

Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities

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ABSTRACT

Once seen as anomalous, facilitative interactions among plants and their importance for community structure and functioning are now widely recognized. The growing body of modelling, descriptive and experimental studies on facilitation covers a wide variety of terrestrial and aquatic systems throughout the globe. However, the lack of a general body of theory linking facilitation among different types of organisms and biomes and their responses to environmental changes prevents further advances in our knowledge regarding the evolutionary and ecological implications of facilitation in plant communities. Moreover, insights gathered from alternative lines of inquiry may substantially improve our understanding of facilitation, but these have been largely neglected thus far. Despite over 15 years of research and debate on this topic, there is no consensus on the degree to which plant–plant interactions change predictably along environmental gradients (i.e. the stress-gradient hypothesis), and this hinders our ability to predict how plant–plant interactions may affect the response of plant communities to ongoing global environmental change. The existing controversies regarding the response of plant–plant interactions across environmental gradients can be reconciled when clearly considering and determining the species-specificity of the response, the functional or individual stress type, and the scale of interest (pairwise interactions or community-level response). Here, we introduce a theoretical framework to do this, supported by multiple lines of empirical evidence. We also discuss current gaps in our knowledge regarding how plant–plant interactions change along environmental gradients. These include the existence of thresholds in the amount of species-specific stress that a benefactor can alleviate, the linearity or non-linearity of the response of pairwise interactions across distance from the ecological optimum of the beneficiary, and the need to explore further how frequent interactions among multiple species are and how they change across different environments. We review the latest advances in these topics and provide new approaches to fill current gaps in our knowledge. We also apply our theoretical framework to advance our knowledge on the evolutionary aspects of plant facilitation, and the relative importance of facilitation, in comparison with other ecological processes, for maintaining ecosystem structure, functioning and dynamics. We build links between these topics and related fields, such as ecological restoration, woody encroachment, invasion ecology, ecological modelling and biodiversity–ecosystem-functioning relationships. By identifying commonalities and insights from alternative lines of research, we further advance our understanding of facilitation and provide testable hypotheses regarding the role of (positive) biotic interactions in the maintenance of biodiversity and the response of ecological communities to ongoing environmental changes.

Key words: facilitation, competition, species interactions, plant–plant interactions, stress gradient hypothesis, facilitation theory.

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I. INTRODUCTION

Once largely neglected, there is nowadays a broad consensus among ecologists that facilitation is a decisive mechanism for maintaining the diversity and structure of a wide range of plant communities (Callaway, 2007). Several attempts have been made to include facilitation into general ecological theory (e.g. Bruno, Stachowicz & Bertness, 2003), of which the stress-gradient hypothesis (SGH) proposed by Bertness & Callaway (1994) has been the most influential. Based on the notion that biotic interactions are dependent on environmental conditions (Gause, 1934) and the apparent prevalence of empirical studies reporting facilitative interactions under harsh environments (deserts, salt marshes and intertidal habitats), the SGH predicts that the frequency of facilitative and competitive interactions varies inversely across stress gradients. Thus, facilitation is expected to be more common in stressful conditions than in more mesic ones (Bertness & Callaway, 1994). While the SGH has significantly increased the awareness of positive plant–plant interactions worldwide, it has also been actively debated during the last decade (Maestre, Valladares & Reynolds, 2005, 2006; Lortie & Callaway, 2006; Malkinson & Tielbörger, 2010), and controversies regarding how plant–plant interactions respond to changes in environmental conditions remain largely unresolved (Holmgren & Scheffer, 2010; Soliveres *et al.*, 2011; He, Bertness & Altieri, 2013). In spite of this controversy, assumptions of the SGH are commonly applied to current modelling approaches (Lin *et al.*, 2012) or to studies linking facilitation with other lines of research (Bruno *et al.*, 2003; Santoro *et al.*, 2012). It is time to resolve these issues, particularly if we aim to refine our predictions of how plant communities respond to disturbances or environmental

pressures such as those forecasted for future scenarios under ongoing global environmental change (Brooker, 2006). Moreover, the SGH is beginning to be extended to life forms other than vascular plants such as soil lichens, invertebrates or mammals (Bowker, Soliveres & Maestre, 2010; Barrio *et al.*, 2012; Fugère *et al.*, 2012), and a solid theory would help this research to advance further and faster.

Broadening and improving facilitation theory involves not only focusing on the behaviour of pairwise interactions along environmental gradients, but also considering the drivers and consequences of such interactions for plant communities and ecosystems. Thus, we need to understand how interactions among multiple species behave and how frequent they are in natural ecosystems, and also know their relative importance as a driver of community attributes (diversity, structure, species dynamics) and related ecosystem functions (e.g. productivity, stability, nutrient cycling). Such a shift in the focus of facilitation research from pairwise interactions to the community and ecosystem levels would also stimulate the further development of novel fields, of which the evolutionary consequences of facilitative interactions is among the most promising.

The aim of this review is to provide a unifying framework to solve current controversies regarding the behaviour of plant–plant interactions across environmental gradients. We use this framework to advance our understanding in other poorly studied topics such as: (i) how plant–plant interactions affect structure and function of plant communities and their response to ongoing global environmental change, (ii) how facilitation affects the evolution of interacting plants, and (iii) how facilitation research can be linked to other active lines of inquiry, such as plant invasions, woody encroachment, or the biodiversity–ecosystem-functioning relationship. We finally identify research gaps and propose

future directions and experimental approaches that contribute to the further advancement of the theory and applications of positive plant interactions.

II. PLANT–PLANT INTERACTIONS AND THE ENVIRONMENT: CLARIFYING CONCEPTS AND RECONCILING APPARENTLY OPPOSING VIEWS

The exceptions to the original predictions of the SGH found in several empirical studies (Kitzberger, Steinaker & Veblen, 2000; Tielbörger & Kadmon, 2000; Maestre & Cortina, 2004; Butterfield *et al.*, 2010; Soliveres *et al.*, 2011; López *et al.*, 2013) have fuelled a long-standing and active debate among ecologists about the nature of the response of plant–plant interactions to environmental changes. While some studies defend monotonic increases of the frequency or importance of positive interactions towards higher stress levels (Lortie & Callaway, 2006; He *et al.*, 2013), others suggest that there is either a lack of a general response to changes in stress (Maestre *et al.*, 2005) or that the relationship between facilitation and abiotic stress can take multiple shapes, depending on the nature and co-occurrence of the stress factors involved, or the non-linearity of the response of plant species to the environment (Smit *et al.*, 2007; Smit, Rietkerk & Wassen, 2009; Maestre *et al.*, 2009b; Holmgren & Scheffer, 2010; Malkinson & Tielbörger, 2010). We believe that these apparently opposing views can be largely reconciled by clarifying the scale of focus in each study (Fig. 1). First, the original predictions made by Bertness & Callaway (1994) focused on a community-level response, but these predictions have been in most cases only tested with one or a few pairwise interactions. The second important issue is how we define stress, and thus the harshness of a given environment, and whether this concept is solely applicable to particular species (as we believe) or to whole communities whose species differ widely in their ecological adaptations. These two points have crucial implications on how we understand the response of plant–plant interactions to changes in the environment, and are discussed below.

