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Facilitation in plant communities: the past, the present and the future

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18

1 **Summary**

- 2 1. Once neglected, the role of facilitative interactions in plant communities has
3 received considerable attention in the last two decades, and is now widely
4 recognised. It is timely to consider the progress made by research in this field.
- 5 2. We review the development of plant facilitation research, focussing on the
6 history of the field, the relationship between plant-plant interactions and
7 environmental severity gradients, and attempts to integrate facilitation into
8 mainstream ecological theory. We then consider future directions for
9 facilitation research.
- 10 3. With respect to our fundamental understanding of plant facilitation,
11 clarification of the relationship between interactions and environmental
12 gradients is central for further progress, and necessitates the design and
13 implementation of more complex experiments than generally undertaken to
14 date.
- 15 4. There is substantial scope for exploring indirect facilitative effects in plant
16 communities, including their impacts on diversity and evolution, and future
17 studies should attempt to connect the degree of non-transitivity in plant
18 competitive networks to community diversity and facilitative promotion of
19 species co-existence, and explore how the role of indirect facilitation varies
20 along environmental gradients.
- 21 5. Certain ecological modelling approaches (e.g. individual-based modelling),
22 although thus far largely neglected, provide highly useful tools for exploring
23 these fundamental processes.
- 24 6. We consider the links between plant facilitation and evolution. Unusual
25 evolutionary responses might result from facilitative interactions in plant

communities, and consideration of facilitation might lead to re-assessment of the evolution of plant growth forms.

7. Improved understanding of facilitation processes has direct relevance for the development of tools for ecosystem restoration, and for improving our understanding of the response of plant species and communities to key environmental change drivers.

8. Attempts to apply of our developing ecological knowledge would benefit from explicit recognition of the potential role of facilitative plant-plant interactions in the design and interpretation of studies from the fields of restoration and global change ecology.

9. Despite the undoubted progress made in this field in the last 20 years considerable research challenges still exist. Tackling these challenges will not only advance the field of plant facilitation research, but also community ecology in general.

Keywords: facilitation, positive plant interactions, communities, competition, environmental gradients, review, environmental change, ecological theory

Introduction

Plants interact in many different ways, both negative and positive. They compete for light, nutrients, space, pollinators, and water, but at the same time protect one another from the impacts of herbivores, potential competitors, or extremes of climate, and provide additional resources through canopy leaching, microbial enhancement, mycorrhizal networks and hydraulic lift.

1 There has been a particular resurgence of interest in the positive, non-trophic
2 interactions that occur between physiologically independent plants, and that are
3 mediated through changes in the abiotic environment or through other organisms -
4 both plant and animal (for reviews see Hunter & Aarssen 1988; Callaway 1995;
5 Flores & Jurado 2003; Bruno *et al.* 2003). Substantial recent research has examined
6 such interactions, exploring in detail the mechanisms by which they take place
7 (Holzapfel & Mahall 1999; Maestre *et al.* 2003a), the way in which they control the
8 structure and function of communities (Tirado & Pugnaire 2003; Kikvidze *et al.*
9 2005), and their implications for classic ecological theory (Bruno *et al.* 2003, Lortie *et*
10 *al.* 2004a). Furthermore, plant facilitation research is starting to make links to some of
11 the most important current ecological issues including the relationship between
12 biodiversity and ecosystem function, and the impacts of global change (Hooper *et al.*
13 2005; Brooker 2006).

14

15 It is perhaps a suitable time for reviewing the progress made in this field. Has the
16 recent research effort taken this field forward? Given our current understanding, what
17 gaps in our knowledge of facilitative interactions most urgently need to be addressed?
18 Do we know enough about them to understand their role in mediating the impact of
19 environmental change drivers or to use this knowledge to mitigate such impacts? This
20 paper will attempt to answer these questions. Firstly we discuss recent key
21 developments in facilitation research. We then suggest areas where we consider that
22 there are opportunities for future research, and the approaches that might be used to
23 take this work forward. We focus our review in particular on interactions between
24 vascular plants, as they have been the focus of the bulk of plant facilitation studies.

25

1 **Recent developments in plant facilitation research**

2 *“History will be kind to me, for I intend to write it”* – Winston Churchill

3

4 Until recently many ecologists only encountered facilitative plant-plant interactions
5 within a particular context: facilitation of one successional stage by the preceding
6 stage was a recognised, albeit underestimated, component of some theories of
7 succession (Clements 1916; Connell & Slatyer 1977) and had been demonstrated in a
8 number of ecosystems, for example in the classic studies of plant succession in
9 Glacier Bay (Crocker & Major 1955; Chapin *et al.* 1994).

10

11 However, in the late 1980s and throughout the 1990s a number of review papers (e.g.
12 Hunter & Aarssen 1988; Bertness & Callaway 1994; Callaway 1995, 1997; Brooker
13 & Callaghan 1998) pointed out that facilitative plant interactions also operated to
14 regulate plant success and community composition in stable, non-successional
15 communities, and were not merely important during successional change. Although
16 some of these reviews (e.g. Hunter & Aarssen 1988) considered relatively well-
17 recognised types of positive interactions, e.g. the attraction of pollinators (Thomson
18 1978), the positive impact of shrub species on soil nitrogen availability (García-Moya
19 & McKell 1970), the capacity for resource sharing through common mycorrhizal
20 networks (Chiarello *et al.* 1982), and classic nurse plant effects (Went 1942; Fig. 1),
21 they also discussed a developing body of research examining non-trophic interactions
22 between neighbouring plants that either did not fit into these well-recognised
23 categories, or that demonstrated that some facilitative effects (e.g. the nurse plant
24 effect) were more widespread than was previously thought. From these reviews some
25 common themes emerged:

1

2 1. Evidence of facilitative effects between plants tended to come from severe
3 environments, such as deserts, arctic or alpine tundra systems, or salt marshes. It
4 was even proposed that the concentration of ecological research in temperate
5 ecosystems (which were readily accessible and easily studied by many ecologists)
6 might have added to the neglect of facilitation within plant ecology (Brooker &
7 Callaghan 1998), or that “fascination with competition has focused attention on
8 communities where competition is conspicuous” (Bertness & Callaway 1994).

9

10 2. The net interaction between plants resulted from multiple positive and negative
11 interactions (Hunter & Aarssen 1988). For example, plants that competed for
12 nutrients could have simultaneous positive effects through the provision of shelter
13 or protection from herbivory.

14

15 3. The severity of the environment was linked to the balance between positive and
16 negative interactions. Increased environmental severity increased either the
17 potential for or strength of positive relative to negative interactions, and
18 consequently the observable net interactions between neighbouring plants shifted
19 toward facilitation in extreme environments (Hunter & Aarssen 1988; Bertness &
20 Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998).

21

22 These reviews coincided with, and probably contributed to, further increases in
23 interest in the mechanisms and impact of facilitative plant-plant interactions. As well
24 as dealing with “the mistaken notion that positive interactions are not well
25 demonstrated with field experiments” (Callaway 1995) - although competition still

1 clearly dominates consideration of plant-plant interactions within the ecological
2 literature (Fig. 2) - recent studies have explored in detail the issues raised by these
3 reviews. Two topics in particular have received considerable attention, firstly the
4 relationship between plant-plant interactions and environmental severity gradients,
5 and secondly linking facilitative plant-plant interactions into mainstream ecological
6 theory. Because these issues are central to plant facilitation research we now review
7 them in more detail.

