MECHANISMS OF PLANT COMPETITION

A functional comparative approach to facilitation and its context dependence

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Summary

1. Our ability to generalize about broad patterns and outcomes of competitive interactions among plants has improved from a better understanding of functional traits. Facilitative interactions among plants also exhibit strong trait-based patterns; however, very little empirical research has addressed the trait basis of different facilitative mechanisms or the applicability of traditionally defined functional strategies to facilitation.

2. We present a series of predictions regarding the trait basis of a variety of facilitative mechanisms based on empirical patterns of trait responses to environmental filters and knowledge of plant–environment feedbacks.

3. Using a leaf-height-seed framework to predict plant responses to facilitative effects of neighbours, we identify two categories of facilitative mechanisms based on similar predicted responses of specific leaf area (SLA), height and seed size: (i) facilitation of low-SLA, large-seeded and tall plants in environments typified by periodically unfavourable conditions; and (ii) facilitation of high-SLA, small-seeded and tall plants in persistently severe environments. We suggest that facilitation related to herbivory will be idiosyncratic with respect to these functional traits.

4. Competition for limiting resources is predicted to reinforce trait-based responses to facilitation in periodically severe environments, particularly under light competition, but to offset facilitative effects to some degree in persistently severe environments. Thus, biotic interactions may have stronger consequences for shifts in trait distributions in environments typified by disturbance, pulsed soil moisture and short growing seasons limited by low temperatures.

5. Facilitative effects, in addition to facilitative responses, may also be regulated by functional traits, but there is much less empirical evidence for links between functional traits and ameliorative effects on the environment. However, we predict that leaf area index or other integrative traits related to canopy density are likely to be important effect traits for most facilitative mechanisms and should be integrated into more trait-screening programs.

6. Based on the exceptional contribution that trait-based approaches have made for understanding other interactions, we suggest that taking a functional comparative approach to facilitation is an opportunity to improve our ability to identify general patterns and consequences of positive interactions.

Key-words: community assembly, competition, environmental filter, functional strategy, niche, null model

Introduction

Facilitation plays an important role in the assembly of many plant communities (Callaway 2007). These positive interactions can influence community dynamics (Butterfield *et al.* 2010), resilience (Verdu & Valiente-Banuet 2008), ecosystem functioning (Aguiar & Sala 1999) and the evolutionary trajectories of interacting species (Michalet *et al.* 2011). Furthermore, facilitation may increase

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taxonomic (Cavieres & Badano 2009), phylogenetic (Valiente-Banuet & Verdu 2007) and functional (Butterfield & Briggs 2011) diversity. Facilitation has been integrated into many aspects of empirical and theoretical ecology (Brooker *et al.* 2008, 2009; Brooker & Callaway 2009), but most studies have focused on the mechanisms (e.g. resource enhancement and stress reduction; reviewed by Callaway (2007)) and patterns generated by benefactors that enhance beneficiary survival or performance, rather than on the general functional traits of species that might determine broad patterns of facilitative effects and responses.

In contrast, functional traits are widely used in assessing patterns of community assembly (McGill *et al.* 2006; Cornwell & Ackerly 2009), competitive interactions (Gaudet & Keddy 1988; Wilson & Stubbs 2012) and biotic effects on ecosystem functioning (Diaz & Cabido 2001; Gross *et al.* 2008), which suggests that exploring functional traits in the context of facilitation has a great deal of potential to provide new and important insights by allowing us to predict and generalize about facilitative relationships among plant species. There are many examples of species-specific and functional group-specific facilitative relationships in nature (Callaway 1998), yet this potential specificity is obscured in a kaleidoscope of facilitative mechanisms for which trait-based generalization has not been sought. Clear and consistent generality may not occur across all facilitative mechanisms, but we suggest a potential way forward in this overview.