(1) On the importance of multiple plant–plant interaction drivers: insights from pairwise-level approaches

The core of previous research dealing with the response of plant–plant interactions to changes in the environment has focused on studying one or a few pairwise interactions (see Brooker *et al.*, 2008; He *et al.*, 2013 for reviews), and these studies have fed the existing controversy regarding the response of plant–plant interactions to environmental changes. Ecologists generally agree on the existence of multiple factors driving the outcome of pairwise plant–plant interactions. For

example, the performance measure used (Goldberg *et al.*, 1999; Maestre *et al.*, 2005), the nature of the stress factor involved (resource or non-resource; Maestre *et al.*, 2009b), the ontogenetic stage of the interacting species (Stultz, Gehring & Whitham, 2007; Soliveres *et al.*, 2010; Smit & Ruifrok, 2011), the ecological requirements of the interacting plants (Liancourt, Callaway & Michalet, 2005; Chu *et al.*, 2008) or the evolutionary relationships of the species involved (Suzuki & Suzuki, 2012; Soliveres, Torices & Maestre, 2012c), are known to interact with the environment to define such an outcome. Added to this complexity is the fact that multiple environmental stressors, both biotic and abiotic, often co-occur in nature, and jointly shape the response of pairwise plant–plant interactions across environmental gradients (Baumeister & Callaway, 2006; Kawai & Tokeshi, 2007; Smit *et al.*, 2009; le Roux & McGeoch, 2010; Soliveres *et al.*, 2012a). What is the relative importance of these different (a)biotic drivers of pairwise plant–plant interactions? This is difficult to answer since most studies focus on just one or two of these multiple drivers at a time.

Recent evidence suggests that the environment is more important than the species-specific features of the species involved (He *et al.*, 2013). It is known that the environmental conditions, both abiotic and biotic, ‘filter’ those ecological adaptations (either functional traits or evolutionary lineages) that will thrive and those that will not (Webb *et al.*, 2002), and thus the species-specific adaptations that will ultimately be present to interact with their neighbours. The environment can also limit the recruitment, performance or density of potential nurse plants, leading to the waning of positive interactions (Michalet *et al.*, 2006). Moreover, variations in environmental conditions may modulate the groups of functional traits or ecological requirements that are facilitated and those that are not (Butterfield *et al.*, 2013).

We argue, however, that species-specific factors primarily affect the outcome of pairwise interactions, with a secondary role for environmental conditions. As illustrated by Whittaker (1956) in his classic paper on changes in vegetation along aridity gradients in the Great Smoky Mountains, species forming a given community overlap to some degree in their specific requirements, but differ in their ecological optimum [see figs 2 and 3 in Whittaker (1956); discussed in detail in Chase & Leibold (2003)]. Thus, it is reasonable to think that the different pairwise interactions present in a given environment or community will differ in their outcomes depending on features of the interacting species such as ontogenetic stage, functional traits or evolutionary relationships (e.g. Greiner La Peyre *et al.*, 2001; Miriti, 2006; Suzuki & Suzuki, 2012; Soliveres *et al.*, 2012c). Indeed, in most studies including multiple pairwise interactions, species-specific factors of both nurse and beneficiary species shape the response of plant–plant

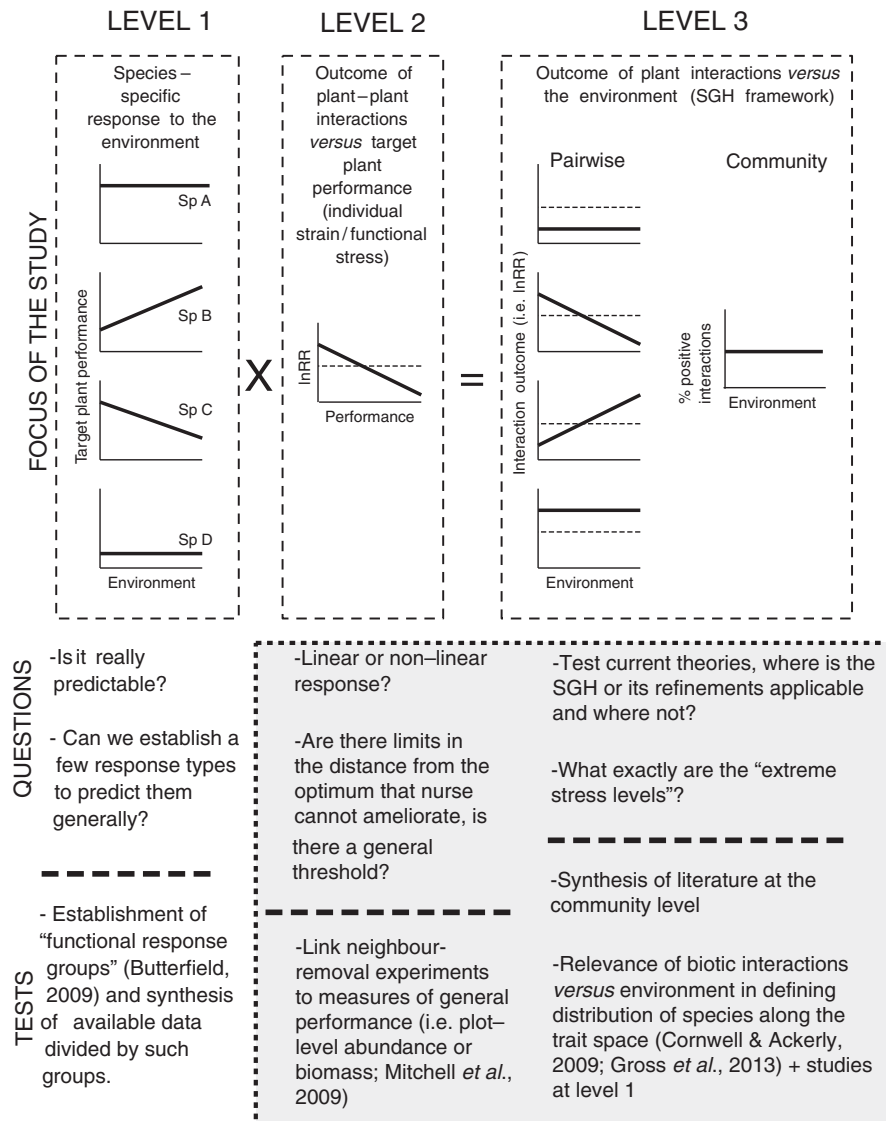


Fig. 1. Different scales of interest typically found in the plant–plant interactions literature, relevant questions regarding their relationship with the environment and suitable tests to answer them. Species-specific (four species, Sp A–D) changes in performance across the same environmental gradient (left box; Level 1) affect the outcome of plant–plant interactions across such gradients (Level 3, pairwise). This affects the frequency of positive interactions found at the community level (Level 3, community). Plant–plant interactions become more positive with decreasing target plant performance in the open; however, for species A and D no changes in their performance are detected through the gradient, and therefore no changes in the outcome of the interactions between these latter species and their neighbours are expected. Discontinuous lines in the panels separate positive (above) and negative (below) plant–plant interaction net outcomes (represented by the InRR [log Response Ratio] index). The grey quadrat surrounds high-priority areas for future research. SGH, stress-gradient hypothesis.

interactions within the same environmental conditions and across environmental gradients (Liancourt *et al.*, 2005; Chu *et al.*, 2008; Soliveres *et al.*, 2012c). Other evidence supports the notion that species-specific features may be more important than the environment in defining the outcome of pairwise plant–plant interactions. For example, environmental filters are relaxed due to the microclimatic amelioration provided by nurse plants (Bruno *et al.*, 2003; Lortie *et al.*, 2004), and this

microclimatic amelioration seems to depend on the specific features of each nurse, rather than on the prevailing environmental conditions (e.g. Gómez-Aparicio, 2009).

