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Trait divergence and indirect interactions allow facilitation of congeneric species

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• *Background* Plant facilitation occurs when the presence of a plant (i.e. a nurse plant) modifies the environment, making it more favourable for the establishment and survival of other species (i.e. facilitated plants), which can germinate and grow nearby. Facilitative associations can be maintained or turned into competition as the facilitated seedling grows. According to the competition-relatedness hypothesis that suggests that closely related species tend to compete more, facilitation turns into competition between phylogenetically close species. However, some examples of facilitation between congeneric species, which are supposed to be closely related species, have been found in nature.
• *Scope* In this work, some examples of congeneric facilitation and subsequent coexistence are reviewed and an attempt is made to explain those exceptions to the competition-relatedness hypothesis.
• *Conclusions* Two mechanisms are proposed that can switch the facilitation–competition balance: trait divergence and indirect interactions. When traits have diverged within the genus, the niche overlap is reduced and competition relaxed, thus allowing the coexistence of congeneric species. The presence of third interplayers (mycorrhizal fungi, seed dispersers, pollinators or pathogens) participating in the interaction between plants can alleviate the competition or enhance the reproduction and allow the coexistence of species that could not coexist in their absence.

Key words: Associational defences, competition, facilitation, indirect interactions, mycorrhizal networks, phylogenetic relatedness, pollination, seed dispersal, trait divergence.

INTRODUCTION

Plant facilitation occurs when the presence of a plant (i.e. a nurse plant) modifies the environment, making it more favourable for the establishment and survival of other species (i.e. facilitated plants). Environmental enhancement by nurse plants may be produced by weakening either biotic or abiotic stress, or resource limitation. When facilitation occurs, there are two possible outcomes depending on the effects that the facilitated plant may have on the nurse plant: the replacement of the nurse species by the facilitated species in a process of succession, or the coexistence of both species (McAuliffe, 1984; Verdú *et al.*, 2009). If the presence of the facilitated plant has stronger negative than positive effects on the nurse plant, the nurse plant will be replaced. If the balance between costs and benefits is neutral or positive, a commensalistic or mutualistic interaction is possible, and then both species can coexist (Valiente-Banuet and Verdú, 2008). Thus, the outcome of the interaction depends on a balance between positive (facilitation) and negative (competition) effects (Callaway and Walker, 1997; Brooker and Callaghan, 1998).

The balance between competition and facilitation depends on several factors such as stress and resource gradients (Brooker and Callaghan, 1998: Pugnaire and Luque, 2001; Van der Putten, 2009), the degree of niche overlap (Dickie, 2005), the life stage of the plants (Verdú *et al.*, 2010) or the presence of indirect interactions (Castillo *et al.*, 2010). Despite this large number of factors potentially affecting the balance between facilitation and competition, Valiente-Banuet and Verdú (2008) demonstrated that the phylogenetic distance between the nurse and the facilitated plant is a good proxy to assess final balance. The underlying rationale of this proxy is Darwin's idea that congeneric species are similar in many habits and constitution, have high overlapping niches and therefore compete more strongly than species of distinct genera (i.e. competition-relatedness hypothesis; Violle *et al.*, 2011). This pattern agrees with that found by Valiente-Banuet and Verdú (2007), who showed that nurse species usually facilitate distantly related species, which have different ecological requirements, and therefore will not compete. When the temporal persistence of the facilitative association was inspected, it was shown that facilitation turns into competition with increasing phylogenetic relatedness (Valiente-Banuet and Verdú, 2008). Accordingly, it could be predicted as a generalization that facilitation will be rare between closely related species. However, there are some examples of facilitation between congeneric species, which are supposed to be closely related, suggesting that this prediction is not always fulfilled, and that other mechanisms might be operating. However, as we discuss with specific examples, the term 'congeneric' refers to a taxonomic rank which does not always reflect short phylogenetic distances.