Several theories have been proposed that indirectly link general concepts of functional strategies to facilitation, most building on the stress-gradient hypothesis (SGH) of Bertness & Callaway (1994). The SGH states that biotic interactions tend to shift from competition to facilitation with increasing environmental severity, resulting in analogies to the competitor - stress-tolerator axis of Grime's (1977) competitor - stress-tolerator - ruderal strategy (CSR) theory. This analogy has been used to predict the intensity and importance of facilitation at broad scales (Callaway *et al.* 2002; Michalet *et al.* 2006), and to explain variation in interaction outcomes among co-occurring species that vary in their competitive ability and stress tolerance (Liancourt, Callaway & Michalet 2005; Butterfield 2009; Maestre *et al.* 2009). However, these conceptual models only incorporate facilitation and functional ecology in general terms, and with further refinement based on explicit incorporation of functional traits, we may better understand the functional basis of facilitation. In fact, the original SGH suggests at least two axes of functional differentiation associated with consumer pressure and physical stress to which responses may involve different functional traits. Bertness & Callaway (1994) also noted the role of facilitation in successional processes, which can be associated with functional traits related to the disturbance–stress tolerance (R–S) or disturbance–competition (R–C) axes of CSR theory, classical r- versus K-selection (Pianka 1970), or other axes of functional differentiation depending upon particular mechanisms (Connell & Slatyer 1977).

Rather than beginning with such highly generalized, often subjective functional strategies, theories for the functional basis of facilitation may be best developed from the 'bottom up', that is from the relationships between specific traits or strategies and different environmental conditions. Whether or not these functional patterns collapse down to one or a few composite axes of functional differentiation, such an approach might shed light on traits involved in facilitation, and whether similar traits apply across diverse facilitative mechanisms and ecosystems to generate more refined theories.

Here, we present a framework for integrating functional traits into our understanding of facilitation in plant communities. We begin by reviewing several studies that have assessed the functional basis of facilitation, then fill in gaps in our empirical knowledge of trait-based facilitation by summarizing shifts in the values of key functional traits in response to environmental variables that are associated with several common facilitative mechanisms (i.e. response traits), as well as the functional traits that may be responsible for generating relevant environmental feedbacks (i.e. effect traits). We use these results to predict how and to what extent the functional strategies associated with facilitation might exhibit generality versus environmental context dependence. Finally, we outline empirical methodologies that can be used to build a trait-based, comparative understanding of the balance between facilitation and competition that will help to refine hypotheses regarding the roles of biotic interactions in community assembly and the regulation of functional diversity.

Evidence for trait-based facilitation

There is empirical support across a variety of ecosystems for functional differentiation among species in both their facilitative responses and effects. For example, Butterfield & Briggs (2011) found that desert shrub species that required nurse plants for establishment had conservative functional strategies [low turnover and high efficiency, *sensu* Wright *et al.* (2004)] both as seedlings and at maturity, whereas species that colonized open ground had the opposite strategy. They attributed these patterns to the consistent light-limited environment beneath canopies versus fluctuating soil moisture in open microsites. Valiente-Banuet *et al.* (2006) found similar patterns in traits of Mediterranean-climate woody plants with respect to facilitative responses, but also found a strong pattern in facilitative effects. Not only did mesic-adapted Tertiary species (deep root systems, large leaves with low specific leaf area (SLA) and more negative minimum pressure potentials) require nurse plants far more than xeric-adapted Quaternary species with contrasting traits, the latter also facilitated the former. Whether Quaternary species are better nurses because of lower niche overlap with Tertiary species (reduced competition), canopy trait values that create a less stressful microenvironment or both is not clear. Similarly, benefactor and beneficiary species could be

categorized as competitive and stress tolerant, respectively, in both mesic grasslands (Liancourt, Callaway & Michalet 2005) and coastal dunes (Forey, Touzard & Michalet 2010) in Europe, but again the specific trait(s) associated with facilitative effects were not studied. In an alpine ecosystem, Schöb, Butterfield & Pugnaire (2012) found strong functional differentiation between species that performed better in cushion plants versus bare ground, with the latter having lower leaf dry matter content (LDMC) and higher SLA (although the SLA pattern switched from low to high elevations).

These examples demonstrate that many traits may be related to facilitation, but suggest that the relevant traits may depend largely on environmental context. While there are few studies that have directly assessed the trait basis of facilitation, the literature is rich with data on functional trait responses to variation in the abiotic environment in ways that can inform trait-based facilitation (Grime *et al.* 1997; Westoby *et al.* 2002; Cornwell & Ackerly 2009; Swenson & Weiser 2010). Most plant–plant interactions occur through direct or indirect modification of the local environment, and thus, the traits that allow species to respond well to such ameliorated environments may help to identify functional responses to facilitation. Identifying facilitative effect traits may be more difficult, as the concept of effect traits has been primarily considered in a narrower context of ecosystem functioning (Lavorel & Garnier 2002; Navas & Violle 2009). Traits associated with facilitative mechanisms such as canopy shade, herbivore deterrence or hydraulic lift may therefore lie outside the bounds of traditionally measured functional traits (Cornelissen *et al.* 2003).