8

9 PLANT-PLANT INTERACTIONS AND ENVIRONMENTAL SEVERITY 10 GRADIENTS

11 Although Hunter & Aarssen (1988) discussed the balance between positive and
12 negative plant-plant interactions, they did not suggest any generic relationships
13 between this balance and environmental gradients. Bertness & Callaway's (1994)
14 paper was central to recent developments in plant facilitation research in that it took
15 such a step, proposing that increases in either the degree of physical stress or
16 consumer pressure would increase the frequency of positive interactions, as under
17 these conditions the potential for such interactions would increase. Callaway &
18 Walker (1997) discussed the possible regulatory effects of climatic conditions and life
19 history stage (see also Callaway 1995) on the balance between positive and negative
20 interactions. Brooker & Callaghan (1998) explicitly framed their model within the
21 context of Grime's (1974, 1977, 1979) definitions of stress and disturbance,
22 concentrating on changes in interactions along gradients of disturbance because of
23 unresolved debate concerning the relationship between competitive interactions and
24 gradients of stress (Tilman 1988; Grace 1991, 1993; Reader *et al.* 1994; Brooker *et al.*

1 2005). However, Brooker & Callaghan's (1998) approach was not without criticism
2 (Bertness 1998).

3

4 Overall, an amalgam of these models has become known as the stress gradient
5 hypothesis or SGH - something of a misnomer considering that the original model of
6 Bertness & Callaway (1994), to which current studies tend to refer, included both
7 stress and consumer pressure. Recently a large number of studies have attempted to
8 test the predictions of the SGH. Many have taken a "high vs. low" approach – i.e. they
9 consider two or perhaps three levels of environmental severity (disturbance and/or
10 stress), and have frequently found that with increasing severity the beneficial impacts
11 of neighbours increase (e.g. Greenlee & Callaway 1996; Pugnaire & Luque 2001;
12 Maestre *et al.* 2003a; Gómez-Aparicio *et al.* 2004; Kikvidze *et al.* 2006a). However,
13 such studies often focus on interactions that are clearly facilitative, and examine one
14 particular species pairing – they do not allow a more general test of changes in the
15 "average" type of interactions found within plant communities (but see Cavieres *et al.*
16 2002, 2006).

17

18 A few studies have attempted to take a broader approach and examine patterns at the
19 community level or across a gradient. For example, Choler *et al.* (2001) found that
20 increasing altitude was associated with increasing frequency of facilitative
21 interactions, but that facilitation also depended on species identity - those species that
22 tended to be facilitated were commonly the ones at the extreme ends of their
23 environmental tolerance (see also Liancourt *et al.* 2005 for a similar example from
24 calcareous grasslands), and that facilitation led to range expansion, a process that has
25 been discussed in detail by Bruno *et al.* (2003) with respect to niche theory. Callaway

1 *et al.* (2002), in a separate study of arctic and alpine plant communities, found a
2 generic shift in the average type of interaction along a large-scale climatic gradient,
3 with facilitative interactions in colder environments and increasingly competitive
4 average interactions in more productive environments. In a study conducted along an
5 aridity gradient, Holzapfel *et al.* (2006) found a steady and consistent shift from net
6 positive or neutral effects to net negative effects of desert shrubs on annual species
7 with increasing water availability. In contrast, but in a study conducted on only one
8 species pair, Maestre & Cortina (2004) found a switch from competition to facilitation
9 and then back to competition along a gradient of decreasing rainfall in a semi-arid
10 steppe system. Similarly, Pennings *et al.* (2003) failed to find support for predictions
11 from the SGH in a study conducted over a large-scale geographical gradient in salt
12 marshes, and Tielbörger & Kadmon (2000a) found that the effect of desert shrubs on
13 annuals shifted from negative to neutral or neutral to positive (depending on the
14 species) with increasing annual rainfall.

15
16 In addition to field tests of the SGH, simple individual-based models have also
17 examined the relationship between the distribution of interactions and environmental
18 severity. Travis *et al.* (2005) found that facilitative interactions were restricted to the
19 most severe environmental conditions when the stress gradient acted upon
20 reproduction, but when it acted upon mortality competitive interactions were again
21 prevalent at the most extreme end of the gradient (Travis *et al.* 2006). These results
22 match the conclusions of Goldberg *et al.*'s (1999) review of field experiment studies
23 that the observed relationship between environmental severity and success depends in
24 part on the measure of success that is used (establishment, biomass accumulation,
25 mortality or reproductive output). However, the conclusions of Goldberg *et al.*'s

review (and studies therein) may themselves be biased by use of inappropriate indices to test the hypotheses examined (Brooker *et al.* 2005; Gaucherand *et al.* 2006).

Additional factors proposed as influencing the outcome of SGH studies include relatively short-term experiments, the confusion of variation in a specific resource or environmental factor with variation in stress - it is noticeable, for example that none of the cited studies that contradict the SGH was explicitly linked to gradients in productivity, the most fundamental metric of stress for a community (Grime 1977; Lortie *et al.* 2004b) - a lack of adequate control for the occurrence of other stress factors or ontogenetic effects (but see Armas & Pugnaire 2005; Miriti 2006; Schiffrers & Tielbörger 2006), or the effects of resource vs. non-resource stress factors (e.g. water availability and vapor pressure deficit; Michalet 2007). Maestre *et al.* (2005), in a meta-analysis of experiments from arid environments, concluded that there was no generic relationship between environmental severity and plant interactions, and that the approach used – e.g. experiments vs. observational studies – had a substantial impact on interpretation of the relationship (see also Dormann & Brooker 2002; Michalet 2006). Maestre *et al.*'s (2005) study led to considerable debate; Lortie & Callaway (2006) concluded that study selection for the analysis was not rigorous, and that differences in stress gradient lengths between studies could have a considerable impact on results, criticisms that have been disputed by Maestre *et al.* (2006).

It is therefore difficult to conclude whether the current uncertainty surrounding the SGH is the result of the analytical approach used (either in the field or statistically), the scale at which processes are examined (i.e. within a community through time, or across a local- or continental-scale environmental gradient) or the type of severity

1 gradient used (resource vs. non-resource or temporal vs. spatial). However, progress
2 in understanding this relationship is crucial, both for enhancing our fundamental
3 ecological knowledge and also for improving predictions of processes such as the
4 impacts of climate change on plant communities or the links between facilitation,
5 diversity and ecosystem function (Loreau & Hector 2001; Bertness & Ewanchuck
6 2002; Brooker 2006). It is important, therefore, that researchers pursue and attempt to
7 resolve this debate, and we return to these issues below in *Facilitation and*
8 *environmental gradients*.

9

10 THE INTEGRATION OF FACILITATION INTO MAINSTREAM ECOLOGICAL 11 THEORY

12 Although positive interactions were a component of the integrated community
13 concept as proposed by Clements (1916), Gleason's (1926) view that communities
14 were simply an assortment of species with similar adaptations to the abiotic
15 environment "has emerged as the favourite among ecologists" (Callaway 1997).
16 When interactions have been addressed in theories of plant community or population
17 ecology (e.g. Grime 1977; Tilman 1988) they have tended to be negative, competitive
18 interactions (except for the handful of well-recognised examples mentioned above).
19 However, given the demonstration that facilitative interactions are widespread and can
20 regulate the success of individuals and the composition of communities, there is
21 clearly a need to revisit mainstream ecological theory in order to integrate within it
22 the role of facilitative interactions.