To find a positive relationship between competition and relatedness, it is necessary that evolutionary conservatism occurs in both traits and niches. When a positive correlation between phylogenetic distance and phenotypic dissimilarity does not exist because of rapid divergence or evolutionary convergence, closely related species can diverge in phenotype more than expected and distantly related species can be more similar than expected. The lack of correlation between phylogenetic and phenotypic distances can account for some 'unexpected' patterns of facilitation between closely related species. For example, Cahill *et al.* (2008) found in a large study involving 124 plant species that the relationships between competition intensity and relatedness were weak compared with the strong relationships between competitive ability and functional traits. Similarly, Uriarte *et al.* (2010) pointed out the importance of studying traits rather than phylogenies to explain the structure of ecological communities.

Another mechanism by which closely related species do not necessarily tend to compete as expected under the competition-relatedness hypothesis is the existence of indirect interactions. Indirect interactions tend to be positive and to alleviate the direct competitive effects (Callaway, 2007). More specifically, indirect facilitation occurs when the indirect positive effect of one species on another, via the suppression of a shared competitor, is stronger than the direct competitive effect (Levine, 1999). This author showed that *Carex nudata* has direct competitive effects on other plant species, as well as indirect facilitative effects, by suppressing a second competitor. Obviously, indirect effects cannot be detected working with pairs of species in the way in which most of the studies about facilitation have traditionally been performed. At the community level, it has been shown that the survival of a facilitated columnar cactus is better explained by the average effects of all its neighbours than by the single effect of its nurse (Castillo *et al.*, 2010). Cactus survival is maximized when the mean phylogenetic distance to all its neighbours is maximized. Indirect interactions can be promoting this coexistence of distantly related species by avoiding host-specific below-ground enemies (e.g. pathogens) or enhancing host-specific below-ground mutualists (e.g. mycorrhizae) with shared phylogenetic predilections (Van der Putten, 2009). Sharing other mutualists, such as pollinators or seed dispersers, may also produce indirect effects with potential benefits for coexisting congeneric species (Hunter and Aarssen, 1998; Sargent and Ackerly, 2008).

In this paper we will focus on trait divergence and indirect interactions (through mutualists and through associational defences) as mechanisms which may allow facilitation between congeneric species. Those mechanisms may modify the balance between competition and facilitation, either separating niches (trait divergence) or turning an antagonistic interaction ($+/-$) into mutualism ($+/+$) or commensalism ($+/0$) by indirect interactions.

TRAIT DIVERGENCE

In *The origin of species*, Darwin postulated that congeneric species tend to be similar in many ecological aspects. This idea has lasted until the present and it is currently receiving renewed interest because the availability of molecular phylogenies allows it to be tested. For example, Burns and Strauss (2011) demonstrated in an experimental test that most species germinate well at conspecific and congeneric sites and less well at confamilial and distant relative sites. This pattern is reversed later, as in terms of survival most species performed better when grown with distant than with close relatives. The authors suggest that more closely related species are more similar ecologically and that is the reason why they germinate under the same conditions. This ecological similarity also leads to species competing intensely for resources after germination, supporting the idea that closely related species have a great niche overlap and that competition may lead to exclusion of one or both species.

One of the mechanisms by which two similar species can coexist is the differential usage of resources (Tilman, 1977). By diverging in traits relevant to the uptake and use of resources, there will be a niche separation, and consequently competition will be relaxed. As the relative importance of both competition and facilitation will determine the outcome of the relationship, when competition is relaxed the relative importance of facilitation increases. During evolutionary time, species accumulate changes and can diverge one from another. Species can diverge in a trait because there has been direct selection on it, or as a by-product of selection on another trait, or because of genetic drift. Trait divergence may be due to old divergences that evolved in another ecological context (Ackerly, 2006) or to character displacement in sympatry due to direct competition (Schluter, 2000*b*; Levin, 2004). Whatever the cause of trait divergence is, it is possible that this trait had not diverged to allow coexistence of two similar species, but it can be useful for that 'goal' (exaptation *sensu* Gould and Vrba, 1982). Early divergence in niche traits can take place in the origin of the clade and can be maintained by evolutionary stasis (Case and Taper, 2000). With time, species can diversify in different habitats, maintaining the divergence in niche traits. Then, when they are brought together to coexist, the niche overlap will be less than expected by phylogenetic relatedness, competition will be less and facilitation between closely related species will be possible.

