FORUM

Strong facilitation in mild environments: the stress gradient hypothesis revisited

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Summary

1. The idea that the role of facilitative interactions increases as environmental conditions become more stressful has become a ruling paradigm in ecology. Here, we review three reasons why positive interactions may actually be more prominent than generally thought under moderately stressful rather than under extreme conditions.

2. First, there is evidence that in some communities the net effect of amelioration of shortage of a limiting resource, such as water under the canopy of nurse plants, may be beneficial under moderate conditions whereas it can be overruled by increased competition for the same resource in very harsh environments.

3. Secondly, we show that even in situations where the relative role of facilitation increases monotonically with stress, the absolute effect should as a rule be largest at intermediately stressful conditions. This is because under the harshest conditions, facilitative amelioration of conditions is insufficient to allow growth altogether. Therefore, while facilitation will expand the range of conditions where an organism may occur, the largest absolute effects on biomass will always occur under less stressful conditions.

4. A third reason why facilitation may be more important under moderate conditions than previously thought is that in any ecosystem, the suite of organisms is adapted to local conditions. This implies that even under conditions that appear benign, facilitation may play an unexpectedly large role as organisms are simply more sensitive than those found under harsher overall conditions.

5. *Synthesis.* We argue that while facilitation will extend the range of conditions where an organism can occur, it should also boost performance of the species well into the more moderate range of conditions. Broadening our search image for facilitative effects towards milder environments will reveal wider than expected prevalence of positive interactions and their effects on stability and diversity in nature.

Key-words: abiotic amelioration, community, competition, grazing, herbivore, nurse plant, plant–plant interactions, positive interaction, predator, stress

Introduction

The recognition of the ubiquitous role played by facilitation in the organization of ecological communities has major implications for theoretical frameworks in ecology (Bruno, Stachowicz & Bertness 2003). In an influential article, Bertness & Callaway (1994) predicted the role of facilitative interactions to increase with the harshness of abiotic or biotic challenges to species. Many studies have confirmed this stress gradient hypothesis (SGH; Callaway 2007). While most work has focused on plant communities (Callaway 2007), results from animal communities tend to be in line with the SGH as well. For instance, in sessile marine animal communities facilitation is more prevalent under harsher conditions (Bertness *et al.* 1999; Stachowicz 2001; Kawai & Tokeshi 2007), and in terrestrial herbivore assemblages small grazers depend on larger ones on sites dominated by nutritionally low quality forage, where larger grazers are essential to promote high quality regrowth (Arsenault & Owen-Smith 2002).

The reasons to expect facilitation under more extreme conditions are intuitively straightforward. Facilitative amelioration of a given stressor is obviously more important if that

stressor is more severe. Together with the fact that facilitating species always have negative impacts as well, this explains why the role of facilitation will tend to diminish as conditions become more benign, and competition will become prevalent (Holmgren, Scheffer & Huston 1997).

The empirical research inspired by the SGH conceptual model has led to rather diverse outcomes depending on the interacting species (Callaway 2007), their ontogenic stage (Miriti 2006; Nuñez *et al.* 2009), the indicators used to evaluate plant performance (Gómez-Aparicio *et al.* 2005), the type of stress factor (Kawai & Tokeshi 2007) and the magnitude of the stress imposed (Kitzberger, Steinaker & Veblen 2000; Tielbörger & Kadmon 2000; Callaway *et al.* 2002; Maestre & Cortina 2004; Holzapfel *et al.* 2006). This has stimulated considerable debate in plant ecology (Maestre, Valladares & Reynolds 2005, 2006; Lortie & Callaway 2006) and has motivated refinements to the original SGH model. Based on the classical work of Grime (1979), Michalet *et al.* (2006) reasoned that the facilitation effects would depend on the life history of the interacting species (stress tolerance vs. competitive ability of benefactor and beneficiary) and that contrary to what is expected by the SGH model, facilitative interactions would probably be insufficient to expand the niche of stress-intolerant competitive species under the most stressful conditions, resulting in a decline in species diversity towards the most stressful end of an environmental gradient. Later on, Maestre *et al.* (2009) expanded these ideas with predictions that fall largely into two categories: (i) facilitation is predicted to increase with stressfulness of conditions when the abiotic stress gradient is not driven by resource limitation (e.g. temperature) or when the beneficiary (facilitated) species is stress tolerant; and (ii) a hump-shaped model with negative interactions overruling facilitation at both ends of the stress gradient is predicted especially when the stress gradient is driven by a resource, such as water or when both benefactor and beneficiary species have similar life histories.