We now need studies aiming to assess to what extent species-specific adaptations depend on different environments and the presence of neighbours, and how this may affect the community-level importance of facilitation under such environmental conditions

(Fig. 1). This will undoubtedly provide a useful link between pairwise and community-level studies, and refine our predictions on the response of plant communities to environmental changes. A combination of the approaches followed by Cornwell & Ackerly (2009; different filters of the community-level trait space) and Butterfield & Briggs (2011; relationship between plant functional traits and a regeneration niche associated with a nurse plant) appears the most promising in this regard (see also Schöb, Butterfield & Pugnaire, 2012; Gross *et al.*, 2013; Hulshof *et al.*, 2013). Moreover, the classification of the species pool into a few relevant groups in the functional trait space regarding the response to the presence of neighbours, and the effect of the latter on their microclimate (i.e. functional response and effect groups; Butterfield, 2009) can help to enhance the reliability and generality of current modelling approaches by introducing biotic interactions in a more refined, yet general, manner (Jeltsch *et al.*, 2008).

(2) Can we predict changes in the outcome of pairwise interactions across environmental gradients?

Regardless of their relative importance, the multiple factors shaping pairwise plant–plant interactions and the interrelationships existing among them make it extremely difficult generally to predict the outcome of plant–plant interactions along environmental gradients. However, we can encapsulate all the species-specific and environmental drivers into a single factor: the distance to the ecological optimum of the beneficiary. In short, the further a given beneficiary species is from its ecological optimum (i.e. the lower the performance of isolated individuals), the more necessary or important will be the presence of a nurse plant (but see Mitchell, Cahill & Hik, 2009 for contradicting findings). This is referred to as ‘individual strain’, ‘functional stress’ or ‘individual stress’ in the literature (Lortie & Callaway, 2006; Gross *et al.*, 2010; Soliveres *et al.*, 2011; Rees, Childs & Freckleton, 2012), and we refer to it here as the ‘individual stress model’. There are multiple examples that support its use, including the higher facilitation found for: (i) drought-maladapted species when water stress is more important (e.g. Liancourt *et al.*, 2005), (ii) grazing-intolerant species under increasing grazing pressure (e.g. Vandenberghe *et al.*, 2009), or (iii) salt-sensitive species in salt marshes (e.g. Greiner La Peyre *et al.*, 2001). Recently, He *et al.* (2013) showed the generality of the individual stress model with a meta-analysis of studies on pairwise interactions across the globe. They showed consistent shifts towards more positive interactions with lower target plant performance in the open (i.e. greater distance from their ecological optimum) in a variety of biomes and growth forms. The authors interpreted their results as strong support for the SGH as originally formulated. However, their results are not linked to the environmental

conditions but to the performance of each particular target species. Therefore, we interpret them as strong support for the direct relationship between the outcome of pairwise interactions and the individual stress experienced by the beneficiary species (Level 2 in Fig. 1).

At this point, we should advise caution when selecting response and predictor variables for testing how plant–plant interactions change along environmental gradients. The selected response variable cannot be a by-product of the predictor (e.g. using survival away from nurse plants as a predictor and then a facilitation index built using this survival and that in the nurses as a response) as these response variables can generate spurious significant relationships and lead to misleading conclusions (Brett, 2004; Rees *et al.*, 2012). In this regard, the ideal approach should probably follow three steps: (i) identify crucial ontogenetic phases for the population of the beneficiary species (i.e. by using matrix-based population models; Salguero-Gómez & De Kroon, 2010), (ii) perform removal experiments or planting experiments using different microsites to quantify the strength of facilitation/competition across these different ontogenetic stages (e.g. Soliveres *et al.*, 2010; le Roux, Shaw & Chown, 2013), and (iii) relate the results to general measures of performance of the population of the beneficiary species (i.e. relative abundance or biomass at the plot scale; Miriti, Wright & Howe, 2001; Mitchell *et al.*, 2009). A complementary future line of inquiry should focus on the linearity or non-linearity of the facilitation distance from the optimum relationship (Malkinson & Tielbörger, 2010), and on the evaluation of thresholds in the distance from the ecological optimum in which the presence of a nurse plant does not suffice to ensure recruitment of a given beneficiary (Kitzberger *et al.*, 2000). If we know the exact shape of this relationship, and the amount of stress that a nurse can alleviate, we can make accurate predictions that can easily be incorporated into models for future species distributions and assemblages of plant communities under different global environmental change scenarios (e.g. Thuiller *et al.*, 2013; Wisz *et al.*, 2013).

(3) Moving from pairwise to community-level interactions: challenges ahead

By using the individual stress model, we can improve our ability to predict the outcome of particular pairwise interactions, but the concept of ‘stress’ cannot be applied to whole communities whose members differ widely in their ecological adaptations. The problem arises when these species-specific stress levels are not linked to the overall environmental conditions. The predictability of any community-level model lacking this link vanishes because such models use these conditions (e.g. climatic data) to predict future distributions and responses of plant communities to changing

environmental scenarios (Bertness & Callaway, 1994; Bruno *et al.*, 2003; Fig. 1).

The link between species-specific stress levels and environmental gradients has led to a proposed modified SGH, which predicts a higher importance and frequency of positive plant–plant interactions at moderate levels of stress (Holmgren & Scheffer, 2010). The peaking of facilitation at moderate levels of stress is supported by other theoretical models and empirical research at the community level (Hacker & Gaines, 1997; Hacker & Bertness, 1999; Michalet *et al.*, 2006). Other studies, however, provide support for linear and monotonic increase of the importance of facilitation at the community level (e.g. Armas, Rodríguez-Echeverría & Pugnaire, 2011; Dohn *et al.*, 2013). Recently, a conceptual model based on empirical observations was proposed to reconcile contrasting results often found at the community level (Soliveres *et al.*, 2011). This model states that the relationship between environmental gradients and the frequency of facilitative interactions will be predictable (either linear or unimodal) if the environmental gradient is driven by a single stressor and most species in the community perform similarly under this stress factor (discussed in Michalet *et al.*, 2006; Holmgren & Scheffer, 2010). When multiple unrelated stress factors are present within the environmental gradient, or when there is high variability in the ecological requirements among the species pool, a relationship between the frequency of positive plant–plant interactions and environmental harshness should not be expected (Soliveres *et al.*, 2011; López *et al.*, 2013; Soliveres & Maestre, 2014).

To answer community-level predictions on how the frequency of positive plant–plant interactions changes across differing environmental conditions, we must necessarily use data gathered at the community level (Soliveres & Maestre, 2014). Data gathered at the level of single or a few species pairs is insufficient to test the generality of predictions from the SGH, to understand under which conditions these predictions are valid or not, and to assess the importance of factors shaping the outcome of plant–plant interactions at the community level across environmental gradients (Fig. 1). Moreover, although much has been discussed about the collapse of facilitative interactions under ‘extreme conditions’ (Molina-Montenegro *et al.*, 2012; Callaway, 2013; Verwijmeren *et al.*, 2013), neither the threshold (if any) between what is considered ‘extreme’ or ‘mild/moderate’ environmental conditions nor the factors driving it have been defined. Does our perception of what is ‘extreme’ vary with the community being studied and with the environmental adaptations of the occurring species? Is the co-occurrence of diverse stress factors what makes an environment ‘extreme’? Or is it just that we denote the conditions when facilitation collapses as ‘extreme’?