The process known as adaptive radiation can also lead to trait divergence. Adaptive radiation is the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage. It involves the differentiation of a single ancestor into an array of species that inhabit a variety of environments and that differ in the morphological and physiological traits used to exploit those environments (Schluter, 2000*a*). When colonizing a habitat with non-exploited niches, there will be a period of fast evolution, where species will diverge in order to occupy those niches. This niche divergence may, over time, allow the coexistence of closely related species which diverged during an adaptive radiation (Ackerly, 2006). Some examples are given below of coexistence of congeneric species mediated by trait divergence.

Verdú and García-Fayos (2003) have found facilitation between two species of the genus *Juniperus*: *J. sabina* and *J. communis* (Fig. 1A). They showed that *J. communis* recruits significantly better under *J. sabina* than on the open ground, and that this fact is correlated with a microenvironment modification under *J. sabina*. Trait divergence can be easily detected by inspecting the phenotypic differences between

FIG. 1. Two cases of congeneric facilitation: (A) *Juniperus communis* (erect shrub) facilitated by *Juniperus sabina* (prostrate shrub); (B) *Euphorbia balsamifera* (dendroid shrub) facilitating *Euphorbia canariensis* (cactoid shrub).

J. communis and *J. sabina*: *J. sabina* has scale-like leaves, and a prostrate and creeping growth form which develops in a centrifugal pattern to form an elliptical shrub of up to 20 m diameter; *J. communis* has needle-like leaves and grows as an erect shrub up to 2·5 m tall. A number of physiological characteristics related to gas exchange and water use efficiency are also different between both species (Verdú *et al.*, 2004). *Juniperus sabina*, because of its prostrate growth and its large diameter, is a good nurse: it can act as a seed trapper and modify the microenvironment of a relatively large area, allowing the recruitment of several species. In the presence of the drastic morphological and physiological differences mentioned above, niche overlap will be lower than expected by relatedness, competition between both species will then be relaxed and therefore their coexistence will be allowed. The balance between facilitation and competition depends in this case on the life stage. In later stages of life, *J. communis* growth is greater in isolated than in *J. sabina*-associated individuals, although *J. sabina* growth is not significantly affected by the presence of *J. communis* (Verdú *et al.*, 2004). However, even in this life stage, although competition exists, the profound trait divergence between both species must be allowing their coexistence. In an area adjacent to where Verdú and García-Fayos (2003) reported the close

association between *J. sabina* and *J. communis*, there are four congeneric junipers coexisting: *J. communis*, *J. oxycedrus*, *J. thurifera* and *J. phoenicea*. The former two species belong to the section *Juniperus* whereas the three latter species belong to the section *Sabina*. Trait divergence is notably less between species within than among sections. For example, a conspicuous difference between sections is that section *Juniperus* is characterized by needle-like leaves whereas section *Sabina* is characterized by scale-like leaves. We have recorded the frequency with which junipers grow in close proximity with species of their same section vs. the other section in four plots of 30×10 m^2 each (E. Beltrán *et al.*, unpubl. res.). While the abundance did not differ between sections (104 vs. 111 individuals in sections *Sabina* and *Juniperus*, respectively), spatial association between junipers followed a clear pattern: we found 54 cases for association between junipers belonging to different sections and only three occurring between junipers within the same section ($\chi^2_1 = 45 \cdot 6$, $P \ll 0 \cdot 0001$). This result supports the hypothesis of trait divergence-mediated coexistence.

The phenotypic differences of both species can be tracked in the phylogeny of the genus (Mao *et al.*, 2010). We find that the divergence of *J. sabina* and *J. communis* ancestors is very old; it took place 45 million years ago (Mya), at the very beginning of the clade. To put this time span in the context of the age of diversification of other angiosperms, it is remarkable that the divergence between *J. communis* and *J. sabina* is much older than some families, and even some orders. For instance, Bell *et al.* (2010) dated the most recent common ancestor of the family Ericaceae as 14 Mya and that of the order Nymphaeales as 38 Mya. In this time span, both *Juniperus* lineages have had time to diverge in some morphological and physiological parameters, ultimately leading to reduced niche overlap. Nowadays this trait divergence allows the coexistence of these two species, although it took place long before the species coexisted, and probably in another environmental context.

