established seedlings was positively correlated with the phylogenetic distance to the nearest relative, suggesting strong competition with closely related neighbors because of the similarity in their niches. Finally, survivorship of juveniles (3–14 years) was not dependent on the nearest relative but on the interactions with all its neighbors in such a way that survival was maximized under a phylogenetically diverse neighborhood.

Phylogenetic separation promotes species coexistence in vegetation patches by enhancing facilitation and reducing competition. Supporting this idea, the highest seed crops of *Mimosa luisana*, a key nurse in Mexican deserts, occur in individuals inhabiting patches with distant relatives (L Sortibrán, M. Verdú, & A. Valiente-Banuet, submitted). This finding demonstrates that not only facilitated species but also nurses may obtain benefits from the facilitation interaction, opening thus the possibility to consider facilitation as a mutualism in which multiple distantly related partners affect fitness reciprocally. The mutualistic nature of facilitation is a research avenue deserving further effort (Bronstein 2009). Coexistence of species in multispecific patches is thus enhanced by living in phylogenetically diverse neighborhoods.

Living in multispecific patches also produces many indirect interactions with third interplayers, such as mycorrhizal fungi or pathogens. Indirect interactions allow species coexistence because they tend to be positive and to alleviate the direct competitive effects (Callaway 2007). Indirect facilitation may occur when the indirect positive effect of one species on another, via the suppression of a shared antagonist (e.g., pathogen) or via the facilitation of a shared mutualist (e.g., mycorrhizal fungi), is stronger than the direct competitive effect (Levine 1999). Most of the research on the importance of third interplayers in the outcome of plant facilitation interactions has focused on belowground microorganisms (Van der Heijden & Horton 2009, Van der Putten 2009), and phylogenetic signatures are also emerging in these complex networks of interactions (Montesinos-Navarro et al. 2012a,b).

A well-known belowground process related to facilitation is the establishment of fully mutualistic symbiotic associations between plants and mycorrhizal fungi (Casanova-Katny et al. 2011). Plants provide carbon compounds to the fungi. In return, fungi provide multiple functions to plants, such as nutrient supply limitation, protection against pathogens and toxic compounds, and an increase of nutrient uptake thanks to the mycelium being extended over a large surface area

(Selosse et al. 2006; Sikes et al. 2009, 2010). The mycelium can interconnect many plants, forming a mycorrhizal network through which resources are shared (Van der Heijden & Horton 2009). Facilitated plants may benefit from plugging into the mycorrhizal networks established between the adult plants acting as nurses. Ultimately, mycorrhizal fungi, by enhancing plant nutrient uptake, could alleviate competition among plants allowing their coexistence (Fitter 1977, Malcová et al. 1999). This scenario seems to be the most frequent, as shown by a recent review indicating that plugging into the network of adult plants was positive for seedling growth in 48% of the cases, negative for 25%, and neutral for 27% (Van der Heijden & Horton 2009).

Phylogenetic signal: the tendency of closely related species to resemble each other morphologically or ecologically

The growth benefits for plants have been experimentally shown to be dependent on the phylogenetic diversity of the fungi with which they interact; plants interacting with a suite of distantly related fungal species grow larger than plants interacting with a suite of closely related fungi (Maherali & Klironomos 2007). This outcome reflects the phylogenetic conservatism of functional traits in fungi (Powell et al. 2009); distantly related fungi tend to be functionally different and therefore to provide plants with more complementary functions (i.e., pathogen protection and phosphorous uptake) than closely related fungi, which tend to be functionally redundant.