Identifying relevant traits also requires identifying the particular resources or stresses that limit plant performance within a particular environment – the abiotic filters – and in many systems, this is difficult. A trait related to a facilitative response or effect in one context may be meaningless in another or even have opposite consequences for performance; for example, in two case studies from arid and alpine ecosystems, beneficiaries have higher and lower LDMC than colonizers, respectively (Butterfield & Briggs 2011; Schöb, Butterfield & Pugnaire 2012). To address this complexity, links between specific functional traits and a variety of facilitative mechanisms may help to identify important differences in the nature of stress and stress amelioration by neighbours. By summarizing empirical relationships between functional trait responses to and effects on a variety of environmental filters, we can begin to ask: what are the expected commonalities and differences in functional strategies associated with facilitation under different environmental contexts?

Facilitative response and effect traits

FACILITATIVE RESPONSE TRAITS

Many different functional traits may regulate biotic responses to environmental variation. Rather than attempt to consider all of them, we focus on three traits that probably have been the most frequently measured and likely to be relevant under most circumstances: SLA, asymptotic height at maturity and seed mass. This leaf-height-seed (LHS) scheme was proposed by Westoby (1998) as an empirically simplified analogue to the CSR model of Grime (1977) and has been adopted by many ecologists (Weiher *et al.* 1999; Golodets, Sternberg & Kigel 2009; Laughlin *et al.* 2010) as a way to generalize about the traits that contribute to particular interactions and community organization. While other traits are likely to be more relevant in specific conditions, the LHS scheme is thought to represent biophysically independent axes of functional differentiation that should generally correspond with other, less readily measurable traits (Westoby 1998).

Based on the literature, functional responses to facilitation predicted for LHS fall into several basic categories (Table 1). The one common predicted response across all facilitative mechanisms is an increase in the number of relatively tall species within a community. This loosening of environmental restrictions on tall plants is variously associated with reduced demands on water transport (Moles *et al.* 2009; Poorter *et al.* 2010), reduced risk to exposed perennating tissues (Körner 1998) or reduced allocation to roots (Mokany, Raison & Prokushkin 2006), or structural integrity (Iida *et al.* 2012). This pattern of facilitation of taller plants is indeed found in arid systems (Butterfield & Briggs 2011), but has not been directly tested in others. In contrast to height, SLA and seed mass demonstrate varying responses to the range of environmental filters that facilitation modifies in different environments (Table 1). Furthermore, with the exception of response to indirect facilitative effects via amelioration of herbivory, the responses of these two traits are inversely correlated with one another (i.e. in circumstances where high-SLA species are selected against, so too are low-seed-mass species, and vice versa).

The inverse responses of SLA and seed mass to environmental variation fall into two general categories. First, facilitation of low-SLA, high-seed-mass species otherwise excluded by harsh environmental filters is expected when neighbours buffer disturbances, resource fluctuations or frost intensity, all of which may be more or less associated with protection from periodically unfavourable conditions. Species with low SLA tend to be excluded from environments with short growing seasons or windows of opportunity, as can occur after physical disturbances (Kuehner & Kleyer 2008; Kyle & Leishman 2009), brief precipitation pulses in arid ecosystems (Butterfield & Briggs 2011) and in cold environments at high altitudes or latitudes (Niinemets 2001). In these cases, the slower rate of return on longer-lived leaves with low SLA (Reich, Walters & Ellsworth 1992; Wright *et al.* 2004) may exclude them from environments with short favourable intervals. Small seeds provide another opportunity for coping with such environments, in which their higher relative growth rates may allow them to respond to relatively short windows of opportunity in disturbed (Grime *et al.* 1997), pulsed

Table 1. General responses of specific leaf area (SLA), height and seed mass to different environmental filters and interaction mechanisms, grouped by solid lines based on similar trait responses. Environmental filter indicates the primary environmental factor limiting trait distributions, where filter effect indicates selection of the environmental filter on that trait (e.g. a negative effect indicates exclusion of species with relatively high values of a given trait, and vice versa). For each facilitative mechanism, the predicted effect on trait values is based on loosening of the relevant environmental filter. A '/' indicates no effect of that filter on the focal trait distribution. Water and nutrient reduction in neighbours via competition are presumed to have the same effects as similar environmental filters, whereas light competition effects are drawn directly from the competition literature. Trait responses shaded grey are associated with predicted responses to facilitative and competitive mechanisms in isolation, while the matrix in the lower right indicates the predicted net trait responses to facilitation and competition. Superscript numbers correspond with references provided in Appendix S1 (Supporting information).