Other cases of congeneric facilitation are produced between species of the genus *Euphorbia*. In the Canary Islands, *E. canariensis* is facilitated by *E. balsamifera* (B. Mies, University Duisburg-Essen, Germany pers. comm.; J. Ollerton, University of Northampton, UK, pers. comm.; Fig. 1B). *Euphorbia balsamifera* is the first plant to grow near the coast on fresh lava fields and it allows other plants, such as *E. canariensis* and many shrubs, to establish underneath it (Mies, 1998). These two *Euphorbia* species have very different morphologies: the dendroid *E. balsamifera* forms an intricately branched, rounded shrub of variable height and has thick, semi-succulent, gnarled, spineless stems, while *E. canariensis* is a cactoid plant, growing to 3 m high, with succulent quadrangular or pentagonal stems. There are also great physiological differences between *E. balsamifera*, with a C$_3$ metabolism, and *E. canariensis*, with the ability for crassulacean acid metabolism (Mies and Aschan, 1995; Mies, 1998). Again, morphological and physiological differences may lead to reduced niche overlap and allow coexistence between congeners. A similar case can be found in Sidi Ifni (Morocco), where the dendroid *Euphorbia regis-jubae* facilitates the cactoid *Euphorbia officinalis* (P. Rey and J. Alcántara, Universidad de Jaen, Spain, pers. comm.).

Tracing back the divergence of the split between *E. canariensis* and *E. balsamifera* may provide information on whether the interaction has been produced recently after adaptive ecological radiation in the Canary Islands or anciently after allopatric speciation and posterior island colonization (Whittaker and Fernández-Palacios, 2007; Carine and Schaefer, 2010). By using dated phylogenies (Barres *et al.*, 2011; Christin *et al.*, 2011), we find that the most recent common ancestor of both species is very old. The two species belong to different subgenera: *E. canariensis* belongs to the subgenus *Euphorbia* while *E. balsamifera* belongs to the subgenus *Rhizanthium*. Those subgenera diverged >35 Mya. In fact, this is the maximum phylogenetic distance between two *Euphorbia* species. During that time, both lineages diverged in many ecological traits that now allow them to coexist in new environments. *Euphorbia balsamifera* is considered a remnant of the drought-adapted Tertiary vegetation of northern Africa (Mies, 1998), whereas *E. canariensis* is endemic to the Canary islands, providing evidence that each lineage evolved in different environmental contexts and that the interaction has been produced very anciently after allopatric speciation.

This long divergence time, as in *Juniperus*, would eventually fit to the hypothesis that facilitation occurs between phylogenetically distant species. In other words, congeneric species are not necessarily closely related species. It remains to be discovered whether facilitation and coexistence between closely related species mediated by rapid trait divergence after adaptive radiation has occurred in nature. A recent divergence may make it easier to identify the specific traits responsible for coexistence. In our *Juniperus* and *Euphorbia* examples, divergence was so ancient and the phenotypes so different between neighbours that we could not attribute coexistence to any specific trait. When the specific traits responsible for coexistence are unknown, phylogeny becomes helpful because it contains a lot of information about the similarity between neighbouring species not captured by our phenotypic measures (Verdú *et al.*, 2012).

INDIRECT INTERACTIONS

Sharing mutualists

Establishment of mycorrhizal associations. Coexistence can also be mediated by a third interplayer. The best studied case of indirect interactions related to facilitation is the establishment of symbiotic associations with fungi (Dickie *et al.*, 2002; Van der Heijden and Horton, 2009). Mycorrhizal networks play a key role in plant communities by facilitating and influencing seedling establishment, by altering plant–plant interactions and by supplying and recycling nutrients. Although some mycorrhizal networks can be beneficial for those who are plugged into them, that is not always the case. Mycorrhizal networks can have no effect or negative effects on the plants which are interacting through the network (Johnson *et al.*, 1997; Van der Heijden and Horton, 2009).