23

24 Recent studies have attempted such integration. Bruno *et al.* (2003), in a study that
25 focussed strongly on evidence from coastal and marine ecosystems, discussed revision

1 of niche theory to include the potential for expansion of the realised niche by
2 facilitation (as empirically demonstrated by Hacker & Gaines 1997; Choler *et al.*
3 2001), positive density-dependence at high population densities, inclusion of
4 facilitation in the diversity-invasibility paradigm, and the role of dominant species in
5 regulating local diversity.

6

7 The severity gradient issue in particular is fundamental to classic theories of species
8 diversity. One of the first attempts to explore the role of facilitation as a regulator of
9 diversity was that of Hacker & Gaines (1997) who, working from the humped-back
10 model of diversity (Grime 1973; Huston 1979), suggested a conceptual scheme in
11 which the positive effects of facilitation on biodiversity (species richness) increase
12 from intermediate to very high environmental severity, in line with predictions from
13 the SGH. Michalet *et al.* (2006) further developed these ideas, suggesting that
14 facilitation promotes diversity at medium to high environmental severity levels by
15 expanding the range of stress-intolerant competitive species into harsh physical
16 conditions (as discussed by Bruno *et al.* 2003 and demonstrated by e.g. Choler *et al.*
17 2001), but that when environmental conditions become extremely severe the positive
18 effects of the benefactors wane and diversity is reduced, indicating that biotic
19 interactions shape both sides of the humped-back curve of diversity. Perhaps one of
20 the most striking examples of the potential importance of facilitation for the
21 maintenance of biodiversity is that described by Valiente-Banuet *et al.* (2006). They
22 found that a large number of ancient Tertiary plant lineages, which evolved under
23 much wetter climatic conditions than found in the Mediterranean-climate ecosystems
24 where they now live, have been preserved by facilitative nurse plant effects from
25 modern Quaternary species. In the absence of such interactions the flora of these

1 regions would be significantly altered, and facilitative interactions have therefore
2 played “a central role in the preservation of global biodiversity”.

3

4 As a consequence of these recent attempts to integrate facilitation into at least some
5 classic ecological theories, researchers have gained new insight into these classic
6 theories, and have also started to redress the excessive dominance of the
7 individualistic paradigm of community composition. However, considerable advances
8 still need to be made in this integration process, and it will probably take a significant
9 amount of time for a more integrated community concept (as proposed by Lortie *et al.*
10 2004a) to become widespread in ecological thinking.

11

12 **Looking to the future**

13 These short reviews highlight ongoing and new areas of debate, and illustrate the
14 significant potential for future research into plant facilitation. In this section we
15 discuss what we consider to be some of the most interesting topics for future research
16 and, where possible, the approaches by which they could be taken forward.

17

18 **IMPROVING OUR UNDERSTANDING**

19 *Facilitation and environmental gradients*

20 To understand the shifting balance between positive and negative interactions along
21 environmental gradients, and changes in the dominant type of interactions, we must
22 design and implement more complex experiments. These should, whenever possible,
23 include the following aspects: (i) several co-occurring stress factors (e.g. temperature
24 and water availability in arid areas and Mediterranean mountains), (ii) several levels
25 within each stress factor, ideally accounting for a wide range in the variation of each

factor (Fig. 3), and (iii) different target and nurse species, in order to control for species-specific responses in competitive and facilitative ability and tolerance to stress (e.g., Tielbörger & Kadmon 1995; Callaway 1998; Choler *et al.* 2001; Gómez-Aparicio *et al.* 2004; Liancourt *et al.* 2005). Of particular interest in testing the SGH are experiments conducted at the extreme end of severity gradients where benefactors may themselves be limited. Experiments should also attempt to isolate the environmental factors affected by potential benefactors (to provide a mechanistic explanation for severity-interaction relationships), evaluate different performance variables (e.g. survival, growth, physiological status), attempt to account for factors such as initial biomass effects (Goldberg *et al.* 1999; Kikvidze *et al.* 2006b), provide a fine characterization of abiotic conditions, and be conducted over time periods long enough to cover different life-stages in the studied species (e.g. Gómez-Aparicio *et al.* 2004; Miriti 2006; Schiffers & Tielbörger 2006). We acknowledge that taking into account all these issues when designing and conducting field experiments is challenging and costly. To overcome some of the experimental limitations, we recommend complementing them with observational studies conducted at the community level in multiple sites. When combined with appropriate statistical tools – such as structural equation models – these studies would allow us to assess multi-species interactions over broad geographical gradients, and to tease out the relative influence of different stress factors on them (Kikvidze *et al.* 2005).

In parallel to a rejuvenated research effort on plant interactions and severity gradients, we must start to rigorously address the issue of the importance of facilitative interactions. Simply because a process is detectable it does not mean that it plays a predominant role in regulating plant success or community composition. Plant

community composition is commonly seen as being regulated by a series of filters including chance biogeographical events, local abiotic environmental conditions, and interactions with other species (Grime 1998; Lortie *et al.* 2004a). By differentially regulating the success of individuals, such processes can operate as selective forces (see *Connecting facilitation to evolution*). The relative impact of each filter is not fixed, but such variation is rarely discussed, although there is a general assumption that filters operate to regulate distribution at different scales, e.g. chance biogeographical events are considered most important for regulating distributions at the regional scale and biotic interactions for regulating distributions at the local scale (but see Callaway & Ridenour 2004 and Valiente-Banuet *et al.* 2006 for examples of interactions determining ranges at a global scale). Central to these discussions, but frequently ignored, are the issues of the importance and intensity of interactions (Welden & Slauson 1986; Grace 1991; Corcket *et al.* 2003a; Brooker *et al.* 2005; Gaucherand *et al.* 2006; Grime 2007). Although the intensity of plant-plant interactions (absolute biomass impact) may remain unaltered along an environmental gradient, their importance (the impact of plant-plant interactions relative to other processes) may vary. The questions then arising are when and where are facilitative interactions not only detectable but playing a key role, and does this role vary depending upon whether we are considering (for example) community composition or evolutionary processes?

The issue of the changes in the relative importance of interactions along severity gradients is one of the most promising for community ecology research. The few studies considering both the importance and intensity of interactions demonstrate that they might or might not change in parallel (Brooker *et al.* 2005; Gaucherand *et al.*

2006), and that a detectable effect on biomass need not necessarily translate into a fitness effect (Goldberg *et al.* 1999). We should start to isolate these different measures of facilitative interactions, and we predict that facilitation is likely to be important relative to other “filters” when and where climate stress (e.g. aridity) or disturbance (e.g. grazing) is *high but not excessive* so that well-fitted benefactor species (e.g. “nurses”) are able to grow and significantly ameliorate stress or provide protection from disturbances. Important facilitation would be indicated when these interactions enable a *considerable* number of beneficiary species to survive and reproduce in the *immediate vicinity of benefactor species*. Both low environmental severity and excessive stress or disturbance would prevent facilitation from having a significant role, either in regulating the composition of the community or as a selective force. Field studies are now needed that can test these simple predictions by considering explicitly the importance of interactions along environmental gradients (e.g. Gaucherand *et al.* 2006).