Another relevant issue when upscaling from the pairwise to the community scale is that plants do not interact just in pairs, but rather form multiple species assemblages (e.g. Verdú & Valiente-Banuet, 2011; Saiz & Alados, 2011b). Under this multiple-species scenario, even competitor species may be facilitated if one of them excludes a third common competitor species (Levine, 1999; Brooker *et al.*, 2008). However, we know very little of how frequent these indirect positive interactions are, and under which environments or for which plant functional groups these interactions prevail. Indirect interactions among woody adults and seedlings, mediated by competition with grasses, have been reported in different ecosystems (Maestre, Cortina & Bautista, 2004; Cuesta *et al.*, 2010; Saccone *et al.*, 2010). In one of the very few attempts to study the interplay between indirect interactions and climate, Cuesta *et al.* (2010) showed that indirect positive effects prevailed in the wetter periods while direct facilitation was predominant during drought. Similar results were found in a more extensive study (Schöb, Armas & Pugnaire, 2013a), suggesting that indirect interactions prevail under more productive conditions.

Plants, especially in harsh environments, tend to form clumps of multiple species that interact with one another. Under such conditions, not only indirect interactions are important, but also the existence of non-hierarchical competitive networks (intransitive networks, equivalent to the rock-paper-scissors game in which no single dominant species prevails; Gilpin, 1975). These intransitive competition networks are important, yet poorly explored, mechanism for the maintenance of plant diversity (Laird & Schamp, 2006). Although intransitive networks are based on competition, and not on facilitation, the presence of nurse plants may enhance the degree of intransitivity, and therefore increase species diversity at the community level (Soliveres *et al.*, 2011). Intransitivity is more likely to occur under more heterogeneous conditions (Allesina & Levine, 2011), such as those favoured by the presence of nurse plants. A nice example, although not discussed by the authors in their original paper, is provided by Cavieres *et al.* (2005). These authors found evidence of how changes in the competitive networks promoted by the cushion *Azorella monantha* may reduce competitive exclusion among their neighbouring plants. Although intransitive interactions have been studied mostly using mathematical models, due to difficulties in studying them empirically, new tools are becoming available to quantify changes in the degree of intransitivity in competitive networks among neighbouring species from observational data (Soliveres *et al.*, 2011; Ulrich *et al.*, 2014). These methodological advances open the door to assessing the frequency of intransitive loops within plant communities, and to evaluating how nurse plants, other trophic levels, or the environment affect such frequency.

The application of network theory into facilitation research has also shed substantial insights on the role of different drivers of plant–plant interactions, namely evolutionary relationships, disturbance or density-dependent effects, on the structure of the interactions among the multiple species forming plant communities (Verdú *et al.*, 2009; Verdú & Valiente-Banuet, 2011; Saiz & Alados, 2011b). Network approaches have also been used to assess how keystone species affect interactions among the rest of the species within a community (Saiz & Alados, 2011a). We believe that network approaches may serve, among other things, to identify keystone nurse species that have disproportionate (regarding their abundance) positive effects on other species, which can help in focusing species selection in restoration efforts. Overall, these new tools and approaches offer great potential to study multiple species interactions, and hence to provide new insights into the importance of interspecific interactions on plant communities. The evidence mentioned above also indicates that the consideration of multiple-species interactions may completely change our view of how plant–plant interactions at the community level are affected by environmental conditions, and will further increase the reliability of conceptual, mathematical and empirical models aimed at predicting how these interactions will respond to ongoing global environmental change.

III. EVOLUTIONARY ASPECTS OF PLANT FACILITATION

A key theme in ecological and evolutionary studies is how, and to what degree, ecosystems – and organisms living therein – deal with the rapid human-induced climate and land-use changes (Vitousek *et al.*, 1997; Sala *et al.*, 2000). Classically, studies have focused on one-way adaptations of organisms to changing environments by natural selection (Jump & Peñuelas, 2005). However, species also create their own environment, and thus that of the species interacting with them (i.e. niche construction *sensu* Odling-Smee, Laland & Feldman, 2003). This is another, albeit largely ignored, evolutionary pathway. A recent synthesis (Castellanos & Verdú, 2012) shows that biotic factors, including the interaction with neighbouring plants, are stronger evolutionary selection forces than abiotic factors in plants. Empirical evidence also shows that species interactions largely drive the response of ecosystems to environmental changes (Cardinale, Palmer & Collins, 2002; Gilman *et al.*, 2010). What then are the long-term consequences of facilitation for the interacting plants and their environment? Previous work has aimed at providing a theoretical framework for the evolutionary implications of facilitation (Laland, Odling-Smee & Feldman, 1996; Bronstein, 2009; Thorpe *et al.*, 2011; Liancourt *et al.*, 2012) and

it is not our intention here to develop them further. Rather, we focus on including empirical evidence supporting or contradicting what we believe are the most important implications of facilitation on evolution, and on providing future guidelines and suggesting potential experiments to advance this topic further.

Typically, studies on the evolutionary consequences of species interactions have focused on plant–pollinator, seed–disperser, and plant–herbivore interactions (Thorpe *et al.*, 2011). Interactions between plants have been much less considered as a mechanism for evolutionary adaptations. Thus far, this theme has received very little attention, and available studies have mostly focused on theoretical and conceptual work (Brooker *et al.*, 2008; Bronstein, 2009; Thorpe *et al.*, 2011; Liancourt *et al.*, 2012; but see Aarssen & Turkington, 1985; Ehlers & Thompson, 2004; Valiente-Banuet *et al.*, 2006). While the evolutionary implications of environmental changes have been evaluated multiple times (reviewed in Castellanos & Verdú, 2012), there is a great need for studies testing patterns of evolution in response to the presence of neighbours. So far, evidence suggests that facilitative interactions help to preserve lineages less adapted to more recent environmental (both abiotic and biotic) conditions, working as an ecological ‘time machine’ for maladapted lineages (*sensu* Lortie, 2007). A crucial example for the latter is that recent (quaternary) lineages have preserved older (tertiary) drought-maladapted ones through the drier climatic conditions found during the quaternary period (Valiente-Banuet *et al.*, 2006). Whether or not this preservation of biodiversity by benefactor species through sharp environmental changes has occurred at other times in the past, or may occur in the future, is a topic deserving further attention (McCluney *et al.*, 2012; Blois *et al.*, 2013).