Environmental filter	Trait	Filter effect on trait	Facilitative mechanism	Competitive mechanism			
				None	Light	Water	Nutrients
	SLA		None		−[25-27]	−[21,9]	−[15]
	Height				+[18]	−[12]	−[5,30]
	Seed				+[28,29]	+[14,16,17]	+[28]
Disturbance	SLA	+[1,2]	Disturbance buffer	−	− −	− −	− −
	Height	−[3,4,5]		+	++	/	/
	Seed	−[6,7]		+	++	++	++
Pulsed resources	SLA	+[8]	Resource fluctuation buffer	−	− −	− −	− −
	Height	−[8]		+	++	/	/
	Seed	−[8]		+	++	++	++
Low temperature	SLA	+[9,10,11]	Increased temperature	−	− −	− −	− −
	Height	−[12,13]		+	++	/	/
	Seed	−[14]		+	++	++	++
Water stress	SLA	−[9,10,15]	Reduced evapo-transpiration	+	/	/	/
	Height	−[12]		+	++	/	/
	Seed	+[14,16,17],/[14]		−	/	/	/
High temperature	SLA	−[9,10]	Reduced temperature	+	/	/	/
	Height	−[12]		+	++	/	/
	Seed	+[14]		−	/	/	/
Low fertility	SLA	−[15]	Enhanced fertility	+	/	/	/
	Height	−[5,18]		+	++	/	/
	Seed	+[19],/[20]		−,/	/	/	/
High salinity	SLA	−[21]	Reduced salinity	+	/	/	/
	Height	−[18]		+	++	/	/
	Seed	?		?	+	+	+
Herbivory	SLA	/[22],/+[23,24]	Herbivore deterrence	/,/−	−	−	−
	Height	−[22],/		+,/	+	/	/
	Seed	+[17]		−	/	/	/

(Butterfield & Briggs 2011) and frost-prone (Moles *et al.* 2005) environments. Nurse plants may relax these conditions by reducing the negative impacts of disturbance and effectively lengthening disturbance intervals, buffer fluctuations in soil moisture and nutrients typical of arid ecosystems by shading or hydraulic lift, and extending the growing season by buffering frosts.

The second general category of predicted facilitative responses involves the improved performance of high-SLA and low-seed-mass species in the presence of neighbours because of reduced evapotranspiration, temperature or salinity, and increased fertility. In environments where these mechanisms are relevant, restrictions on high-SLA species are likely to be due to their relatively low resource use efficiency. High-SLA species also may not be able to maintain favourable water relations or temperature levels in arid and hot environments (Niinemets 2001; Wright, Westoby & Reich 2002; Wright *et al.* 2004) and require higher levels of nutrients and water content to achieve their characteristically high maximum photosynthetic rates

(Niklas *et al.* 2007). Thus, the potential benefits of high photosynthetic rates may be more than offset by unmet resource demands, and in this case, a nurse species may ameliorate these resource restrictions by producing more benign and/or resource-rich local environments. Restrictions on small-seeded species are likely associated with limited energy stores and weak initial radicle development that may limit access to nutrient pools (Guerrero-Campo & Fitter 2001; Hallett, Standish & Hobbs 2011). Neighbours may buffer small-seeded species from extreme conditions that lead to rapid mortality, and also enhance shallow soil moisture and mineral nutrient pools that sustain growth. It is interesting to note that persistent water stress versus pulsed soil moisture predicts different SLA and seed mass responses to facilitation, which may provide useful insights into precisely how soil moisture limitation influences community assembly in different environments.

Predicted functional responses to protection from herbivory fall into a separate category, in part due to a

potentially positive correlation between seed and SLA responses (e.g. small-seeded and low-SLA species may be relatively intolerant to herbivore damage), but also because of difficulties of differentiating tolerance and avoidance associated with SLA and height. Seed mass may exhibit the most consistent response to herbivory of the LHS traits, where relatively small-seeded species are most negatively impacted (Moles & Westoby 2004), likely due to relatively low energy reserves for recovery from defoliation. Protection by unpalatable neighbours may provide a longer enemy-free establishment period for small-seeded species, so they can grow large enough to tolerate herbivory. Low-SLA species may also be most sensitive to herbivory, because of the investment necessary to replace their relatively costly leaf tissues (Wright & Cannon 2001), and may therefore benefit more from herbivore protection than high-SLA species. However, low-SLA species may be avoided by herbivores because of generally lower nutrient content, thereby weakening the potential relationship between SLA and herbivory. Similarly, tall species are often excluded from herbaceous communities with high grazing intensity and may be facilitated by unpalatable neighbours (Cingolani, Posse & Collantes 2005), although the same pattern may not hold across different growth forms (Vesk, Leishman & Westoby 2004). Thus, variation in SLA and height responses to herbivory may be attributed to avoidance and tolerance strategies as well as characteristics of the herbivores themselves, creating greater potential for idiosyncratic relationships between functional traits and facilitation associated with herbivory.