Indirect interactions and facilitation

Interest in the effects of indirect interactions among species that occupy different trophic levels has been ongoing and has increased in recent years (Root 1973; Menge 1976; Hay 1986; Wootton 1994; Rousset & Lepart 2000; Corcket *et al.* 2003b; Seifan & Kadmon 2006), but complex indirect interactions *within* a trophic level, or among competitors (Aarssen 1992; Miller 1994; Levine 1999; Callaway & Pennings 2000; Tielbörger & Kadmon 2000b) have received much less attention. The outcomes of pair-wise interactions therefore shape our thinking and thus community theory (Connolly *et al.* 2001), with pair-wise studies of competitive interactions leading to the perspective that competitive hierarchies in plant communities are transitive, or

1 linear, with each species out-competing all those that are lower in the hierarchy. From
2 this we might conclude that the only outcome of strong competition in communities at
3 equilibrium is the exclusion of some or most members. However, this overlooks
4 potential positive effects that occur in multi-species communities due to non-transitive
5 “networks” of interactions (Aarssen 1992). When interactions take place among many
6 species at the same time, the competitive suppression of one species (B) by another
7 (A) can decrease the latter’s competitive effect on a third species (C) (Fig. 4a) thus
8 leading to the phenomenon of indirect facilitation.

9

10 The occurrence of indirect facilitation may depend on complementarities in the
11 interactions between species and, therefore, the identities or traits of the organisms
12 involved (Huisman & Weissing 1999; Huisman *et al.* 2001). For example, in our
13 model system (Fig. 4) indirect facilitation is most likely when pairs of plants (A-B, B-
14 C) compete for different resources, for example light for the first species pair, and
15 water or nutrients for the second (Levine 1999; Pagès & Michalet 2003; Siemann &
16 Rogers 2003; Kunstler *et al.* 2006). Plant characteristics other than resource uptake
17 ability may create such species-specific interactions, and thus non-transitive
18 interaction networks and indirect interactions (Pagès *et al.* 2003; Callaway & Howard
19 2006; Kunstler *et al.* 2006). Production of allelopathic chemicals may be such a trait
20 because of their potential for highly species-specific effects (Callaway & Howard
21 2006). If the existence of multiple interaction mechanisms among coexisting species
22 increases the potential for strong indirect interactions, indirect facilitation should be
23 more common in communities where several limiting factors co-occur with similar
24 strengths, whereas in environments with one dominant limiting factor, such as xeric,
25 N-poor, or low light conditions, indirect facilitation should be less important.

1

2 Gradients of diversity will influence, and be influenced by, indirect facilitative
3 interactions. Indirect facilitation should be more common in species-rich communities
4 (Miller 1994; Dodds 1997). It may have the potential to sustain the coexistence of
5 high species diversity by reducing the potential for competitive exclusion (Czaran *et*
6 *al.* 2002; Laird & Schamp 2006) and may be the dominant facilitative process in more
7 productive environments (given the predicted reduction in direct facilitative effects).
8 Indirect facilitation among competitors therefore challenges assumptions about
9 competition consistently leading to exclusion and has interesting evolutionary
10 implications. For instance, Scheffer & van Nes (2006) have shown that indirect
11 facilitation can result in a system in which “look-a-like” species are more likely to
12 coexist than dissimilar species, as increased similarity is likely to lead to non-
13 transitive networks. However, as with the evolutionary effects of direct facilitative
14 interactions (see *Connecting facilitation to evolution*), the evolutionary consequences
15 of indirect facilitative effects have generally been overlooked.

16

17 There is, therefore, substantial scope for further exploring the role of indirect
18 facilitative effects in plant communities, including their impacts on diversity and
19 evolution. Future studies, using artificial manipulations of diversity or modelling
20 approaches (see *Development of models incorporating plant facilitation*) should: i)
21 attempt to assess the conditions under which we might expect the greatest level of
22 non-transitivity within plant communities; ii) connect the degree of non-transitivity in
23 plant competitive networks to community diversity and facilitative promotion of
24 species co-existence; iii) explore how the role of non-transitivity and indirect
25 facilitation varies along gradients both of diversity and system productivity, and in

1 relation to direct facilitative effects; iv) explore, perhaps through multi-species
2 evolutionary modelling, the potential for indirect facilitative effects to drive or limit
3 niche differentiation, and how such processes might vary along gradients of diversity
4 and environmental severity.

5

6 *Development of ecological models incorporating plant facilitation*

7 Although a broad suite of modelling approaches is available, and despite their likely
8 relevance and utility, they have not yet been widely employed in furthering our
9 understanding of the role of facilitative interactions in plant communities. This
10 represents a significant missed opportunity.

11

12 Recent work illustrates the potential for relatively simple models to provide some
13 generic insights into the dynamics of communities that are structured with a mixture
14 of positive and negative interactions. Yamamura *et al.* (2004) studied the evolution of
15 mutualistic interactions and highlighted the importance of local spatial structure in
16 determining the outcome of interactions among a mutualistic and a cheater species.
17 Travis *et al.* (2005) extend this approach to plant facilitation issues, demonstrating
18 that positive interactions are most likely towards the harsh end of environmental
19 gradients, although this depends to on whether the gradient primarily influences
20 reproduction or survival (Travis *et al.* 2006). More recently Brooker *et al.* (2007) have
21 used these models to explore the potential impact of facilitative and competitive
22 interactions on the capacity of species to track a moving “climate envelope”. The
23 spatial arrangement of species with particular traits (as determined initially by
24 interactions), along with the rate of climate change and level of long-distance
25 dispersal, interact to regulate the capacity of species to track their climate envelope.

1 Interestingly, the comparatively slow-growing facilitators are not consistently driven
2 to extinction within the model community: if climate change is sufficiently slow, and
3 dispersal distance sufficiently low, the facilitators can continue to dominate the
4 habitat into which competitors are attempting to expand, and can thus limit the range-
5 shifting capacity of competitors (Brooker *et al.* 2007).

6

7 These models are a move in the right direction, but they do not yet properly represent
8 facilitation as most empirical plant ecologists have described it. In the mutualism
9 models that have been adapted for facilitation research the interaction term is
10 commonly $+/+$ (Odum 1968), i.e. reciprocal benefit. However, although mutualistic
11 interactions between neighbouring plants are possible, and may be more common than
12 currently expected (Pugnaire *et al.* 1996), the impact of the beneficiary on the
13 benefactor may range from positive to zero ($+/0$ commensalism), and some
14 interactions might even be classified as parasitic ($+/-$). Future modelling should
15 therefore start to clearly distinguish between mutualism and facilitation. Such a
16 distinction would, for example, be important in determining the outcome of
17 evolutionary modelling studies – facilitative interactions may have very different
18 evolutionary impacts from mutualistic interactions, and may also evolve under
19 different circumstances. By allowing evolution of competition and facilitation kernels
20 (which represent the strength of the negative and positive influence of neighbouring
21 plants in relation to their proximity) it could be systematically tested under which
22 circumstances (frequency of interactions, gene flow, etc.) facilitation might evolve as
23 an evolutionary stable strategy. Modelling could also explore the potential for
24 different life history characteristics (such as dispersal, dormancy, time to first
25 reproduction, self compatibility) to evolve in response to the balance between

1 facilitation and competition present within a local community. Furthermore, two-
2 species models could be extended to multi species models enabling, for example, the
3 dynamics of indirect interactions to be examined in detail, including the conditions
4 under which this type of effect is likely to be observed in natural systems, and how its
5 community and evolutionary impacts might compare to those of direct facilitative
6 effects.

7

8 We also suggest that there is a need to develop modelling approaches that can
9 accommodate variation in the role of facilitative interactions along environmental
10 gradients, both in space and time. If the spatial extents of positive and negative effects
11 differ, the net outcome of interactions will be highly dependent on the spatial relation
12 of the individual plants. Few, if any, experiments in the literature provide the
13 parameters necessary for models that can incorporate such effects, and thus adopting
14 this approach might need explicitly matched field experimental studies. Overall,
15 therefore, modelling studies dealing with interactions should combine the key
16 elements of neighbourhood models - individuals with an explicit location, a basal
17 extension where no other plant can exist, and a zone of influence on which
18 interactions with other plants occur (Stoll & Weiner 2000) - with the inclusion of
19 facilitation through, for example, facilitation kernels in addition to competition
20 kernels. Models of this type have the potential for a wide range of both strategic
21 application (providing general insights into the types of dynamics that might be
22 observed) and tactical application (providing specific predictions regarding particular
23 communities in particular geographic locations).