A second major research line in the relationship between facilitation and evolution is how facilitation works as a process driving speciation. In line with the individual stress model, recent work highlights the importance of plant–plant interactions to maintain local maladapted ecotypes within a given species (Jensen & Ehlers, 2010). These results suggest that local plant communities may be much more co-evolved than assumed so far. Besides abiotic conditions, the evolutionary grazing history is also an important determinant of the outcome of plant–plant interactions. The ‘naïve’ (without grazing history) phenotype of the palatable *Persicaria longiseta* strongly benefits from protection against browsing, while its grazing-adapted phenotype does not (Suzuki & Suzuki, 2012). Interestingly, this study suggests that adaptations to grazing can occur within a relatively short time span (decades to centuries), which is much faster than assumed in the classical studies on evolutionary grazing history (>10000 years; Mack & Thompson, 1982; Milchunas, Sala & Lauenroth, 1988). This is supported by the fact that biotically selected traits

hold fewer genes and therefore drive faster adaptation than abiotically driven traits (Louthan & Kay, 2011). The notion that evolutionary processes commonly take place at ecological timescales has opened up the opportunity to study feedbacks between ecology and evolution (i.e. eco-evolutionary dynamics: Carroll *et al.*, 2007; Pelletier, Garant & Hendry, 2009; Schoener, 2011). The example of Suzuki & Suzuki (2012) is the first that places (positive) plant–plant interactions in this exciting field, and we see strong potential for novel empirical studies within this eco-evolutionary context.

There are several remaining questions regarding the role of facilitation as a speciation process. The main one is that, to generate new species, facilitative interactions do not need just to enhance the performance of maladapted ecotypes, but also to promote reproductive isolation. An obvious, yet poorly explored, mechanism is that facilitative interactions change flowering phenology of such maladapted ecotypes, thus promoting reproductive isolation from the better adapted ecotypes. Another pathway of reproductive isolation may occur when a nurse plant protects beneficiary plants against grazing, which reduces the production of flowerheads and seeds of beneficiaries outside the canopy of the nurse (Bossuyt, De Fre & Hoffmann, 2005). Studies addressing these pathways are key to assessing the role of facilitation as a driver of speciation.

To understand fully the role of facilitation in the evolution of plants, the nurse plants should also be considered (Bronstein, 2009). Two recent examples show that facilitation may come with a cost for the facilitator (Michalet *et al.*, 2011; Schöb *et al.*, 2013b); thus, what are the advantages of being a facilitator? Facilitation might come with benefits for the facilitator when the fitness of the population is increased by the beneficiary *via* promotion of seed and leaf size (Cranston *et al.*, 2012), seed dispersal (by attractive seeds of the beneficiary), pollination (attractive flowers of the beneficiary), shared defenses, or the exact opposite (decoy; beneficiary distracts enemies of the nurse), but evidence thus far is very scarce. If we can establish how general these positive and negative outcomes for nurses are, we will undoubtedly be able to understand the implications of plant–plant interactions in the evolution of plant communities better. Only a handful of studies have considered the reciprocal effects of plant–plant interactions to date (e.g. Michalet *et al.*, 2011; Lortie & Reid, 2012; Schöb *et al.*, 2013b). We see a strong need for novel experimental, descriptive and modelling studies aiming to unravel the conditions under which facilitation can lead to evolutionary adaptations among the interacting plant species. Such studies would include field measurements of trait variability of nurse and beneficiary species, in each other's presence and absence, combined with reciprocal transplant studies to identify signals for possible local adaptation to neighbouring plants (similar to Grøndahl & Ehlers, 2008; Liancourt & Tielbörger, 2011). In

addition, greenhouse or common garden studies on the second- and third-generation offspring from these different populations are needed to test for the heritability of the measured altered traits. Laboratory experiments with controlled lines of both beneficiary and nurse plants in manipulated mesocosm environments would be needed to test under what conditions genetic variation due to the presence of the neighbour evolves. Modelling studies would allow populations of multiple nurse and beneficiary plants (community approach) to evolve over longer times under different scenarios (variable interaction strengths, interaction types, sets of species traits, environmental stressors and their combinations). In addition, long-term studies of species invasions are an excellent opportunity to investigate not only how invading species evolve different interactions within the novel communities (Callaway *et al.*, 2012), but also how these invaded communities, and their members, respond to the invader in evolutionary terms (Lau, 2006; Pakeman *et al.*, 2009).

Lastly, it has been hypothesized that systems with ubiquitous facilitative interactions may exhibit highly unstable dynamics, with some alternative states leading to local extinction (also referred to as 'evolutionary suicide'; Gyllenberg & Parvinen, 2001; Kefi *et al.*, 2008). This occurs when facilitated species, which succeed thanks to the presence of nurse species, competitively exclude the latter, preventing their own recruitment in the next generation (see Valiente-Banuet, Vite & Zavala-Hurtado, 1991, for an empirical example). This leads to either the local extinction of both nurse and facilitated species, or to sharp reductions in their population sizes (see Ferriere & Legendre, 2013, for a recent review on this topic). How this theoretical instability in communities driven by facilitation is linked to the evolutionary persistence of positive interactions observed in real world communities (e.g. Valiente-Banuet *et al.*, 2006) is certainly a major topic to address to understand fully the evolutionary implications of plant–plant interactions. The scarce existing studies point to the spatial component as a crucial attribute to consider when investigating the conundrum between the persistence of positive plant–plant interactions and the low stability of facilitation-driven communities. For example, Kefi *et al.* (2008) found that short-distance seed dispersal generates patchy patterns that allow facilitation-driven populations to escape extinction, while those populations characterized by long-distance dispersal become extinct under the same conditions. Along the same lines, Filotas *et al.* (2010) found that facilitation-driven populations with less spatial interconnectedness were more stable than those that were highly connected. Until now, modelling has been the only available approach to address this issue. Hopefully, by investigating long-term datasets in well-studied systems showing cyclical succession (such as the Saguaro systems in Valiente-Banuet

et al., 1991) will we be able to assess empirically the insights gained by modelling approaches.

IV. RELATIVE IMPORTANCE OF PLANT–PLANT INTERACTIONS FOR COMMUNITY STRUCTURE AND FUNCTIONING: IDENTIFYING GAPS IN OUR KNOWLEDGE

The importance of plant–plant interactions as a driver of plant communities has been a subject of debate since the 1980s (Welden & Slauson, 1986; Goldberg & Barton, 1992). Welden & Slauson (1986) proposed differentiation between the intensity (with *versus* without neighbour) and the importance (neighbour *versus* the remaining environmental factors affecting target plant performance) of plant–plant interactions. Although not free from caveats (Rees *et al.*, 2012), this differentiation between intensity and importance helped to clarify contrasting results in the literature regarding plant–plant interactions (e.g. Brooker *et al.*, 2005), and even could be exported to other active lines of inquiry in ecology, such as the relationship between disturbance and diversity, or the response of plant species to global environmental change (Kikvidze, Suzuki & Brooker, 2011). Most recent research and conceptual advances on this topic have focused on the importance of plant competition and facilitation for individuals and populations of single species (e.g. Rees *et al.*, 2012 and references therein). However, the relative importance of plant–plant interactions *versus* other variables as drivers of community attributes and ecosystem functions has been largely overlooked.

It is well known that both positive and negative interactions affect the richness of plant communities (e.g. Goldberg & Barton, 1992; Hacker & Gaines, 1997; Bruno *et al.*, 2003), and that the positive effects of nurse plants can cascade to insects (e.g. Lortie & Reid, 2012), biological soil crusts or microbial communities (Maestre *et al.*, 2009a). However, how many species within a community depend on nurses or, in other words, what the importance is of positive plant–plant interactions for the maintenance of plant diversity, and over what spatio-temporal scales these interactions are important, is largely unknown (see discussion on this topic in Ricklefs, 2008, 2009; Brooker *et al.*, 2009). Empirical studies (e.g. Cavieres & Badano, 2009; Soliveres *et al.*, 2011) and theoretical work (Brooker, 2006) illustrates that facilitative interactions may influence a high proportion of the species forming a community, and that they can buffer against negative impacts from climate change. However, to what extent and under which conditions this buffering effect should be expected is very poorly understood (but see Cavieres *et al.*, 2014; Soliveres & Maestre, 2014). As an example, Sala *et al.* (2000) predicted that up to 40% of actual plant communities will change in

composition because of changing environmental conditions. How these predictions would change if they included positive interactions is a question that deserves to be explored.