COMPETITIVE AND NET RESPONSES

Positive and negative effects of neighbours often occur simultaneously (Callaway & Walker 1997). Thus, to fully understand the net response of plants to their neighbours based on functional traits, responses to competition should also be considered. Based on empirical responses of LHS to three specific resources – light, water and mineral nutrients – in the literature, we assessed how the negative effects of neighbours on those resources might restrict species based on their trait values.

The predicted trait-based responses to competition are remarkably similar across the three most common limiting resources, when these resources are considered in isolation. Small-seeded species are expected to suffer stronger negative impacts of competition for light (Leishman & Westoby 1994; Poorter & Rose 2005), water (Moles & Westoby 2004) or mineral nutrients (Schwinning & Weiner 1998) than large-seeded species, and this is the same for high-SLA species for light (Kitajima1994; Walters & Reich 1999; Markesteijn & Poorter 2009; Poorter *et al.* 2009), water (Niinemets 2001; Poorter *et al.* 2009) or mineral nutrients (Wright, Westoby & Reich 2002). Relatively, short plants are expected to be the most negatively affected by competition for light (Givnish 1995), whereas taller plants may perform worse in competition for water (Ryan

& Yoder 1997) or nutrients (Bongers, Engelen & Klinge 1985; Tilman 1988).

Depending upon the mechanisms, simultaneous responses to competitive and facilitative effects of neighbours may either reinforce or counteract one another (Fig. 1). This can make it harder to generalize about net
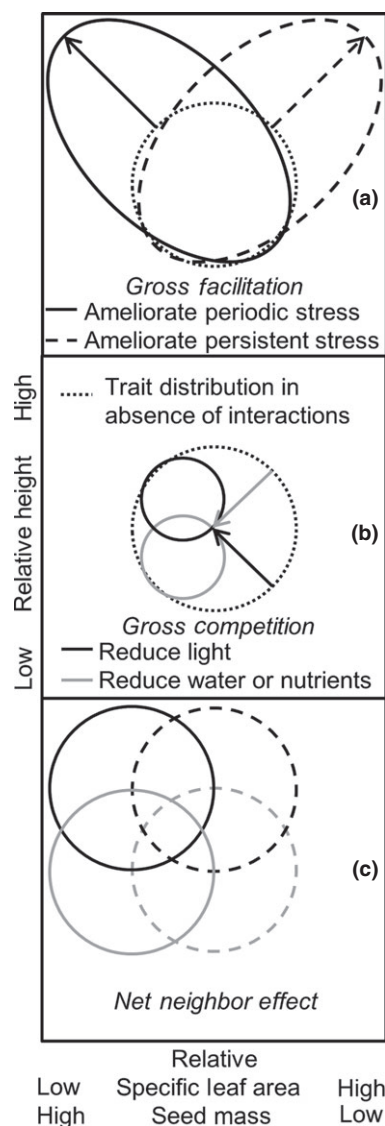
Fig. 1. Predicted trait-based responses of plant communities to facilitative and competitive effects of neighbours. Periodically stressful conditions include disturbance, pulsed precipitation and frost. Persistently stressful conditions include persistent drought, soil infertility, high salinity and high temperatures (see text for discussion). The local trait distribution generated by the environmental filter alone, which can be measured on isolated individuals or through neighbour removals, is represented by the central dotted circle. Facilitation expands the local trait distribution (a), while competition causes a contraction of the trait distribution (b). The net effect (c) is either a shift in the local trait distribution if facilitation and competition influence different ends of the distribution, or no net effect on the distribution if they influence the same end of the distribution (e.g. dashed grey line; amelioration of persistent stress coupled with competition for water or nutrients).