24

25 *Connecting facilitation to evolution*

1 Recent studies have indicated that facilitation may act as an evolutionary force. For
2 example, Scheffer & van Nes (2006) predicted that indirect facilitation may drive
3 convergence of species' niches, and Valiente-Banuet *et al.* (2006) suggested that
4 facilitation is a source of stabilising selection for the regeneration niches of ancient
5 Tertiary species within Mediterranean-climate ecosystems.

6

7 When we consider the evolutionary impacts of interactions, we can readily visualise
8 the “competitor” syndrome that might evolve in response to strong and consistent
9 negative interactions in productive environments: a high, dense canopy of wide-
10 spreading leaves, rapid potential RGR, high morphological plasticity, etc. (a classic C-
11 strategy species; Grime 1977). However, given the multiple positive and negative
12 interactions that occur between individuals in severe environments, it may not be
13 straightforward to predict the evolutionary response to facilitative interactions, as both
14 facilitative and competitive mechanisms may evolve in response to facilitation. A
15 simple hypothetical example demonstrates the unusual and interesting evolutionary
16 processes that could result. In a two-species system, species A is facilitated by species
17 B, but any negative effects of species A could select for those B individuals that are
18 weaker facilitators (either by selecting against the key facilitation trait or in favour of
19 an avoidance mechanism in species B; Fig. 5a). However, an alternative second
20 selective force might favour individuals of species A with lower negative impacts on
21 their benefactor (Fig. 5b).

22

23 One key trait that may come under such selection within the context of an assemblage
24 comprising facilitators and facilitated is dispersal. In our simple model it would seem
25 likely that selection might favour dispersal kernels in the facilitated species that map

1 onto those of the facilitator, for example through the evolutionary convergence of
2 dispersal agents, while conversely in the facilitating species selection might favour
3 dispersal kernels leading to the establishment of plants that can escape the negative
4 consequences of competition from the facilitated (Fig. 4a), unless the level of
5 competition is itself reduced (Fig. 4b). If strong benefits from facilitation act as
6 selective forces against large competitive effects they might have a key role in
7 explaining patterns of plant strategies, which are commonly interpreted independently
8 of the role of facilitation. Similarly, selection acting on characteristics such as the
9 balance between reproduction by clones and seed may vary depending on the nature
10 or balance of interactions – reproduction by seed may aid dispersal and be favoured
11 by avoidance of competition whereas clonal growth may be selected for by facilitation
12 in the immediate vicinity of the parent plant. It is interesting to speculate that the
13 reduced competitive effect or enhanced clonality of stress tolerant species may in part
14 result from selection in favour of enhanced facilitation. As stated by Brooker &
15 Callaghan (1998) “It may be the case that we already have evidence of the
16 evolutionary impact of positive plant-plant interactions, but have never examined it in
17 the light of this possible interpretation”.

18
19 In our model system the outcome of the selective process will depend not only upon
20 the frequency and relative strength of the interactions, but also upon evolutionary
21 constraints on specific traits – is evolution of an avoidance mechanism in B (e.g.
22 through altered dispersal) more likely than reduced competitive impact from A (e.g.
23 through increased niche differentiation)? The evolution of life history traits will play
24 an important role in determining the spatial dynamics of an assemblage, resulting in a
25 continuous interaction between evolutionary dynamics related to the interactions and

1 the spatial ecology of the system. The extension of relatively simple models (e.g.
2 Travis & Dytham 1999; Travis 2002) could explore the interplay between ecological
3 and evolutionary dynamics that might result from these types of effects. However,
4 given the potential complexity involved, including variability in the two-way nature
5 of facilitation, a simple starting point for evolutionary studies might be to ask whether
6 all facilitative interactions provide common selective forces, from this predicting
7 patterns of traits, and then exploring whether traits vary in the expected manner along
8 environmental gradients in association with quantification of the importance and
9 intensity of interactions.

10

11 APPLYING OUR UNDERSTANDING

12 *Facilitation and ecosystem restoration*

13 In the face of current rapid degradation of terrestrial ecosystems worldwide, there is
14 an increasing need for the development of novel, low-cost and efficient restoration
15 techniques for maintaining ecosystem function and services (e.g. Ormerod *et al.* 2003;
16 Hobbs *et al.* 2006). Because facilitation has been recognized as an important
17 structuring force in natural plant communities, it is being increasingly discussed as an
18 ecological mechanism which could be exploited for developing vegetation restoration
19 tools, particularly for extreme environments (Maestre *et al.* 2001; Padilla & Pugnaire
20 2006).

21

22 Arid ecosystems offer perhaps the best current opportunity for exploring this
23 application, and it is well illustrated by the study of Gómez-Aparicio *et al.* (2004).
24 They examined, in water-limited Mediterranean environments, the use of naturally-
25 occurring shrubs as nurse plants for reforestation, and found consistently over the

1 course of a 4-year study that shrubs had a beneficial effect on tree seedling survival
2 and growth. Such a result directly contradicted traditional reforestation management
3 practice, wherein shrubs were thought to compete with tree seedlings, and were thus
4 removed prior to the planting of seedlings (see also Castro *et al.* 2004). Unfortunately,
5 the majority of studies that address the use of nurse plants for restoration in arid
6 systems are usually conducted over shorter time frames, i.e. fewer than two growing
7 seasons (e.g. Maestre *et al.* 2001, 2003b, 2004; Barchuk *et al.* 2005; Drezner 2006).
8 Given the temporal variability in facilitative interactions in these systems (Tielbörger
9 & Kadmon 2000; Miriti 2006), this may be an insufficient period over which to assess
10 whether nurse plants have a net beneficial effect, and longer-term studies are clearly
11 needed. Furthermore, these previous studies commonly planted beneficiary species
12 under existing nurse plants. However, in extremely degraded semi-arid ecosystems
13 nurse plants may themselves be lost (Gibson & Brown 1991). In such cases
14 management for nurse plant re-establishment may be necessary as a first step, but it
15 would be important to consider whether, overall, the use of nurse plants was the most
16 effective way of driving benefactee re-establishment.

17
18 Novel techniques currently being developed in agro-ecosystems and polluted areas
19 demonstrate the wide range of possible uses of facilitative interactions for
20 environmental management. Facilitation can operate via increased pollinator visits
21 which lead to greater crop yields (Ricketts *et al.* 2004), enhanced water status of crops
22 growing with species capable of hydraulic lift (Pate & Dawson 1999; Sekiya & Yano
23 2004), the transfer of symbiotically fixed nitrogen from legumes to non-legumes
24 species (Jensen 1996; see also Hauggaard-Nielsen & Jensen 2005 for a review of
25 facilitative root interactions in agro-ecosystems), or phytostabilisation by

1 metallicolous nurse plants in heavy metal polluted environments (Frérot *et al.* 2006).
2 There may, therefore, be a wide range of facilitative mechanisms, in addition to the
3 classic nurse plant effect, that could act as the basis for restoration tools.