For these benefits to occur, plants should be selecting the fungi with which to interact. In contrast to the traditional view of a lack of specificity in the interaction between plants and mycorrhizal fungi, recent complex network analyses show that these interactions do not occur at random in nature, but follow a nested pattern like many other mutualistic interactions (Chagnon et al. 2012, Montesinos-Navarro et al. 2012a). Another line of evidence supporting that plants and mycorrhizal fungi do not interact at random in natural communities is the existence of a phylogenetic signal in the interaction (Montesinos-Navarro et al. 2012b). The identity of the fungi with which each plant interacts is crucial to establish a long lasting facilitative interaction with other plants because facilitation is stronger between pairs of plant species differing in their associated mycorrhizal fungi, suggesting that different fungi provide complementary and not redundant functions (Montesinos-Navarro et al. 2012b). An important complementary function provided by different species of mycorrhizal fungi is protection against pathogens (Sikes et al. 2009). Using structural equation modeling to analyze greenhouse experiments, Sikes et al. (2010) detected that changes in plant biomass were associated with different mycorrhizal lineages providing different functions (phosphorous uptake and protection against pathogens) for different plant species. The complexity of interactions between plants, mycorrhizal fungi, and pathogens can also be deciphered in natural communities, where structural equation modeling has revealed that a high phylogenetic diversity of mycorrhizal fungi promotes facilitation among plants both directly and indirectly through the reduction of phylogenetic diversity of pathogenic fungi (A. Montesinos-Navarro, J. G. Segarra-Moragues, A. Valiente-Banuet, & M. Verdú, submitted).

Altogether these results highlight the importance of the phylogenetic identity of the neighbor plants to establish a positive interaction. Mesocosm experiments indicate that plants are able to integrate information not only about nutrients but also about neighbors in such a way that foraging strategies are strongly modified by the presence of a competing neighbor (Cahill et al. 2010). If plants may proactively modify their behavior to avoid competition with neighbors, it is tantalizing to hypothesize that plants may also modify their behavior to cooperate with plants that provide them with additional resources, as complementary mycorrhizal fungi or shared defenses.

7. COEXTINCTION CASCADES

Positive interactions occurring in ecological communities form complex networks with a well-defined architecture contributing to biodiversity persistence (Rezende et al. 2007). Similarly, the rate at which these species go extinct depends on the structure of the network and the phylogenetic signature of the interactions (Rezende et al. 2007). Network thinking has permeated many fields of ecology and evolution, resulting in a recent explosion of studies on the properties and consequences of network structure in biological systems (Proulx et al. 2005). As a result of the traditional overlook of positive interactions in the field of ecology and evolution, most ecological networks were developed to study negative interactions, especially predation (food webs). It was not until 1987 that positive interactions appeared formally analyzed in the ecological network literature (Jordano 1987). Since then, we have found that networks involving positive interactions, for example mutualisms between seed dispersers and plants, pollinators and plants, or cleaner and client fishes, share common properties (Bascompte & Jordano 2007). All these networks are characterized by a nonrandom nested structure of interactions in which specialists tend to interact with a subset of the species with which generalists interact. The nested structure of the network makes communities robustly protected against extinction (Memmott et al. 2004).

Facilitation network: a set of nurse species connected with facilitated species through facilitation interactions

Following this framework, Verdú & Valiente-Banuet (2008) proposed to visualize the complexity of multiple facilitation interactions as a network constituted by nurse species interacting with their facilitated species. The analysis of facilitation networks of Mexican desert communities revealed similar properties as mutualistic networks. Nurses and facilitated species do not interact randomly but follow a highly nested pattern in which a few generalist nurses facilitate a large number of species while the rest of the nurses facilitate only a subset of them. As generalist nurses tend to be the most abundant species in the community, the nested pattern of interactions confers to communities governed by facilitation robustness against extinction. This result at the ecological scale supports the evolutionary role of facilitation buffering older lineages from extinction along the Tertiary-Quaternary climatic change (Valiente-Banuet et al. 2006).