trait-based responses to neighbours, rather than gross facilitative and competitive effects in isolation. Facilitative mechanisms that generally exhibit reinforcing trait-based selection with competition include buffering of temporally dynamic limitations such as disturbance, pulsed resources or low temperatures. In these cases, facilitation results in an expansion of the trait distribution in the direction of taller plants with large seeds and low SLA (Fig. 1a), while competition for nutrients or water results in a contraction of the trait distribution that eliminates shorter plants with small seeds and high SLA; competition for light results in a similar contraction of seed and SLA values, but also eliminates taller plants (Fig. 1b). The net result is a relocation of the trait distribution, rather than a change in its volume, with the strongest shift occurring with buffering of dynamic limitations coupled with competition for nutrients or water (Fig. 1c). In cases where facilitation ameliorates more persistent limiting factors such as persistent water stress, high temperatures, low fertility and salinity, the expansion towards taller plants with small seeds and high SLA (Fig. 1a) is counteracted by competition for nutrients or water, which itself would cause a contraction in the opposite direction of the trait distributions (Fig 1b). The net effect is no change in the trait distributions, although competition for light may reinforce the facilitative selection for taller plants (Fig. 1c). Finally, with respect to herbivory, facilitation of low-SLA species may be reinforced because of competition for light water or nutrients, whereas facilitative benefits to low-seed-mass species may be negated by competition (not shown in figure), although again relationships between LHS traits and herbivory may be highly variable.

The simultaneous effects of facilitation and competition have important implications for the distributions and spatial patterning of functional traits within communities. In circumstances where competition and facilitation exhibit reinforcing selection, one tail of the trait distribution contracts while the other expands, the net result being a relocation of the trait distribution rather than an expansion or contraction. This relocation of trait space may nevertheless enhance functional diversity in low-productivity or frequently disturbed ecosystems where vegetative cover is low, with the unmodified trait distribution occurring in bare patches and the relocated trait distribution occurring beneath or next to suitable nurse plants (Butterfield & Briggs 2011).

Synergistic versus counteracting selection by competition and facilitation also presents an interesting prediction regarding the prevalence of net positive interactions among plants. Assuming that gross facilitative and competitive effects are of similar magnitude, net facilitation may be expected to occur more frequently in the presence of dynamic conditions of disturbance, precipitation pulses and frost than in environments typified by persistent water stress, high temperatures, low fertility or salinity, although places with persistent stress or resource limitations are often also characterized by highly dynamic conditions; for

example alpine and desert ecosystems. This follows from the prediction that in dynamically stressful environments, facilitation and competition create local microenvironments that synergistically select for species with particular trait values, whereas persistently stressful environments are those in which competitive and facilitative effects counteract one another. The relative intensity of gross facilitative and competitive effects, however, varies along gradients of environmental severity, and net facilitation certainly occurs in the latter set of environments. Ontogenetic niche shifts may also result in strong facilitative effects for juveniles that shift to competition at maturity (Schupp 1995; Miriti 2006), creating the potential for strong net facilitation in persistently severe environments. However, all else being equal, net facilitation may be prevalent along a broader range of environmental conditions when trait-based responses to facilitation and competition are similar, and potentially restricted to the most severe environments when trait-based responses to facilitation are counteracted by responses to competition.

In summary, the predicted responses of three fundamental functional traits – SLA, height and seed mass – to the facilitative effects of neighbours fall into at least three categories, one typified by periodically unfavourable conditions, a second by persistent unfavourable conditions and a third by herbivory. In the context of general functional strategies, the first category results in species with conservative functional strategies (i.e. stress tolerators or K-selected species) occurring in environments otherwise dominated by more ruderal species. The second category includes facilitation of species with relatively acquisitive trait values (i.e. competitive species in the CSR triangle), while protection from herbivory may result in facilitation of either competitive or stress-tolerant species. None of the facilitative mechanisms considered here are likely to enhance the performance of ruderal species. Including simultaneous competitive effects of neighbours suggests that under dynamically unfavourable conditions, functional responses to facilitative effects of neighbours are likely to be reinforced, while facilitative responses may be counteracted in more persistently stressful environments. While the balance between competition and facilitation, and thus associated functional responses, is likely to vary along any of the aforementioned environmental gradients, we predict that the net effects of biotic interactions on local trait distributions are likely to be strongest in environments typified by strong cycles of favourable and unfavourable periods.