4

5 Sutherland *et al.* (2004) proposed that “Much of current conservation practice is based
6 upon anecdote and myth” (as demonstrated by the study of Gómez-Aparicio *et al.*
7 (2004) discussed above). It would appear that in the case of restoration in severe
8 environments there are opportunities to move away from this situation and apply our
9 developing ecological knowledge. The acknowledgement of facilitation in studies of
10 restoration, particularly within environments that are difficult to restore, would help to
11 raise facilitation’s profile as a tool for natural resource conservation and management.
12 Furthermore, applied facilitation research also has significant unexploited potential
13 for advancing the science of restoration ecology in general. The explicit consideration
14 of facilitation when exploring key topics in this research area, such as stable
15 alternative states (Suding *et al.* 2004) or the links between ecosystem
16 structure/function and restoration success (Cortina *et al.* 2006), will likely shed new
17 light on our understating of these issues and, more importantly, may further help
18 managers and practitioners to develop effective tools to achieve the desired restoration
19 targets, both in terms of species composition/structure and functional status.

20

21 *Facilitation and global change*

22 Climate change, nitrogen deposition, biological invasions and land use change have
23 been suggested as the current major threats to global biodiversity (Sala *et al.* 2000;
24 CBD 2003), and significant evidence is accumulating of the role of interactions,

1 including facilitative ones, in mediating the impact of these environmental change
2 drivers on natural communities (Brooker 2006; Maestre & Reynolds 2006, 2007).

3
4 Several studies have demonstrated the importance of facilitation for the maintenance
5 of biodiversity in arctic and alpine habitats (e.g. Choler *et al.* 2001; Callaway *et al.*
6 2002). These habitats are predicted to be amongst the most sensitive to global
7 warming (Guisan & Theurillat 2000; ACIA 2004). Based on the original SGH, some
8 authors have predicted a general shift in species interactions from more strongly
9 positive to more strongly negative as these environments warm and become less
10 severe (e.g., Klanderud 2005; Klanderud & Totland 2005). In support of this basic
11 prediction, experiments that evaluated the impact of enhanced nitrogen availability in
12 these ecosystems (simulating the expected effect of climate change on nutrient
13 mineralization rates) mostly reported increased competitive interactions (e.g., Chapin
14 *et al.* 1995; Bret-Harte *et al.* 2004; Klanderud & Totland 2005). Similarly, in a North
15 American arctic tundra system, where artificially advanced snowmelt (a phenomenon
16 expected under global warming) created a more severe environment through increased
17 early-season frost events, neighbours increasingly facilitated the survival, growth and
18 reproduction of *Empetrum nigrum* (Wipf *et al.* 2006). However, Shevtsova *et al.*
19 (1997) reported that the positive effects of elevated temperature on the growth and
20 reproduction of *Vaccinium vitis-idaea* and *Empetrum nigrum* in subarctic Finland
21 were amplified by the presence of neighbours – in this instance a reduced level of
22 environmental severity (warming) lead to an increased impact of facilitative
23 interactions. These findings support the argument (discussed above) that the
24 relationship between gradients of environmental severity and the relative role of
25 interactions is more complicated than set out in the original SGH. At first glance we

1 might conclude that such a pattern supports the recently proposed humped-back
2 relationship (Michalet *et al.* 2006) – if these environments are on the high severity
3 side of the hump, then decreased severity might increase the impact of facilitative
4 interactions. However, it is notable that the increased role of facilitation with
5 decreasing severity found by Shevtsova *et al.* (1997) occurs within an environment
6 that is apparently less severe than, for example, the open tundra systems studied by
7 Chapin *et al.* (1995) and Wipf (2006) and in which the opposite pattern was observed.
8 Such apparently contradictory findings support the propositions that the perception of
9 environmental severity is to some extent species-specific, and that the response of
10 interactions to environmental severity at the individual species level may not reflect
11 the trend of average interactions within a community.

12
13 Invasive species are another critical global change driver. In the study of biological
14 invasions, interactions are considered crucial in determining the success of exotics
15 (e.g. Daehler 2003; Simberloff *et al.* 2003; Vilà *et al.* 2004). Most studies have
16 focused on negative interactions as the main drivers of invasive success (e.g.,
17 Callaway & Aschehoug 2000; Colautti *et al.* 2004; Mitchell *et al.* 2006). However, a
18 number have also reported that facilitation by other exotics (Simberloff & Von Holle
19 1999) or by natives (Maron & Connors 1996; Richardson *et al.* 2000; Lenz & Facelli
20 2003; Cavieres *et al.* 2005) can promote exotic invasion. For instance, Maron &
21 Connors (1996) reported that the nitrogen-fixing native shrub *Lupinus arboreus*
22 facilitates the establishment of exotic species by ameliorating soil nutrient shortage.
23 Cavieres *et al.* (2005) found that the cushion plant *Azorella monantha* facilitates the
24 establishment of the exotic species *Taraxacum officinale* in the high-alpine zone of
25 the Andes of central Chile by providing microsites with milder microclimatic

1 conditions. Reinhart *et al.* (2006) showed how seedlings of the invasive tree *Acer*
2 *platanoides* had higher densities, recruitment, and survival, and less photoinhibition
3 and water stress when beneath conspecific canopies than when growing under
4 adjacent native *Pseudotsuga menziesii* trees; they related these differences to the
5 environmental modification created by the invaders. Interestingly, invasion can also
6 be “resisted” by greater diversity of native species (e.g. Zavaleta & Hulvey 2004;
7 Fargione & Tilman 2005), another mechanism by which facilitation of natives may
8 help resist the influx of invasive species.

9

10 Improving our understanding of facilitative interactions is therefore of direct
11 relevance to understanding the impacts of environmental change drivers on
12 biodiversity. For example, resolution of debate concerning the SGH may enable us to
13 more accurately predict changes in the role of interactions in response to
14 environmental change, or the conditions under which interactions might restrict or
15 enhance biodiversity change, for example through the influx of invasives. However, it
16 is not necessarily the case that radical new experiments are needed to explore these
17 issues. As with restoration ecology, simply recognising the potential role of
18 facilitation, and including it within both experimental designs and the interpretation of
19 ecosystem responses, could provide us with valuable insights into facilitation both as
20 a mediator of global change and a fundamental ecological process.

21

22 **Conclusions**

23 Our coverage cannot hope to be fully comprehensive in an essay review such as this.
24 Other relevant topics which we have touched upon at best only briefly include the
25 possible impacts of facilitation on ecosystem function (Hector *et al.* 1999), the use of

1 indices in plant interaction studies (as hotly debated with respect to competition
2 indices; Markham & Chanway 1996; Freckleton & Watkinson 1997a, b; Markham
3 1997; Freckleton & Watkinson 1999), or the possible contrasting consequences of
4 diffuse and species-specific facilitation (e.g. the general facilitative effects of
5 neighbours in alpine environments compared to the specific one-on-one facilitative
6 impacts of nurse plants). However, we have covered what are widely recognised as
7 some of the central current issues for plant facilitation research, and should perhaps
8 now answer the questions posed at the outset of this review.

9

10 Firstly, has the recent substantial research effort taken this field forward? Yes,
11 undoubtedly, both in terms of developing general models and in exploring some of
12 their underlying complexity, and also in raising general awareness of the widespread
13 and important role of facilitative interactions in plant communities.