Interactions among plants also influence other important diversity attributes, such as functional and phylogenetic diversity (Webb *et al.*, 2002; Valiente-Banuet & Verdu, 2007; Cornwell & Ackerly, 2009; Soliveres, Torices & Maestre, 2012b; Gross *et al.*, 2013), and the composition and spatial pattern of entire plant communities (reviewed in Callaway, 2007; Brooker *et al.*, 2008). Separate lines of inquiry, on the other hand, have repeatedly demonstrated how these different attributes (richness, functional and phylogenetic diversity or spatial pattern) play a crucial role in the functioning of ecological communities and the services they provide (e.g. Díaz *et al.*, 2007; Kefi *et al.*, 2007; Maestre *et al.*, 2012). Our aim here is to merge both bodies of knowledge to address the importance of plant–plant interactions as drivers of the structure and functioning of ecological communities. We first discuss how nurse plants can affect the structure of plant communities and then the potential implications of such effects on their functioning.

(1) Plant–plant interactions as drivers of community composition and structure: linking results at the individual and landscape spatial scales

The importance of plant–plant interactions for species richness, spatial pattern and or composition varies across community types and environments (Kikvidze *et al.*, 2005; Cavieres & Badano, 2009; Mitchell *et al.*, 2009; Soliveres *et al.*, 2011). This variation seems jointly to depend on the prevailing environmental conditions and the density and functional traits of nurses (Breshears, 2006; Verwijmeren *et al.*, 2013). Nurse plants generally ameliorate the environment beneath their canopies (i.e. positive patch-level effect), and this generates some degree of environmental heterogeneity at the landscape scale (i.e. differing water, nutrient and light conditions beneath nurse canopies than outside). This seems the main reason why nurses increase species richness and affect species composition at the landscape level (Tewksbury & Lloyd, 2001; Cavieres & Badano, 2009).

However, very few studies have related the response of these positive effects at the level of the individual plant to changes in the density of the potential nurse plant within the landscape. Literature focusing on woody encroachment (i.e. the increase in woody plant densities into former grasslands) suggests that if the density of woody plants (which also can act as nurses) increases at the landscape level, it will reach a point at which habitat heterogeneity decreases rather than increases, which could reduce the positive effect of nurses on community structure attributes (Breshears, 2006). A unique empirical example for this is found in Riginos

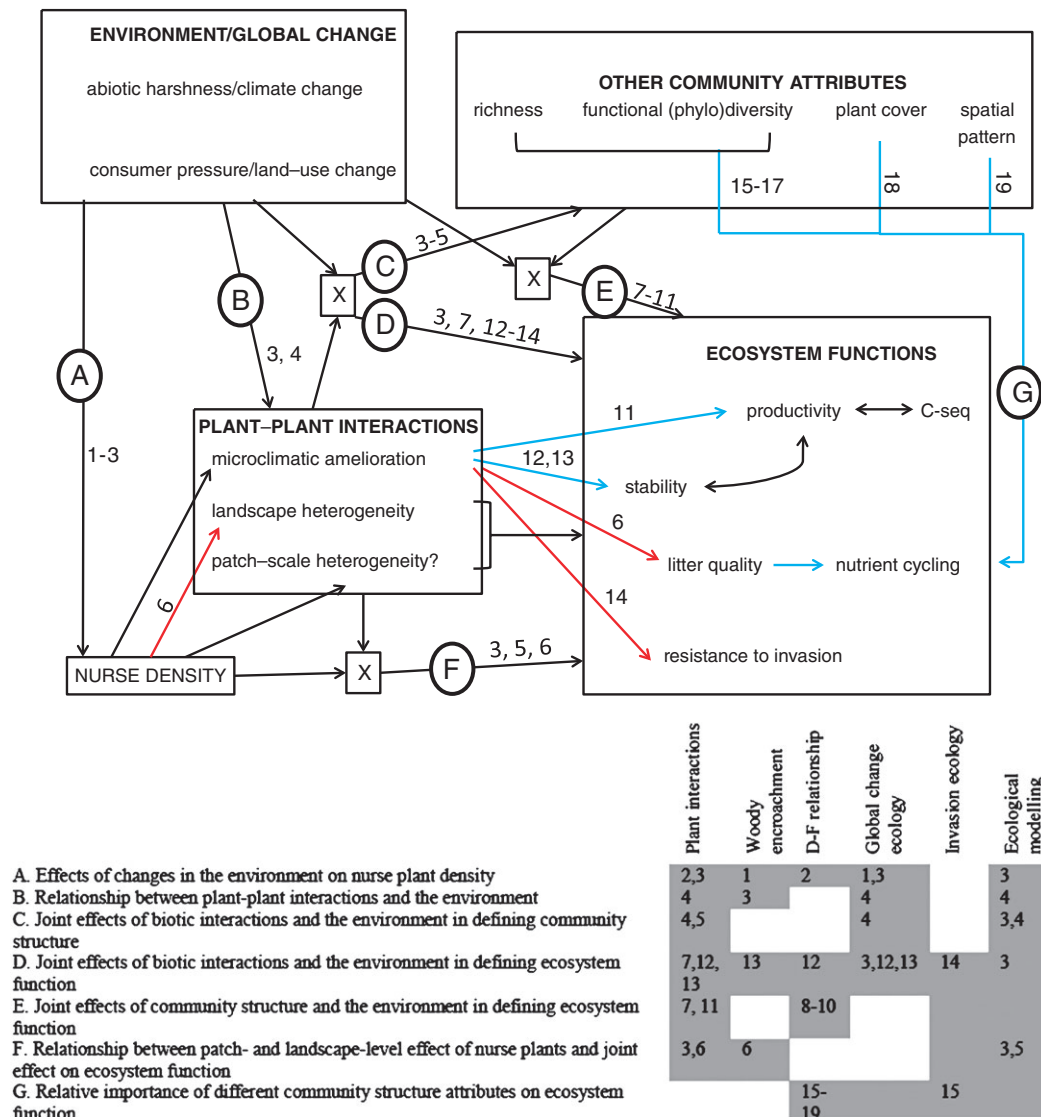


Fig. 2. Conceptual model highlighting positive (in blue) and negative (in red) relationships between community and environmental attributes, and their effects on several ecosystem functions. Black single-headed arrows indicate likely but poorly studied relationships. X = interactions between two different components of the model (D = between plant-plant interactions and environmental conditions; F = between nurse plants' effects at the patch level *versus* their density within the landscape), there is no general agreement in their outcome and cross-discipline studies are needed to solve these discrepancies. Important studies, relevant to particular parts of the model are identified with numbers and listed in the highlighted table (bottom right). 1, Van Auken (2000); 2, Michalet *et al.* (2006); 3, Verwijmeren *et al.* (2013); 4, this study; 5, Soliveres *et al.* (2012c); 6, Riginos *et al.* (2009); 7, Mulder *et al.* (2001); 8, Steudel *et al.* (2012); 9, Jucker & Coomes (2012); 10, Maestre *et al.* (2012); 11, Cardinale *et al.* (2002); 12, Butterfield (2009); 13, Wilby & Shachak (2004); 14, Reinhart (2010); 15, Zavaleta *et al.* (2010); 16, Forest *et al.* (2007); 17, Díaz *et al.* (2007); 18, Maestre & Escudero (2009); 19, Kefi *et al.* (2007). C-seq, carbon sequestration.

et al. (2009), who found that the effect of *Acacia* trees on species richness, plant biomass and soil fertility was strongly positive, but became negative with increasing tree density at the landscape scale (but see Soliveres & Eldridge, 2013).