Mycorrhizal networks allow the exchange of resources among plants which are plugged into them. Thus, the ability to plug into the network is essential to take part in the facilitation process. As ecological interactions tend to be

evolutionarily conserved (Gómez *et al.*, 2010), closely related plants will be able to interact with the same species of symbionts and, thus, to plug into the same network. Most mycorrhizal fungi are not host specific and have intermediate to broad host ranges, although some ectomychorrhizal fungi of the Boletales order have narrow (at the genus level) host ranges (Molina *et al.*, 1992). Network specificity depends on fungus identity, plant identity and neighbourhood composition (Van der Heijden and Horton, 2009). This specificity will in turn determine which and how many species will participate in the network.

On one hand, when specificity is high only plant species which share the same symbionts will be able to plug into the network, and that is more likely if species are closely related. In this case, there will be a lot of niche overlap, but the benefits of belonging to the network may balance the greater costs of competition. On the other hand, when specificity is low we expect to have a greater phylogenetic dispersion in the network, because a wide range of plant species will be able to plug into the network and then the costs of plant–plant competition will be minimized if species have different niches (and that is more likely when species are phylogenetically distant). According to that, we hypothesize that nurse species can facilitate congeneric species when the specificity of the mycorrhizal network is high due to the evolutionary conservatism of the plant–fungus interaction (i.e. when the fungus species tends to interact with closely related species of plants (Shefferson *et al.*, 2010; Jacquemyn *et al.*, 2011). In this situation, the closer the phylogenetic distance between the nurse plant and the facilitated plant, the higher the possibility for both plants to benefit from the fungus but, at the same time, the higher the competition between them. Facilitation of conspecifics may be advantageous in terms of sharing the mychorrhizal network benefits but disadvantageous in terms of plant competition. However, facilitation of congeners may relax plant competition while benefiting from the mycorrhizal network.

The balance between the costs of competition and the benefits of sharing a mycorrhizal network has been described for congeneric *Quercus* species (Dickie *et al.*, 2002, 2005). Some species of the genus *Quercus* appear to require ectomycorrhizae to establish in a community. A lack of ectomycorrhizae seems to be a significant limitation for *Quercus*. Two cases of facilitation in the genus were studied: between *Quercus macrocarpa* and *Quercus ellipsoidalis* (Dickie *et al.*, 2005) and between *Quercus rubra* and *Quercus montana* (Dickie *et al.*, 2002). *Quercus macrocarpa* seedlings grow better when they establish near a *Q. ellipsoidalis* tree, and so do *Q. rubra* seedlings when growing near *Q. montana*. This enhanced growth is due to the establishment of a mycorrhizal network which allows greater nitrogen incorporation and the movement of carbon compounds among the plants which are plugged into the network.

The ectomycorrhizal network must have a relatively high specificity, as both ectomycorrhizae infection and seedling growth in *Q. rubra* are enhanced when growing near a congeneric (*Q. montana*), and not when growing with a phylogenetically distant species (*Acer rubrum*) (Dickie *et al.*, 2002). The advantages of sharing resources through a mycorrhizal network with a relatively high specificity are evident in terms of growth, but there are also costs in terms of competition. These costs can be inferred from the spatial distribution of trees and seedlings because *Q. macrocarpa* seedlings grow better when they establish at a certain distance from a *Q. ellipsoidalis* tree: far enough to reduce competition, close enough to share a mycorrhizal network (Dickie *et al.*, 2005).

The effects of facilitation in *Quercus* depend on life stage. The mycorrhizal network has strong positive effects on the establishment of seedlings. During the establishment, the resources allocation is critical. Plants which are not plugged into a mycorrhizal network will have to invest in maintenance rather than growth. Early establishment is a period where seedling mortality is high, and mortality can be strongly affected by plant size (Lawson *et al.*, 1999). Thus, when seedlings are plugged into a mycorrhizal network and can invest in growth in early stages of life, then they avoid the high mortality rates. From the third year, once the seedling is established, the importance of competition for light increases and the net effects of the network can decrease or even become negative, surpassing a stage of net facilitation. During the early establishment phase in *Quercus* (the first 2 years), the amount of N in the leaves is strongly correlated with mycorrhizal infection. In later stages of life (up to the third year) this correlation disappears, probably reflecting that there are other factors affecting N leaf content from this moment (Dickie *et al.*, 2005). The balance between costs and benefits along the ontogeny of the interaction will determine the net effect of the indirect association on the coexistence of the nurse with the facilitated plant.