14

15 Secondly, what gaps in our knowledge of facilitative interactions need to be
16 addressed? Clarification of the relationship between interactions and environmental
17 gradients is central for further progress, and necessitates the design and
18 implementation of more complex experiments than undertaken to date. There is also
19 substantial scope for exploring indirect facilitative effects, including their impacts on
20 diversity and evolution, and future studies should attempt to connect the degree of
21 non-transitivity in plant competitive networks to community diversity and facilitative
22 promotion of species co-existence, perhaps exploring how the role of indirect
23 facilitation varies along environmental gradients. Certain ecological modelling
24 approaches could provide highly useful tools for exploring these fundamental
25 processes, and also clearly lend themselves to studying the unusual evolutionary

1 responses that might result from facilitative interactions, perhaps even leading to re-
2 assessment of the evolution of plant growth forms.

3
4 Thirdly, do we know enough about facilitative interactions to understand their role in
5 mediating the impact of environmental change drivers, or to use this knowledge to
6 mitigate such impacts? The answer to this question is probably no. We know enough
7 to recognise that improved understanding of facilitation processes is directly relevant
8 to both ecosystem restoration (and may form the basis of restoration management
9 tools), and to understanding the response of plant species and communities to key
10 environmental change drivers such as invasive alien species and global change.
11 However, attempts to apply of our developing ecological knowledge to these fields
12 are at an early stage, and would benefit from explicit recognition of the potential role
13 of facilitative plant-plant interactions in the design and interpretation of studies of
14 restoration and global change ecology.

15
16 It is clear, therefore, that considerable research challenges exist, but that expanding
17 our fundamental understanding of facilitation, applying that knowledge to key
18 ecological problems, and attempting to further integrate our developing knowledge of
19 facilitation into mainstream ecological theory will undoubtedly bring an improved
20 understanding of both plant facilitation and community ecology in general.

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9 **References**

- 10 Aarssen, L.W. (1992) Causes and consequences of variation in competitive ability in
11 plant communities. *Journal of Vegetation Science*, **3**, 165-174.
- 12 ACIA (2004) *Arctic Climate Impact Assessment*. Cambridge University Press,
13 Cambridge.
- 14 Armas, C., Ordiales, R. & Pugnaire, F.I. (2004) Measuring plant interactions: A new
15 comparative index. *Ecology*, **85**, 2682-2686.
- 16 Armas, C. & Pugnaire, F.I. (2005) Plant interactions govern population dynamics in a
17 semi-arid plant community. *Journal of Ecology*, **93**, 978-989.
- 18 Barchuk, A.H., Valiente-Banuet, A. & Díaz, M.P. (2005) Effect of shrubs and
19 seasonal variability of rainfall on the establishment of *Aspidosperma quebracho-*
20 *blanco* in two edaphically contrasting environments. *Austral Ecology*, **30**, 695-
21 705.
- 22 Bertness, M.D. (1998) Searching for the role of positive interactions in plant
23 communities. *Trends in Ecology and Evolution*, **13**, 133-134.
- 24 Bertness, M. & Callaway, R.M. (1994) Positive interactions in communities. *Trends*
25 *in Ecology and Evolution*, **9**, 191-193.

1 Bertness, M. & Ewanchuk, P.J. (2002) Latitudinal and climate-driven variation in the
2 strength and nature of biological interactions in New England salt marshes.
3 *Oecologia*, **132**, 392-401.

4 Bret-Harte, M.S., García, E.A., Scaré, V.M., Whorley, J.R., Wagnern, J.L., Lipper,
5 S.C. & Chapin, F.S. (2004) Plant and soils responses to neighbour removal and
6 fertilization in Alaskan tussock tundra. *Journal of Ecology*, **92**, 635-647.

7 Brooker, R.W. (2006) Plant–plant interactions and environmental change. *New*
8 *Phytologist*, **171**, 271-289.

9 Brooker, R.W. & Callaghan, T.V. (1998) The balance between positive and negative
10 plant interactions and its relationship to environmental gradients: a model. *Oikos*,
11 **81**, 196-207.

12 Brooker, R., Kikvidze, Z., Pugnaire, F.I., Callaway, R.M., Choler, P., Lortie, C.J. &
13 Michalet, R. (2005) The importance of importance. *Oikos*, **109**, 63-70.

14 Brooker, R.W., Travis, J.M.J., Clark, E.J. & Dytham, C. (2007) Modelling species’
15 range shifts in a changing climate: The impacts of biotic interactions, dispersal
16 distance and the rate of climate change. *Journal of Theoretical Biology*, **245**, 59-
17 65.

18 Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003) Inclusion of facilitation into
19 ecological theory. *Trends in Ecology & Evolution*, **18**, 119-125.

20 Callaway, R.M. (1995) Positive interactions among plants. *Botanical Review*, **61**, 306-
21 349.

22 Callaway, R.M. (1997) Positive interactions in plant communities and the
23 individualistic-continuum concept. *Oecologia*, **112**, 143-149.

24 Callaway, R.M. (1998) Are positive interactions species-specific? *Oikos*, **82**, 202-207.

- 1 Callaway, R.M. & Aschehoug, E.T. (2000) Invasive plants versus their new and old
2 neighbors: a mechanism for exotic invasion. *Science*, **290**, 521-523.
- 3 Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R.,
4 Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze,
5 D. & Cook, B.J., (2002) Positive interactions among alpine plants increase with
6 stress. *Nature*, **417**, 844-848.
- 7 Callaway, R. M. & Howard, T. G. (2006) Competitive networks, indirect interactions,
8 and allelopathy: a microbial viewpoint on plant communities. *Progress in Botany*,
9 **68**, 317-335
- 10 Callaway, R.M. & S.C. Pennings. (2000) Facilitation may buffer competitive effects:
11 indirect and diffuse interactions among salt marsh plants. *American Naturalist*,
12 **156**, 416-424.
- 13 Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the
14 evolution of increased competitive ability. *Frontiers in Ecology and Evolution*, **2**,
15 436-443.
- 16 Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic
17 approach to interactions in plant communities. *Ecology*, **78**, 1958-1965.
- 18 Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M. & Gómez-Aparicio, L. (2004)
19 Benefits of using shrubs as nurse plants for reforestation in Mediterranean
20 mountains: a 4-year study. *Restoration Ecology*, **12**, 352-358.
- 21 Cavieres, L., Arroyo, M.T.K., Penaloza, A., Molina-Montenegro, M. & Torres, C.
22 (2002) Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of
23 the Chilean Patagonian Andes. *Journal of Vegetation Science*, **13**, 547-554.
- 24 Cavieres, L., Badano, E.I., Sierra-Almeida, A., Gómez-González, S. & Molina-
25 Montenegro, M.A. (2006) Positive interactions between alpine plant species and

1 the nurse cushion *Laretia acaulis* do not increase with elevation in the Andes of
2 central Chile. *New Phytologist*, **169**, 59-69.

3 Cavieres, L.A., Quiroz, C.L., Molina-Montenegro, M.A., Muñoz, A.A. & Pauchard,
4 A. (2005) Nurse effect of the native cushion plant *Azorella monantha* on the
5 invasive non-native *Taraxacum officinale* in the high-Andes of central Chile.
6 *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 217-226.

7 CBD (2003). *Interlinkages between biological diversity and climate change. Advice*
8 *on the integration of biodiversity considerations into the implementation of the*
9 *United Nations Framework Convention on Climate Change and its Kyoto*
10 *protocol*. Secretariat of the Convention on Biological Diversity, Montreal.

11 Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995)
12 Response of Arctic tundra to experimental and observed change in climate.
13 *Ecology*, **76**, 694-711.

14 Chapin, F.S., III, Walker, L.W., Fastie, C.L. & Sharman, L.C. (1994) Mechanisms of
15 primary succession following deglaciation at Glacier Bay, Alaska. *Ecological*
16 *Monographs*, **64**, 149-175.