Finally, the positive effects of different plant functional groups, such as trees, shrubs, herbs, cushion plants or grasses, on their neighbours are widely variable because

of their different morphology (Gómez-Aparicio, 2009), and these growth forms dominate under differing habitats and environments. Thus, understanding how environmental conditions, the functional traits of the nurses, and the relationship between the facilitative role of individual nurses and their density within the landscape affect ecosystem attributes is an extensive field for future research (Fig. 2).

(2) Effects of plant–plant interactions on ecosystem functioning

If studies focused on the different drivers of the importance of plant–plant interactions for community attributes such as richness, composition or spatial pattern are scarce, those focusing on ecosystem functioning are even rarer. The few available studies deal with the effect of facilitative interactions on ecosystem productivity and stability (Mulder, Uliassi & Doak, 2001; Cardinale *et al.*, 2002; Wilby & Shachak, 2004; Butterfield, 2009), the increase in alien plant invasions due to the microclimatic amelioration provided by nurses (Bruno *et al.*, 2003; Cavieres *et al.*, 2005; Reinhart, 2010), or the relative importance of plant–plant interactions on nutrient cycling and soil fertility (reviewed in Callaway, 2007; see also Maestre *et al.*, 2010). However, an increasing amount of studies are dealing with the effect of nurse plants on the functional diversity of their neighbours, or use phylogenetic diversity as a proxy to assess functional diversity. Due to the tight link between changes in functional and phylogenetic diversity, such as those promoted by nurses, and changes in ecosystem functioning (e.g. Díaz *et al.*, 2007; Forest *et al.*, 2007), we can use studies on the effects of facilitation on functional and phylogenetic diversity to provide a first link between facilitation among plants and ecosystem functioning.

The first step, therefore, would be to assess how plant–plant interactions respond to the environment to affect functional traits of neighbouring species (Butterfield & Callaway, 2013; Gross *et al.*, 2013), and how these changes in functional traits relate to different ecosystem functions. It must be noted that those traits affected by the presence of a given nurse (response traits *sensu* Lavorel & Garnier, 2002) can differ widely from those affecting ecosystem processes (effect traits *sensu* Lavorel & Garnier, 2002; see also Butterfield, 2009). Thus, to link properly the effects of nurse plants on neighbours' functional traits, and these traits to important ecosystem processes, we need to consider the existing relationship between response and effect traits. According to the framework proposed by Lavorel & Garnier (2002), those response traits related to the nutrient amelioration commonly provided by nurses are likely to be involved in nutrient cycling or productivity and, therefore, should be those considered when linking plant–plant interactions to ecosystem processes. For example, the few available studies on this topic suggest that plants growing beneath a nurse show higher leaf N contents and lower C/N ratios (Riginos *et al.*, 2009). These response traits may also play a role as effect traits by promoting litter decomposability. Therefore, plants growing beneath nurses are likely to show higher decomposition rates than those growing in open areas, mimicking the behaviour found for cultivated *versus* wild plants, or high-resource *versus* low-resource habitats (García-Palacios *et al.*, 2013). On the other hand,

response traits related to grazing protection are likely to be less relevant to ecosystem processes (Lavorel & Garnier, 2002), and thus can be of little importance to link plant–plant interactions and ecosystem functioning.

As in the assessment of facilitation as a driver of speciation (see Section III above), it is also necessary to know which facilitative interactions provide common selective forces for certain trait values, how these selective forces change with environmental conditions and how the favoured trait values affect different ecosystem functions. Again, following the individual stress model, it is unlikely that we will find common selective forces in the future, as the trait values favoured by facilitation are likely to change depending on the species-specific adaptation of each beneficiary species and the prevailing environmental conditions (Fig. 1; see also Butterfield & Callaway, 2013). Thus, generalizations about the effects of facilitation on ecosystem functioning are extremely difficult, as different functional traits are facilitated under different environments (Butterfield & Callaway, 2013). However, some commonalities arising from the current literature can help us to draw a first set of testable hypotheses to foster research in this topic. Overall, available empirical evidence suggests that facilitative interactions affect ecosystem functioning by (i) promoting higher productivity and litter quality (e.g. Cardinale *et al.*, 2002; Schöb *et al.*, 2012), which enhances nutrient cycling and C fixation, (ii) buffering the reduction of functional diversity expected under harsher environments (Schöb *et al.*, 2012; Gross *et al.*, 2013), which can promote the stability of plant productivity (Cardinale *et al.*, 2002; Wilby & Shachak, 2004) and promote ecosystem functioning under harsher scenarios (e.g. Mulder *et al.*, 2001), and (iii) reducing community resistance to alien plant invasions due to the microclimatic amelioration promoted by nurses (Cavieres *et al.*, 2005; Reinhart, 2010). It is interesting to note that facilitation seems particularly important to maintain rare and subordinate species (Gross *et al.*, 2013), which have been highlighted as crucial for the maintenance of ecosystem functions because of their low functional redundancy (Lyons *et al.*, 2005; Mouillot *et al.*, 2013).

The effects of facilitative interactions in the above-mentioned ecosystem-function-related variables will likely depend on the environment. In this regard, it seems clear that more functional diversity approaches (Schöb *et al.*, 2012, 2013a; Butterfield & Callaway, 2013; Gross *et al.*, 2013) are needed to establish general patterns on the importance and sign of the effect of plant–plant interactions on functional diversity, and how this may relate to ecosystem functioning under differing environmental conditions. Apart from the indirect effects mediated through their influence on neighbouring plants, it is obvious that nurses have their own direct effects on ecosystem functioning. Normally, they capture more resources *via* run-off and provide shade and milder environmental conditions,

Table 1. Main topics addressed in this review, identifying the main gaps in our knowledge that should be addressed by future research, recommending approaches to address them (see text for examples) and listing theoretical improvements expected from such research