These refinements to the SGH model are thought provoking. However, as acknowledged by Maestre *et al.* (2009), detailed predictions are difficult without a mechanistic understanding of the nature of the stress, the effects of the benefactor species on the stress and the ecophysiological tolerances of the interacting species to the stress. In this article, we use a simple model based on the response of plants to water and light and the effects of plants on the availability of these two resources, to argue that the effects of facilitation may often be more important under relatively benign conditions than in the most stressful situations. Although this point has been made earlier for particular dry plant communities, where the positive effect of nurse plant canopies on microsite microclimate conditions can be overruled by negative effects of competition for soil water (Maestre *et al.* 2009), we will demonstrate that this can be generalized. We will first show that irrespective of whether the relative effect of facilitation declines at the extreme end of the range of conditions or not, the absolute effect of facilitation on performance will be largest under moderately stressful conditions. Subsequently, we will argue that if we compare across regions at larger scales, facilitation will tend to be important

in regions where conditions may seem benign at first glance, simply because organisms adapted to such environments are more sensitive to stress. Our conceptual model is based on two key resources widely studied by plant ecologists, but as we will discuss later, the basic results can be expanded to understand the role of other stressors.

Absolute and relative facilitation effects along stress gradients

A GRAPHICAL MODEL

We will illustrate what may happen to the absolute and relative effects of facilitation along a stress gradient, using a graphical model of the effects of nurse plants (benefactor) on water and light for small plants, such as seedlings growing in their vicinity (beneficiaries). While numerous forms of facilitation are widespread across the plant and animal kingdoms, a particularly large number of studies address this type of facilitation in plant communities (Callaway 2007). It has often been shown that in dry environments, shading by nurse plants may promote growth and survival of plants in the understorey through positive effects on water conditions (Holmgren, Scheffer & Huston 1997). In contrast, light limitation may negatively impact the beneficiaries if the canopy of the benefactor becomes denser (Forseth, Wait & Casper 2001; Valladares & Pearcy 2002), and in some dry environments competition for soil moisture may counteract the positive effects of reduced transpiration rates often found under the canopy (Valladares *et al.* 2008).