Evolutionary conservatism of ecological interactions occurs in all types of interactions and across the entire Tree of Life, indicating that closely related species tend to interact with the same set of species (Gómez et al. 2010). Facilitation interactions are not an exception, because closely related species tend to recruit under the same nurses in the Mexican desert communities governed by facilitation (Verdú et al. 2010). This phylogenetic signal in the interaction through the phylogeny of the facilitated species is consistent with the evolutionary conservatism of the regeneration niche (Valiente-Banuet & Verdú 2007). By contrast, nurses were indifferent to the phylogenetic identity of the seedlings recruiting beneath their canopies because a phylogenetic signal through the nurse phylogeny was not found in any of the facilitation networks analyzed. However, such a signal appeared when facilitated seedlings became adults, indicating that nurses were no longer indifferent to the phylogenetic identity of their associated species. In these adult networks, a phylogenetic signal through the nurse phylogeny indicates that closely related nurses behave similarly in terms of competition with their facilitated species (Verdú et al. 2010). Ultimately, the phylogenetic signal of the interaction between nurses and facilitated species depends on the net balance between facilitation and competition. Phylogenetic information can be used to predict the properties of a facilitation network, such as nestedness and connectance observed in real plant communities, and provide evidence that plant-plant species interactions lead to highly species-specific networks in which the phylogenetic history has a pervasive influence not only on recruitment but also on adult community composition (Verdú & Valiente-Banuet 2011).

An important result from the recognition of the existence of a phylogenetic signal in the facilitation networks is that communities governed by facilitation are more prone to the loss of phylogenetic diversity following an extinction event (Rezende et al. 2007). This outcome is produced because the extinction of several nurses can encompass the extinction of entire clades containing closely related facilitated species. For that reason, it is crucial to have good predictive tools about the dynamics of the communities governed by facilitative interactions. Fortunately, the topology of plant facilitation networks also contains information on the dynamics of the community, the so-called strongly connected components, and it can be demonstrated that facilitation networks exhibit high persistence and robustness against extinction (Alcántara & Rey 2012).

8. BIODIVERSITY MAINTENANCE, SUSTAINABLE DEVELOPMENT, AND COMMUNITY ECOLOGY IMPLICATIONS

All the phylogenetic information that has proven useful in the study of community assembly mechanisms through facilitation might also be useful for conservation purposes. Current threats to biodiversity, such as biological invasions or human overexploitation of natural resources, can be studied under the same phylogenetic framework. The inclusion of phylogenetic data as a proxy for trait similarity for functional traits that are difficult to obtain is currently one of the cost-efficient measures suggested to monitor restoration of biodiversity-based ecosystem services (Montoya et al. 2012). A current concern in conservation biology is the increasing risk of biological invasions leading to negative impacts in natural ecosystems. Facilitation has been invoked as a mechanism producing invasional meltdown, a process in which the negative impacts produced by one invader are magnified by the positive interactions established with another exotic species (Simberloff & Von Holle 1999). Invasional meltdown is produced when an alien species facilitates others, creating a cycle that benefits both invaders. The rationale behind this hypothesis relies on two characteristics of facilitation recently described: (*a*) cyclical dynamics (Verdú et al. 2009) and (*b*) its mutualistic nature (L. Sortibrán, M. Verdú, & A. Valiente-Banuet, submitted). As explained above, these two characteristics have a typical phylogenetic signal left by the fact that nurses usually facilitate, and benefit from, distantly related species. According to this, Parker et al. (2012) has shown that phylogenetic distance is a good predictor of plant success in both native and exotic plant species. These findings support that distantly related species are more likely to benefit from positive interactions with members of the recipient community and that these interactions in the recipient community can promote invasions. Thus, the use of phylogenetic information between invader species may be useful to predict invasional meltdowns.

Human overexploitation of natural resources may produce local extinctions of species. As explained above, the phylogenetic structure of facilitation networks results in great losses of phylogenetic diversity after the extinction of key nurse species in the community (Rezende et al. 2007, Verdú et al. 2010). A dramatic coextinction process has been documented in a desert Mexican community following the human overexploitation of nurse plants for wood (Valiente-Banuet & Verdú 2013). Coextinctions in facilitation networks reverberate in other concomitant networks ultimately collapsing ecosystem services like pollination and seed dispersal and pushing the ecosystem to a point of no return where natural regeneration does not occur. The current challenge is thus to use our knowledge of phylogenetic and complex network methods underlying facilitation processes to apply restoration and sustainable management practices. A combination of phenotypic and phylogenetic information has proved to be a useful tool in nurse-based restoration practices (Verdú et al. 2012), opening the potential for focusing on interaction networks in restoration rather than only on species.