Topic	Gaps in our knowledge	Approach recommended	Theoretical improvements
Pairwise interactions	Relative importance of environment and PPI as drivers of the functional traits (species-specific adaptation) present in a given community	Quantify filtering effects on plant traits of both the environment and PPI Relationship between plant functional traits and the outcome of PPI	Classification of the species pool in functional response groups (<i>sensu</i> Butterfield, 2009) to improve generality and reliability of current model approaches Identify potential benefactor species to enhance success in restoration efforts
	Changes in the performance of species along their ecological optimum	Population models to target crucial ontogenetic stages + experiments to quantify the effect of PPI in such stages	Predict the response of species to environmental changes Improve species distribution models and predict community assemblage under future climatic scenarios
Community-level interactions	Behaviour of PPI across environmental gradients	Community-level studies across gradients driven by different uncorrelated stress factors Quantify the importance of the type of gradient and the diversity of species-specific adaptations as drivers of the response of community-level PPI across differing environments	Predict the role of PPI in the response of ecological communities to global environmental change Quantify the threshold in environmental conditions, if any, that may collapse facilitative interactions
	Importance of interactions among multiple species	Use observational or experimental approaches to quantify the frequency of indirect facilitative interactions and how they behave across differing environments and/or functional groups	Improve our predictions of the importance of PPI for plant communities Application to other research lines (e.g. persistence of shrubs in grasslands, invasion meltdown)
Evolutionary implications	Facilitation as an ecological tardis (<i>sensu</i> Lortie, 2007)	Quantify the role of PPI for the maintenance of diversity across evolutionary scales	Understand better the role of PPI on the maintenance of diversity across evolutionary scales. Improve our predictions of species loss under future environmental scenarios
	Facilitation driving speciation	Apply the individual stress model to intra-specific ecotypes differing in ecological adaptations + link results from different ecotypes to differences in flowering phenology that could promote reproductive isolation and drive to speciation. Quantify the heritability of altered traits/ecotypes by using second- or third-generation seeds in common garden experiments Evaluate fitness costs for the benefactor	Understand better the role of PPI as an evolutionary force driving speciation–extinction Introduction of facilitation into general evolutionary ecology theory
Facilitation and ecosystem functioning	Direct effects of PPI on ecosystem functioning	Quantify the relative importance of PPI on community-level functional/phylogenetic diversity and ecosystem functioning Identify density dependence in the effects of PPI on ecosystem attributes such as diversity, composition or spatial pattern	Unify multiple lines of research to understand better the drivers of ecosystem functioning Quantify how PPI affect ecosystem functioning, and how their effects change across differing environments or biomes
	Traits promoted by PPI and their effect on multiple ecosystem functions	Identify which trait values are favoured by PPI, and link them to different ecosystem functions Assess the role of PPI in multiple ecosystem functions simultaneously	Quantify direct effects on ecosystem functioning promoted by benefactors <i>versus</i> their indirect effects mediated by changing functional traits of their neighbours

Table 1. (cont.)

Topic	Gaps in our knowledge	Approach recommended	Theoretical improvements
	Effects on stability	Evolutionary suicide: investigate the conundrum between the high unstability predicted for facilitation-driven communities and the ubiquitous presence of facilitative interactions in nature Quantify the role of PPI in the maintenance of rare species, which are crucial to maintain stability in multiple functions Link microclimatic amelioration by nurse plants with the stability in the productivity of benefactors	Improve our predictions on the response of communities and ecosystems to global environmental change

PPI = plant–plant interactions.

enhancing soil nutrient cycling and water capture and storage (Puigdefábregas *et al.*, 1999; Tongway & Hindley, 2004). Thus, any study aiming to assess the role of plant–plant interactions in ecosystem functioning should consider both these direct effects and those indirectly mediated by their influence on neighbouring plants (Table 1).

Interestingly, synergistic and antagonistic relationships among different ecosystem functions affected by the presence of nurse plants can be expected, highlighting the need to study the role of facilitative interactions on multiple ecosystem functions simultaneously. For example, the higher species richness promoted by plant–plant interactions may synergistically increase the effects of changes in plant litter quality on nutrient cycling and plant productivity (Fig. 2). However, the increase in alien plant success due to microclimatic amelioration by nurses (e.g. Cavieres *et al.*, 2005) can lead to reductions in both plant diversity and ecosystem functioning (e.g. Stachowicz & Byrnes, 2006). The effects of plant–plant interactions on ecosystem functioning are also density dependent. For example, *Acacia* trees enhance plant productivity when occurring at low densities, but reduce it when occurring at higher densities (Riginos *et al.*, 2009). Furthermore, ecosystem functioning not only depends on functional diversity, but also on the spatial pattern and general cover and biomass of plants (e.g. Kefi *et al.*, 2007; Maestre & Escudero, 2009), which are likely to be affected by plant–plant interactions (e.g. Cardinale *et al.*, 2002; Pueyo *et al.*, 2008). While very few studies have evaluated the relative importance of attributes such as spatial patterns and species diversity simultaneously on ecosystem functioning, even less have simultaneously studied how plant–plant interactions affect such ecosystem attributes and the ecosystem functions affected by them (but see Kikvidze *et al.*, 2005; Mitchell *et al.*, 2009; Maestre *et al.*, 2010). More of these studies are needed if we are to understand the importance of plant–plant interactions as drivers of community structure and functioning. Apart from purely empirical approaches, mathematical modelling

(e.g. Filotas *et al.*, 2010) can be really helpful when addressing the complex interplay among the factors modulating the role of plant–plant interactions on ecosystem functioning.

V. CONCLUSIONS

(1) Current apparently opposing views regarding the SGH, which remain debated in the literature, can be reconciled when clearly considering and determining the species-specificity of the response, the nature of the stressor considered, and the scale of interest (pairwise interactions or community-level responses). We believe that the application of these straightforward recommendations (Fig. 1) is essential for the further development of facilitation theory and for improving our understanding and predictions of how plant communities will respond to ongoing global environmental change. These advances can also further our understanding on the evolutionary and ecological implications of plant–plant interactions for plant communities.

(2) We identified gaps in our knowledge that should be a priority for future studies. For example, we emphasized the need to address thresholds in the amount of stress that a benefactor can alleviate, and the linearity or non-linearity of the behaviour of pairwise interactions along distances from the beneficiary's ecological optimum.

(3) We also need more community-level studies and approaches assessing interactions among multiple species to understand better the consequences of facilitative interactions for the structure of whole communities (Table 1).

(4) The SGH is rapidly expanding towards fields other than plant ecology, for which it was originally designed. It is likely that the SGH and its modifications (Fig. 1) might be applicable to other sessile organisms once the specific mechanisms that underlie their interactions have been assessed. However, for more mobile animal communities, the application of the SGH may lead to

different predictions compared to plants and sessile organisms (Barrio *et al.*, 2012), particularly at the extreme ends of environmental gradients. Development of facilitation theory for these other communities is only just beginning and there is ample room for theoretical, empirical and modelling studies.

(5) Empirical studies on the evolutionary aspects of facilitation are clearly needed. While it is now recognized that facilitation can play an important role in the maintenance of genetic diversity, very few studies have tested how positive species interactions affect the generation of new species. There is a strong need for novel experimental, descriptive and modelling studies aiming to unravel under what conditions facilitation can lead to evolutionary adaptations among interacting plant species. Such studies should also include the evolutionary aspects for the nurse species, as well as the evolutionary (grazing) history of the interacting species. We see high potential in invasion ecology as a field to test these ideas.

(6) Research on the relative importance of plant–plant interactions as drivers of community structure and functioning may benefit from approaches dealing with the interactions between environmental conditions, nurse density within landscapes and the effects of individual nurses at the scale of individual plant patches.

(7) Studies addressing the direct and indirect (mediated through their influence on the functional traits of their neighbours) effects of plant–plant interactions will help us to understand better the effects of such interactions on multiple ecosystem functions. Performing such studies across environmental gradients will help to predict the importance of biotic interactions as a driver of the response of ecological communities to ongoing global change (Fig. 2).

(8) There are multiple challenges ahead in facilitation research, and novel conceptual, empirical and modelling studies are needed to advance ecological theory with respect to facilitation.

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