Attraction of pollinators and seed dispersers. Other indirect effects may occur if the establishment of a plant species benefits from living in close proximity to other plant species that attract the same pollinators or seed dispersers (Hunter and Aarssen, 1998; Sargent and Ackerly, 2008). When congeneric species share pollinators or dispersers, then their coexistence may have a benefit.

The best known example of pollinator facilitation is the *Clarkia* system, in which the bee visitation rate to *Clarkia xantiana* significantly increased in the presence of pollinator-sharing congeners (Moeller, 2004). Unlike most of the plant facilitation examples involving a nurse plant facilitating another plant species beneath its canopy, *Clarkia* congeners coexist in the same community but not closely associated. The spatial separation of *Clarkia* congeners avoids the competitive effects which would arise if they were living together. Although the theoretical possibility exists that the competitive costs of living closely associated with other species can be counterbalanced by the benefits of enhanced reproduction, we do not know of any facilitation study addressing this possibility.

Similarly, congeneric species may benefit from growing associated with other species by attracting shared seed dispersers. Again, the competitive costs of living together should be compensated by the benefits of enhanced dispersal. Although facilitation examples of congeneric species sharing seed dispersers exist (Verdú and García-Fayos, 2003), there are no data comparing seed dispersal rates in associated vs. non-associated individuals to test this hypothesis. Further research is clearly needed to fill this gap.

Associational defences

Another mechanism involving a third interplayer could also operate to allow coexistence of congeneric species in a process of facilitation: when the nurse plant defends itself from an above- or below-ground pathogen, the facilitated plant can profit from this defence and contribute to it (Van der Putten, 2009).

Maillette (1988) documented a case of facilitation and coexistence involving three species of the genus *Vaccinium* which were morphologically similar. Each of the species is dominant in a different type of site: *V. myrtilloides* in shaded forests, *V. angustifolium* at krummholz sites and *V. uliginosum* at tundra sites. Her data suggest that, when establishing outside its own area of dominance, a *Vaccinium* species performs less well (in terms of biomass) than in its own area, unless it is in contact with the dominant *Vaccinium* species of the site. The dominant species, in turn, is not affected significantly by the presence of the 'foreign' species. This would establish a relationship of 'apparent' commensalism or even mild mutualism among morphologically similar congeneric species which was unexpected by the author. Maillette (1988) invoked the possibility that protection against diseases and herbivores through volatile compounds may be operating.

Although there are few documented cases in nature of this mechanism of facilitation between congeners, associational defences are well documented in heterospecific (non-congeneric) species. Associational defences can work either by communicating the presence of herbivores or pathogens through airborne signals and activating systemic defence in the neighbours (Heil, 1999), by attracting or maintaining predators or parasites of grazers (Atsatt and O'Dowd, 1976) or by hiding palatable plants from herbivores either by developing morphological (spines) or chemical (toxins, antibiotics, etc.) defences or simply because the presence of many unpalatable species masks the presence of the palatable one.

The role of morphological defences (spinescence, pubescence, sclerophylly, etc.) has been studied far less than traits related to secondary chemistry (Hanley *et al.*, 2007). While some works have shown the protective effect of spiny nurse plants on facilitated plants (Baraza *et al.*, 2006, Vandenberghe *et al.*, 2009), no studies have been carried out using a phylogenetic approach. Given the lack of specificity of the morphological defences, a clear phylogenetic pattern of plant coexistence mediated by sharing this type of defences is not expected.