FACILITATIVE EFFECT TRAITS

Functional traits that determine facilitative effects are likely to be just as diverse as those related to facilitative responses. As a convenient set of traits such as LHS does not currently exist in the context of biotic effects on environmental filters, here we take a more exploratory, or speculative, approach to considering several traits that

may be particularly relevant across most facilitative mechanisms. In fact, we suggest that one functional trait, in particular leaf area index (LAI), may be exceptionally influential. A canopy with high LAI during severe conditions or integrated over the months or years necessary for establishment of beneficiaries may be critical for reducing drought or salinity stress via reduced evapotranspiration rates, as well as minimizing both high- and low-temperature extremes by buffering temperature fluxes. Other facilitative mechanisms tend to be associated with more species-specific functional traits and thus may not extend to functional strategies related to facilitation more generally. For example, soil fertility enhancement may largely be a function of litter quality and quantity (Facelli & Pickett 1991), and protection from herbivory is often because of proximity to an unpalatable neighbour (McAuliffe 1984, 1986). However, palatability is a complex trait that may be a function of highly variable forms of chemical and physical defences. Deep-rooted plants can benefit neighbours in two very different ways, through hydraulic lift in water-limited systems (Zou *et al.* 2005) and possibly by maintaining a buffer against physical disturbances. While these specific traits should be considered in certain conditions, LAI may still play an important role in determining facilitative and competitive effects of neighbours in severe environments.

High LAI may tip the balance between facilitation and competition not only by ameliorating a variety of environmental stresses directly, but also through competition for light (Holmgren *et al.* 2012). High-LAI species tend to reduce light quantity or quality beneath their canopies, thereby having a potentially competitive effect on neighbours (Reinhart *et al.* 2006), even though shade from canopies can be simultaneously highly facilitative through other mechanisms (Baumeister & Callaway 2006). Given the predicted functional responses outlined in the previous sections, in environments where LAI buffers cycles of environmental extremes, the net effects of high-LAI canopies might be predicted to drive strong functional differentiation between beneficiary and nonbeneficiary species and thus strongly increase functional and taxonomic diversity in communities, whereas the net effects may be less pronounced in more persistently stressful environments.

In addition to potentially driving trade-offs between responses to environmental severity and competition for light, LAI may interact with other traits in ways that determine their facilitative effects. For example, protection from herbivory is often a function of the density of plant canopies (Hutto, McAuliffe & Hogan 1986), not just palatability, such that unpalatable neighbours with high LAI may be most effective in protecting palatable plants. Effects of litter quality on soil fertility are also strongly influenced by the amount of litter produced (Facelli & Pickett 1991), not just its composition, which may be strongly correlated with LAI. Effects of rooting depth on soil moisture via hydraulic lift are certainly accentuated by the shade created by high-LAI canopies (Zou *et al.* 2005),

and the resistance of deep-rooted plants to physical disturbance may translate into a stronger above-ground facilitative effect if that neighbour also has a dense, high-LAI canopy. Variation in LAI may therefore explain a great deal of variation in facilitative effects of neighbours, even if it is due to interactions with other traits.

Facilitative effect traits can be compared with general functional strategies much the same as facilitative response traits, although the linkages may be less clear when comparing taxa with very different growth forms (e.g. herbaceous versus woody). In water-, light- or nutrient-limited environments, high LAI may be associated with high competitive ability or inversely with low 'stress tolerance', because high-LAI canopies require substantial water and nutrient transport coupled with light availability to support high rates of photosynthesis (Sterck *et al.* 2011). However, high LAI may also be associated with persistent access to resources and high leaf longevity in some water-limited systems (Nilsen, Sharifi & Rundel 1984) and with buffering of extreme temperatures in other systems (e.g. alpine cushion plants; Badano *et al.* 2006), thereby corresponding with more conservative functional strategies. This context dependence might be expected for such a complex trait as LAI and may reduce the utility of general functional strategies for categorizing species' facilitative effects across different environmental conditions. High litter quality, however, tends to be consistently associated with resource-acquisitive functional strategies because of relationships between leaf nutrient content and photosynthetic capacity, while rooting depth and herbivory defences tend to be associated with more conservative functional strategies. In summary, facilitative effect traits may be associated with traditionally defined functional strategies to varying degrees, although some traits (e.g. LAI) may be related to different functional spectra in different environments, thereby making generalizations about functional strategies and facilitation somewhat system specific.