Following earlier work (Holmgren, Scheffer & Huston 1997; Holmgren 2000), we assume that growth of a plant increases with the availability of water and light (Fig. 1a). We also assume that along gradients from under the canopy of a nurse plant to the open, light will increase, but microsite moisture availability will simultaneously decrease. Microsite moisture is used here as the combined effect of microclimatic conditions and soil water availability on plant water relations. In the model (Fig. 1a), four hypothetical gradients from the canopy to the open are represented by dashed lines (I–IV). Each line represents the gradient in a different climatic situation, from mesic (I) to xeric (IV). The relationship between microsite light and microsite moisture along the gradients is reflected in the projections of the four curves on the bottom plane. In our first situation (Fig. 1a), we assume that the relative change in microsite moisture along the gradient from the open to the canopy is smallest in the most mesic areas (e.g. a very rainy temperate climate) and strongest in the driest areas.
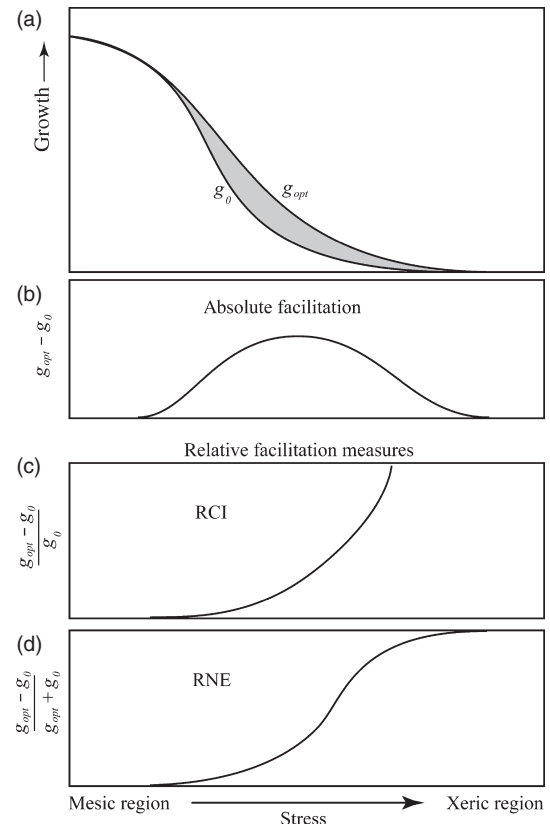
It can be seen from this representation that in dry areas (curve III), the positive effect of improved moisture may overrule the negative effects of shade over part of the gradient from the open to the canopy. As a result, maximum growth (g_{opt} open dots) may appear under a certain optimal level of canopy protection. Since microsite moisture nevertheless decreases with overall drought in an area, the expected gains from facilitative canopy shade eventually decline to zero as we go to xeric environments (curve IV; also, protective canopies will become increasingly sparse in more xeric environments, limiting the

(a)

Growth

(b)
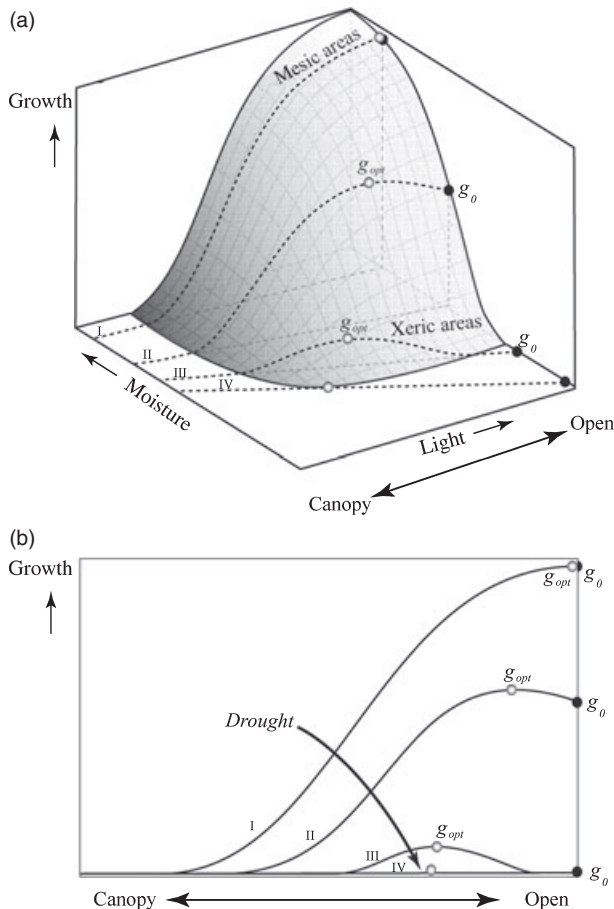
Growth

Fig. 1. Graphical model to illustrate how the growth of seedlings may change along gradients from the canopy to the open (curves I–IV in both a and b). The surface (a) represents growth as a function of light and moisture conditions, assuming a physiological trade-off between drought tolerance and shade tolerance (Holmgren, Scheffer & Huston 1997). From the canopy to the open, light increases, but depending on overall climatic conditions, microsite moisture available to the seedlings decreases. Curves I–IV in both (a) and (b) represent the growth response of seedlings to such correlated changes in light and moisture in four different kinds of environment, from mesic (I) to xeric (IV). The effect of increasingly dry conditions can be seen from the difference between growth in the open (g_0) and growth under an optimal facilitative canopy (g_{opt}) in (b).

shading gradient that will be found). The expected effect of regional climate on the growth of seedlings along a gradient from dense canopy to the open can be compared more easily by plotting the growth curves (I through IV) in two dimensions (Fig. 1b).