9. FUTURE AVENUES

Phylogenetic information has proven to be a successful proxy for both plant traits and niches in determining the outcome of plant interactions. The most obvious advance in this field is the ability to obtain better resolved and dated phylogenies accurately describing the relationship between species. Paradoxically, a more complete understanding of the outcome of plant interactions will arrive once phylogenetic information becomes unnecessary because all the relevant information on plant traits and niches is already known. But we are still very far from having complete phenotypes or even from knowing which are the important traits determining the outcomes of interactions. For that reason, obtaining good phenotypic characterization to combine trait-based and phylogeny-based approaches is a promising research avenue. For example, interesting advances in the characterization of chemical phenotypes in ecological studies have recently developed through ecometabolomic techniques (Sardans et al. 2011).

Phenotypic plasticity is another characteristic that needs to be integrated in future studies of facilitation because plasticity may modify the outcome of interactions between plants. Semchenko et al. (2012) show that plant species with limited morphological plasticity depend more heavily on neighbors for microhabitat enhancement, whereas more plastic species are able to minimize the negative effects of harsh microenvironmental conditions produced in the absence of neighbors. Interestingly, phenotypic plasticity, at least for root morphology in response to soil nutrient heterogeneity, is phylogenetically conserved (Kembel & Cahill 2005). Again, phylogenetic information seems a promising tool to predict the response of facilitated species to the nurse effect of neighbors as a function of the phenotypic plasticity.

Integration of community phylogenetics with the modern theory of coexistence, where relative fitness differences between species depends on the magnitude of intraspecific competition (Chesson 2000), is currently a road to pave (Mayfield & Levine 2010). To do that, HilleRisLambers et al. (2012) propose to combine traditional community phylogenetics studies with experimental manipulations of the abiotic or biotic environment and demographic investigations of frequency-dependent population growth. Incorporating experimental approaches where the phylogenetic neighborhood is modified will allow researchers to unambiguously determine the cause and effect of phylogenetic relationships between nurse and facilitated species in facilitation studies (Weber & Agrawal 2012). With demographic studies, we will obtain a picture of the demographic rates of component species beyond the static view of the composition of communities. At present, most of the information that phylogenetics has provided regarding community dynamics comes from temporal snapshots. Integrating phylogenetic information as simple rules governing the community assembly into Boolean networks would help to predict possible trajectories of community dynamics (Campbell et al. 2011).

10. CONCLUSIONS

Plant facilitation is a positive interaction preserving the phylogenetic diversity of ecological communities because it occurs between lineages with different evolutionary histories. The expansion of the evolutionarily conserved regeneration niche produced by facilitation is the ultimate cause of the link between facilitation and phylogenetic diversity. Several proximate causes related to reduced competition and/or increased mutualism between phylogenetically distant species may simultaneously operate to maintain facilitation as a crucial interaction shaping current ecological communities. Both the evolutionary and mechanistic explanations of how phylogenetic diversity is maximized during the process of community assembly provide a solid conceptual framework to bridge the gap between research and conservation (Winter et al. 2012).

SUMMARY POINTS

1. Facilitative interactions occur between species with different regeneration niches.
2. The regeneration niche is evolutionarily conserved, and therefore facilitative interactions tend to occur between distantly related species.

3. Ecological communities governed by facilitation have high phylogenetic diversity.
4. Facilitative interactions shifting to competition over time are those occurring between closely related nurse and facilitated species.
5. The balance between facilitation and competition leaves a phylogenetic signature that allows the study of different ecological processes, such as succession, regeneration dynamics, indirect interactions, and coextinction cascades.

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