Facilitation and trait-based comparative ecology

The relationships among functional traits and particular facilitative mechanisms provide a useful starting point for structuring the results of the myriad of empirical studies of facilitation into a general framework. By explicitly incorporating measurements of functional traits, theory related to facilitation may advance more rapidly in two complementary ways. First, traditional facilitation studies that measure modification of the local environment by neighbours and the performance response of target plants can provide important tests of the links between specific functional traits, as explored here, and the mechanisms by which facilitation occurs. Some existing studies have great comparative potential (Dunne & Parker 1999; Bellingham, Walker & Wardle 2001; Kikvidze *et al.* 2005; Gomez-Aparicio, Valladares & Zamora 2006; Armas, Rodriguez-Echeverria & Pugnaire 2011), and we suggest

that *post hoc* measurements of the traits of the species in these experiments may be used to make new comparisons both within and across studies. Functional traits have not been measured for many of the species that occur in severe environments where facilitation is most influential, and these gaps in our knowledge represent a fruitful area of future research. Second, to complement studies that focus their efforts on quantifying mechanisms directly, removal experiments or spatial-pattern analyses that incorporate a comparative approach by focusing on as many species as possible, rather than one or a few target species, may provide a broader picture of the implications of facilitation while bypassing time and labour-intensive microenvironmental measurements. A combination of these direct and indirect approaches is essential for using trait generalities for predictive models at broad spatial and temporal scales.

Trait-based approaches to facilitation may also help to integrate positive interactions into a rapidly developing body of literature on trait-based empirical models for community assembly (Ackerly & Cornwell 2007; Cornwell & Ackerly 2009; Pillar *et al.* 2009; Götzenberger *et al.* 2012). When compared with randomized assemblages, trait distributions within and across communities can provide insights into community assembly rules that cannot be achieved through traditional approaches based on taxonomic identity. Such models have had substantial impacts on community ecology in recent years (McGill *et al.* 2006; Messier, McGill & Lechowicz 2010). It is important to note, however, that the strength of inferences made from trait-based studies can be low because of alternative processes that can produce similar trait-based patterns; thus, integration of trait-based approaches with experimentation is crucial. For example, competition because of limiting similarity may result in communities with greater-than-expected trait differences among co-occurring species (Weiher & Keddy 1995), but so too can environmental heterogeneity (Cornwell & Ackerly 2009). Restrictive environmental filters may reduce the range of trait values within a community (Cornwell, Schwilk & Ackerly 2006), but so can the competitive effects of a dominant species (Podani 2009). While rarely considered, facilitation too can blur the link between trait pattern and ecological process. Net positive effects can expand the range of trait values within a community, which can produce the same pattern as a less-restrictive abiotic environment (Schöb, Butterfield & Pugnaire 2012). In fact, many studies have demonstrated that functional trait variation within communities is often greater than across relatively broad gradients in environmental variation (Wright *et al.* 2004; Ackerly & Cornwell 2007; Kooyman, Cornwell & Westoby 2010; Gleason *et al.* 2012), a potential consequence of facilitation that is rarely incorporated into trait-based studies of community assembly (Spasojevic & Suding 2011). The balance between simultaneous competition and facilitation will produce even more complex patterns, because improving conditions for a certain set of species

and reducing favourability for others can cause shifts in the mean or clustering of trait distributions but without altering the range (Schöb, Butterfield & Pugnaire 2012). There is no simple solution to these problems, but any attempt to address them will require manipulative experiments and analysis at multiple spatial scales to differentiate pattern from process. An important aspect of any such research will be to recognize the ways in which facilitation acts concomitantly with abiotic filters and competition to influence trait distributions of plant communities.

Conclusions

Our analysis of trait–environment relationships suggests that there is potential for discovering generality in the functional basis of facilitation (e.g. two primary responses in LHS trait space), but a single functional strategy is not likely to be related to facilitation dependence across all systems. This may be due to the variability in traits determining facilitative effects and responses in different abiotic environments, and the complex role facilitation plays in determining net interaction effects (Callaway 1992; Callaway & Mahall 1996). Traits related to the balance between facilitation and competition can have important implications for vegetation structure and dynamics and represent an exciting opportunity to incorporate facilitation into trait-based community ecology. Functional ecology is a rapidly expanding field that is linking the processes that regulate biodiversity and ecosystem functions in powerful new ways, and the design and implementation of experiments seeking to understand the distribution of functional diversity can benefit greatly from accounting for positive interactions among plants, which is one of many alternative processes that need to be critically compared when examining patterns of trait distributions. Achieving this goal will require a combination of manipulative experiments and much more extensive sampling of functional traits in moderate- to high-severity environments where facilitation is most prevalent.

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Supporting Information

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

Appendix S1. References for Table 1.