To see how this affects overall facilitative effects, we consider the difference between growth in the open (g_0) and growth under an optimal facilitative canopy (g_{opt}) (Fig. 2a). This representation reveals that the largest gain in absolute growth should be expected under intermediate climatic conditions (Fig. 2b). There are, however, different ways to quantify the net effect of one species on another. It is common to use a relative indicator of interaction strength. A problem if we want to apply such measures to facilitation under harsh conditions is that growth in the absence of facilitation goes to zero. As a result, the classical Relative Competition Index (Wilson &

(a)

Growth

(b)

Absolute facilitation

$g_{opt} - g_0$

(c)

Relative facilitation measures

$\dfrac{g_{opt} - g_0}{g_0}$

RCI

(d)

$\dfrac{g_{opt} - g_0}{g_{opt} + g_0}$

RNE

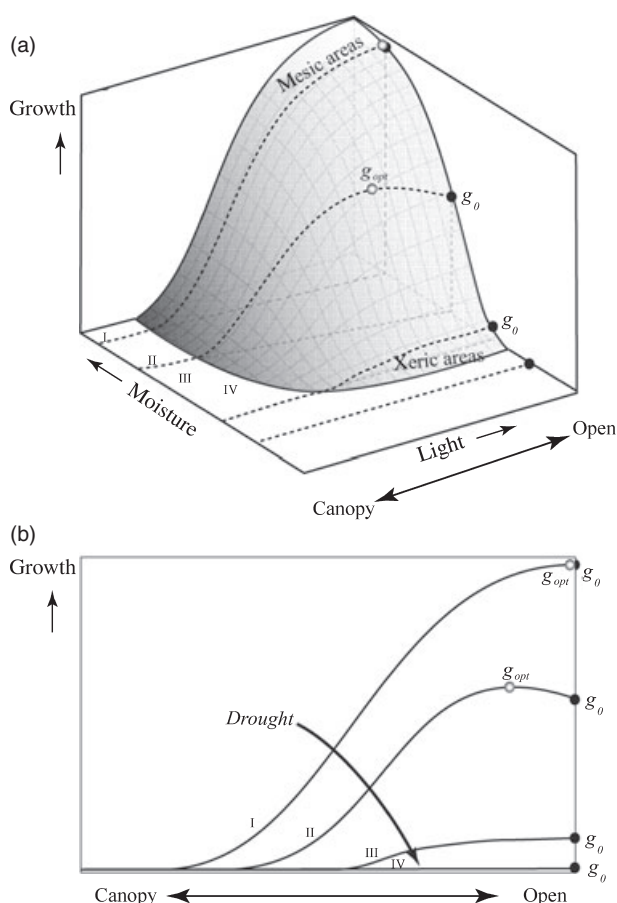Mesic region ⟶ Stress ⟶ Xeric region

Fig. 2. Magnitude of the maximum facilitative effect going from a mesic to a xeric climate inferred from the model presented in Fig. 1. The absolute difference between growth in the open and growth at the optimal level of shade is predicted to be highest under intermediately dry climate conditions (a and b). The relative effect of the canopy measured as the Relative Competition Index (RCI) goes to infinity as growth in the open goes to zero (c). Relative measures of interaction strength avoiding this effect, such as the Relative Neighbour Index (RNE) tend asymptotically to 1 (the maximum) (d) despite the fact that absolute facilitative effects become negligible (see (b)).