Coexistence of palatable and non-palatable congeneric species has been well documented. Atsatt and O'Dowd (1976) described another case of congeneric facilitation in the genus *Trifolium*. *Trifolium repens* is an unpalatable species that, when grown mixed with the congeneric *Trifolium fragiferum*, protects this palatable species from herbivory. Another example was documented by Yeaton *et al.* (1990), where the unpalatable *Pteronia pallens* protects the palatable *Pteronia empetrifolia* from grazers through the production of a hepatotoxin (Prozesky, 1986) which prevents grazers feeding on it and the plants which live underneath it. However, there is no evidence of stable coexistence of the species cited in those examples. In the case of *Pteronia*, there are some extrinsic factors (environmental disturbance) leading to a cyclical pattern of succession that allow the coexistence of both *Pteronia* species. Coexistence in this scenario could be mediated by frequency-dependent selection: when there are many unpalatable individuals, palatable species can grow. Then both species compete and, since the palatable species does not invest in defence, it displaces the unpalatable one. However, when the unpalatable species begins to decrease, the palatable species becomes more evident to herbivores. So herbivores could mediate the coexistence of both species by weakening the density of palatable species.

As in the case of mycorrhizal associations, the coexistence of congeneric species mediated by associational defences through volatile compounds requires that species share the same pathogens and that the interaction has a certain degree of specialization (Cavender-Bares *et al.*, 2009). Since closely related species are likely to share pathogens (Gilbert and Webb, 2007) and defensive compounds in plants are conserved (Agrawal, 2007), we hypothesize that associational defences allowing facilitation between congeneric species will be very specific. If the nurse plant had a broad antibiotic spectrum, a large variety of plant species would be able to profit from this defence, and those which compete less intensely would be able to establish and to be facilitated. However, if the nurse plants have a narrow antibiotic spectrum (i.e. at the genus level), only close relatives will be able to profit from this defence. Then, benefits of defence can balance costs of competition and close relatives will be able to establish near the nurse plant. Further research is needed to test whether this theoretical scenario occurs very often in nature.

CONCLUDING REMARKS

Facilitation and coexistence of congeneric species is rare in the nature, or at least poorly documented. In this paper we have tried to explain some exceptions to the pattern of facilitation between phylogenetically distant species to better understand the mechanisms leading to that general pattern.

The first mechanism allowing congeneric coexistence is trait divergence, as in the cases of coexisting *Juniperus* and *Euphorbia* species. When congeneric species are phenotypically very different, phylogenetic distances may be not very informative about niche overlap. Interestingly, in the cases of *Juniperus* and *Euphrobia*, large phenotypic differences were indeed produced during a long evolutionary time, indicating that congeneric species are not necessarily closely related species. Cases of facilitation among phenotypically different but closely related species produced after adaptive radiation remain to be described.

Likewise, indirect interactions through third interplayers (mycorrhizae or pathogens) may also explain the coexistence of congeneric species if nurse and facilitated plants share the interplayers. Indirect interactions may be benefiting both nurse and facilitated plant species, opening up the possibility of conceiving facilitation as a mutualistic process that can be under selection. Exciting advances in the knowledge of evolution of plant–arbuscular mycorrhizal fungus mutualism show that co-operation between species can be mediated by a reciprocal game in which individuals are able actively to reward good partners or punish less co-operative ones (Kiers, 2011). Similar mechanisms may be at work among coexisting

plants. As Bronstein (2009) pointed out, the research agenda for considering the evolution of facilitation as a mutualism would focus on the study of trait evolution; the continuum from specialization to generalization; the evolutionary origins and maintenance of the interaction; co-evolution of partners; and the prevalence and implications of cheating. Indeed, we have shown that most of these factors are also necessary to explain the observed, but rare patterns of congeneric facilitation in nature. To face this challenge, future work addressed at determining the net effects of the coexistence of neighbouring species mediated by facilitation should provide a good characterization of the phenotypic traits potentially involved in niche overlap. Furthermore, this information should be complemented with accurate estimates of phylogenetic distances based on fossil calibrated phylogenies and avoid estimates based on taxonomic ranks. Finally, it should be considered that third interplayers may change the expected sign of the interaction, and that this complex situation will probably be the rule in nature.

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