Keddy (1986), which puts biomass in the absence of the interaction effect in the denominator, tends to infinity (Fig. 2c). Therefore, other indicators have been proposed more recently, such as the Relative Neighbour Index (Markham & Chanway 1996) and the Relative Interaction Intensity index (Armas, Ordiales & Pugnaire 2004). These tend to a maximum effect of 1 rather than going to infinity (Fig. 2d). Clearly, to make generalizations across environments and species groups we need to quantify the magnitude of interactions between species in a way that allows comparisons. This is an advantage of such relative measures. However, it might be argued that this way of quantifying the role of facilitation overstates the effect of facilitation in harsh environments, as for all practical purposes, measurable facilitation effects will disappear there.

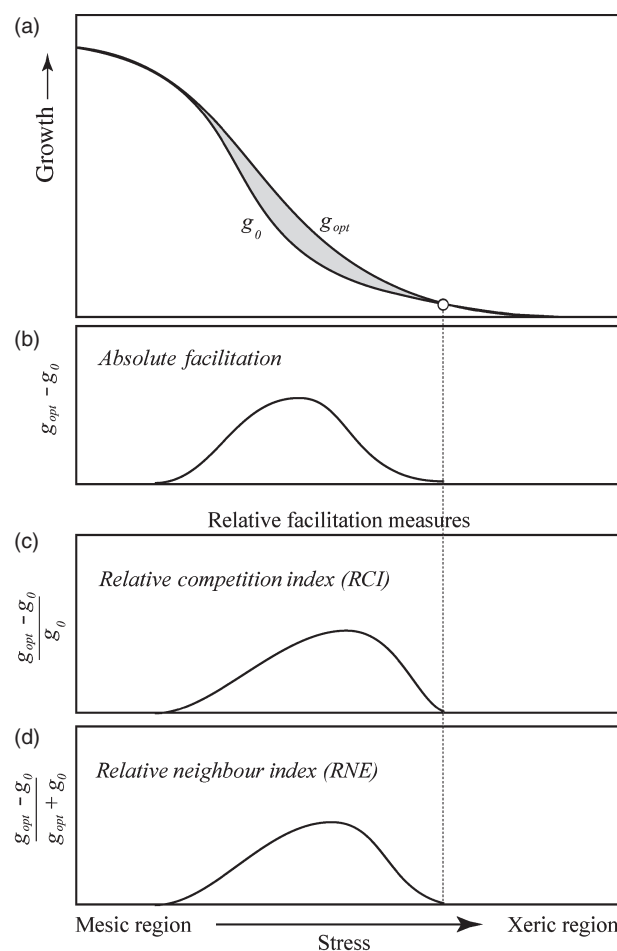CASES WHERE COMPETITION INCREASES UNDER EXTREME CONDITIONS

Microsite moisture conditions in the understorey result from several mechanisms. Although plant canopies often have

cooler and moister air that ameliorates transpiration rates and plant water stress, soil water conditions are more variable. Soil water availability in the understorey results from mechanisms that can act in opposite directions with a net result that is not easily predictable. Lower evaporative demands, improved soil water infiltration and active hydraulic lift all have positive effects on soil water availability in the understorey. However, canopy interception can reduce the amount of water reaching the soil and root competition for water can make understoreys drier than open patches. These negative effects on soil water availability can potentially override the positive ones and as a consequence make conditions drier in shade. So, while the effect of nurse plants on microclimatic conditions is often positive for plants in the understorey, competition for soil moisture may work in the opposite direction. As a result, the net effect of nurse plants on water conditions may be neutral or actually become negative under very dry conditions (Aguiar & Sala 1994; Kitzberger, Steinaker & Veblen 2000; Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Valladares *et al.* 2008). In our graphical model, this situation may be represented by assuming that in xeric systems microsite moisture does not

increase along the light gradient from the open to the canopy (Fig. 3a). As a result, the facilitative effect disappears in the driest systems, and not only the *absolute* effect, but also the *relative* effect of facilitation is highest under moderate conditions (Fig. 4). Some empirical studies have found this hump-shaped pattern. For example, Maestre & Cortina (2004) compared the net effect of the tussock grass *Stipa tenacissima* on the shrub *Pistacia lentiscus* at 10 experimental sites across a gradient of accumulated rainfall in semi-arid Mediterranean steppes. They found that competitive interactions dominated at both extremes of the gradient, whereas facilitation was found under intermediate conditions. In conclusion, our analysis supports the assertion that facilitation may be most important at intermediate stress levels (Michalet *et al.* 2006; Maestre *et al.* 2009). However, it also shows that with respect to *relative* facilitative effects on growth, this hump-shaped pattern is probably limited to particular cases where competition increases under extreme conditions. In contrast,

Fig. 3. As Fig. 1, but assuming that under the driest condition, the net increase of microsite moisture along the gradient from the open to the canopy is lost because of increased competition for soil moisture (see text for further explanation).

Fig. 4. As Fig. 2, but assuming (as in Fig. 3) that under the driest condition, the net increase of microsite moisture along the gradient from the open to the canopy is lost because of increased competition for soil moisture. The dashed vertical line indicates the point in the climatic gradient where the canopy has no net positive effect anymore ($g_{op} = g_0$), and therefore marks the border of the range of conditions for which facilitation is found.

we predict that *absolute* effects of facilitation will always be highest in moderately stressful rather than extreme environments.

BEYOND ABIOTIC STRESS AMELIORATION AND RESOURCE ACQUISITION

Facilitative interactions in plant communities are not only owing to amelioration of harsh abiotic conditions or improvement of resource acquisition, but also commonly arise from protection against herbivores (also called 'associational defence') (Atsatt & O'Dowd 1976). Switches from competitive to facilitative interactions at increasing grazing pressure have been clearly demonstrated in Mediterranean ecosystems (Baraza, Zamora & Hodar 2006), heather vegetation (Brooker *et al*. 2006), Alps woodlands (Smit *et al*. 2007) and the Patagonian steppe (Graff, Aguiar & Chaneton 2007). It is easy to imagine that in most plant communities a net positive effect of facilitation by herbivore protection cannot be expected at very high herbivore density simply because herbivores would eat anything available, including less palatable protective nurse plants. In contrast, at very low herbivore density not much is to be gained, and competition for resources among neighbouring plants will probably override the small protective effects against potential herbivore damage. Indeed, several studies illustrate that such protection against grazing tends to have the most effect at intermediate herbivore pressure (Brooker *et al*. 2006; Smit *et al*. 2007).

In summary, while our graphical model (Figs 1–4) highlights one particular example, various studies illustrate that facilitative interactions may ameliorate stressful conditions only within a certain range. At low levels of stress, positive effects may typically be overruled by competitive impacts, whereas at high stress levels organisms will typically be unable to produce sufficient amelioration to facilitate the survival and growth of others. We therefore predict the maximum absolute effect of facilitation (in terms of biomass gain) to be found under relatively moderate conditions rather than under the most stressful conditions. This implies that, while facilitation can expand the range of conditions where organisms may occur (as stressed in earlier work), performance may be boosted most strongly under more moderate conditions.

Facilitation under seemingly benign conditions

The general focus on the role of positive interactions under harsh conditions also carries some risk of introducing myopia when it comes to our search image for facilitation. For instance, isolated studies have demonstrated that facilitation through shading is essential for seedlings, even in relatively moist regions, such as former rain forest land of central Amazonia (Vieira, Uhl & Nepstad 1994; Ganade & Brown 2002) and New Caledonia (Rigg *et al*. 2002), temperate deciduous forests (Simard & Vyse 2006) or riparian forests (Shararn *et al*. 2009). At first sight, this may seem surprising as most of the literature is on the effect of nurse plants in stressful (dry or alpine) ecosystems of the world. However,
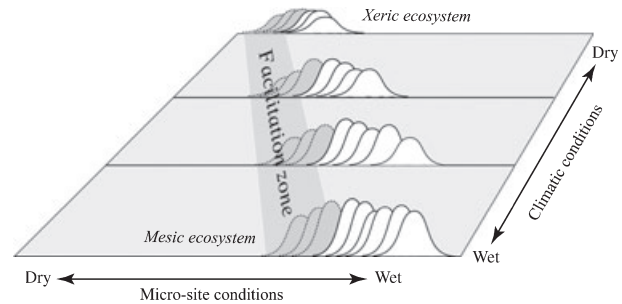
Fig. 5. Schematic representation of the role of facilitative amelioration of water stress in plant communities. In wetter climate zones, microsite conditions tend to be wetter, but species (represented by Gaussian niche curves) are also adapted to wetter conditions than those found in dry climates. As a result, the range of conditions under which species experience water stress that may be ameliorated by a canopy (grey zone) changes with climate. In mesic ecosystems, species that depend on canopy protection (grey Gaussians) occur under much wetter microsite conditions than in xeric ecosystems.

the suite of organisms present in a given ecosystem is of course adapted to the local conditions (Fig. 5). Therefore, apparently minor deviations from the optimal conditions can impose a large stress. Even in tropical and temperate forests where light availability by treefall gaps plays a key role in the maintenance of species diversity, seedlings of the shade-tolerant species that characterize these forests may be unable to grow in larger gaps (Hoffmann 2000; Ganade & Brown 2002). Tropical rain forest species tend to have large leaf area ratio and specific leaf area which increase their vulnerability to higher temperature and water deficit found at higher irradiance. Recent analysis of restoration attempts across ecosystems shows that indeed facilitative interactions play a key role in explaining the success of plant regeneration in tropical and temperate ecosystems (Gómez-Aparicio 2009). While few studies have addressed such situations, one may imagine that in a general sense similar patterns might occur in a wide range of ecosystems (Fig. 5). In a broader context, this also applies for facilitation along grazing pressure gradients where the most sensitive species to grazing are expected to benefit more from associational defence provided by neighbours and to respond more strongly to increasing levels of grazing pressure. Recent field experimental results point in this direction (Vandenberghe *et al*. 2009).

Synthesis

While the role of facilitative interactions has been recognized as a key-structuring force in plant communities early on (Clements 1916), most of our theoretical thinking has long been dominated by competition. Bertness & Callaway (1994) catalysed a change by providing the SGH that has inspired much empirical research in plant communities (Callaway 2007; Brooker *et al*. 2008). This clear and simple conceptual model helped to attract attention to positive interactions in a literature dominated by thinking about competition and predation. Simple theoretical models in ecology have historically played a

key-catalysing role in advancing our understanding and stimulating research. However, as with any scientific theory, such models can invoke myopia (Chamberlin 1897; Carpenter *et al.* 2008). The eye-opening SGH has led to a focus on extreme environments in the search for facilitation effects. Some authors have already pointed out that in particular cases competition may overwhelm facilitative effects when conditions become very harsh (Michalet *et al.* 2006; Maestre *et al.* 2009). However, we argue that it may be the rule rather than the exception to find large facilitation effects under moderate rather than extreme conditions. One reason is that, as growth tends to zero under the most extreme conditions, the absolute positive effects on growth and survival will typically be largest at intermediate conditions (Fig. 2). A quite independent reason why facilitation is more important than one might expect under the moderate conditions in moister ecosystems is the relatively lower drought tolerance of the plants species adapted to these environments. In seemingly benign environments organisms will tend to be more sensitive to stress, and may depend on facilitation more than we would expect at first sight (Fig. 5). As facilitation has fundamental implications for the stability and functioning of communities (Butterfield 2009), it is important to recognize that the role of facilitation is not limited to extreme environments. A too-narrow focus on extreme environments would bias our view of the overall role of facilitation in ecological communities.

Acknowledgements

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