17 Chiariello, N.R., Hickman, J.C. & Mooney, H. (1982) Endomycorrhizal role for
18 interspecific transfer of phosphorus in a community of annual plants. *Science*,
19 **217**, 941-943.

20 Choler, P., Michalet, R. & Callaway, R.M. (2001) Facilitation and competition on
21 gradients in alpine plant communities. *Ecology*, **82**, 3295-3308.

22 Clements, F.E. (1916). *Plant succession. Carnegie Institute Publication #242*.
23 Carnegie Institute, Washington.

24 Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion
25 success explained by the enemy release hypothesis? *Ecology Letters*, **7**, 721-7333.

- 1 Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural
2 communities and their role in community stability and organization. *American*
3 *Naturalist*, **111**, 1119-1144.
- 4 Connolly, J., Wayne, P. & Bazzaz, F.A. (2001) Interspecific competition in plants:
5 How well do current methods answer fundamental questions? *American*
6 *Naturalist*, **157**, 107-125.
- 7 Corcket, E., Liancourt, P., Callaway, R. & Michalet, R. (2003a) The relative
8 importance of competition for two dominant grass species as affected by
9 environmental manipulations in the field. *Ecoscience*, **10**, 186-194.
- 10 Corcket E., Callaway, R.M. & Michalet, R. (2003b) Insect herbivory and grass
11 competition in a calcareous grassland: results from a plant removal experiment.
12 *Acta Oecologica*, **24**, 139-146.
- 13 Cortina, J., Maestre, F.T., Vallejo, V.R., Baeza, J., Valdecantos, A. & Pérez-Devesa,
14 M. (2006) Ecosystem function and restoration success: are they related? *Journal*
15 *for Nature Conservation*, **14**, 152-160.
- 16 Crocker, R.L. & Major, J. (1955) Soil development in relation to vegetation and
17 surface age at Glacier Bay, Alaska. *Journal of Ecology*, **43**, 427-448.
- 18 Czarán, T.L., Hoekstra, R.F. & Pagie, L. (2002). Chemical warfare between microbes
19 promotes biodiversity. *Proceedings of the National Academy of Sciences*, **99**, 786-
20 790.
- 21 Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien
22 invasive plants: implications for conservation and restoration. *Annual Review of*
23 *Ecology and Systematics*, **34**, 183-211.
- 24 Dodds, W. K. (1997). Interspecific interactions: constructing a general neutral model
25 for interaction type. *Oikos*, **78**, 377-383.

- 1 Dormann, C.F. & Brooker, R.W. (2002) Facilitation and competition in the high
2 Arctic: the importance of the experimental approach. *Acta Oecologica*, **23**, 297-
3 301.
- 4 Drezner, T.D. (2006) Plant facilitation in extreme environments: the non-random
5 distribution of saguaro cacti (*Carnegie gigantea*) under their nurse associates and
6 the relationship with non-linear architecture. *Journal of Arid Environments*, **65**,
7 46-61.
- 8 Fargione, J.E. & Tilman, D. (2005) Diversity decreases invasion via both sampling
9 and complementarity effects. *Ecology Letters*, **8**, 604-611.
- 10 Flores, J. & Jurado, E. (2003) Are nurse-protégé interactions more common among
11 plants from arid environments? *Journal of Vegetation Science*, **14**, 911-916.
- 12 Freckleton, R.P. & Watkinson, A.R. (1997a) Measuring plant neighbour effects.
13 *Functional Ecology*, **11**, 532-534.
- 14 Freckleton, R.P. & Watkinson, A.R. (1997b) Response to Markham. *Functional*
15 *Ecology*, **11**, 536.
- 16 Freckleton, R.P. & Watkinson, A.R. (1999) The mis-measurement of plant
17 competition. *Functional Ecology*, **13**, 285-287.
- 18 Frérot H., Lefèbvre C., Gruber W., Collin C., Dos Santos, A. & Escarré J. (2006)
19 Specific interactions between local metalicolous plants improve the
20 phytostabilization of mine soils. *Plant and Soil*, **282**, 53-65.
- 21 García-Moya, E. & McKell, C. (1970) Contribution of shrubs to the nitrogen
22 economy of a desert-wash plant community. *Ecology*, **51**, 81-88.
- 23 Gaucherand, S., Liancourt, P. & Lavorel, S. (2006) Importance and intensity of
24 competition along a fertility gradient and across species. *Journal of Vegetation*
25 *Science*, **17**, 455-464.

1 Gibson, C.W.D. & Brown, V.K. (1991) The effects of grazing on local colonisation
2 and extinction during early succession. *Journal of Vegetation Science*, **2**, 291-300.

3 Gleason, H.A. (1926) The individualistic concept of plant association. *Bulletin of the*
4 *Torrey Botanical Club*, **53**, 7-26.

5 Goldberg, D.E., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. (1999) Empirical
6 approaches to quantifying interaction intensity: competition and facilitation along
7 productivity gradients. *Ecology*, **80**, 1118-1131.

8 Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J. & Baraza, E.
9 (2004) Applying plant positive interactions to reforestation in Mediterranean
10 mountains: a meta-analysis of the use of shrubs as nurse plants. *Ecological*
11 *Applications*, **14**, 1128-1138.

12 Grace, J.B. (1991) A clarification of the debate between Grime and Tilman.
13 *Functional Ecology*, **5**, 583-587.

14 Grace, J.B. (1993) The effects of habitat productivity on competition intensity. *Trends*
15 *in Ecology and Evolution*, **8**, 229-230.

16 Greenlee, J.T. & Callaway, R.M. (1996) Abiotic stress and the relative importance of
17 interference and facilitation in montane bunchgrass communities in western
18 Montana. *American Naturalist*, **148**, 386-396.

19 Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344-
20 347.

21 Grime, J.P. (1974) Vegetation classification by reference to strategy. *Nature*, **250**, 26-
22 30.

23 Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and
24 its relevance to ecological and evolutionary theory. *American Naturalist*, **111**,
25 1169-1194.

- 1 Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. Wiley, Chichester.
- 2 Grime, J. P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and
3 founder effects. *Journal of Ecology*, **86**, 902-910.
- 4 Grime, J.P. (2007) Plant strategy theories: a comment on Craine (2005). *Journal of*
5 *Ecology*, **95**, 227-230.
- 6 Guisan, A. & Theurillat, J.P. (2000) Assessing alpine vulnerability to climate change,
7 a modelling perspective. *Integrated Assessment*, **1**, 307-320.
- 8 Hacker, S.D. & Gaines, S.D. (1997) Some implications of direct positive interactions
9 for community species diversity. *Ecology*, **78**, 1990-2003.
- 10 Hay, M.E. (1986) Associational defenses and the maintenance of species diversity:
11 turning competitors into accomplices. *American Naturalist*, **128**, 617-641
- 12 Hauggaard-Nielsen, H. & Jensen, E.S. (2005) Facilitative root interactions in
13 intercrops. *Plant and Soil*, **274**, 237-250.
- 14 Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M.,
15 Dimitrakopoulos, P.G., Finn, J.A, Freitas, H., Giller, P.S., Good, J., Harris, R.,
16 Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley,
17 P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J.,
18 Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D.,
19 Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward,
20 F.I., Yachi, S. & Lawton, J.H. (1999) Plant diversity and productivity experiments
21 in European grasslands. *Science*, **286**, 1123–1127.
- 22 Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A.,
23 Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D.,
24 Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R. &

1 Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the
2 new ecological world order. *Global Ecology and Biogeography*, **15**, 1-7.

3 Holzapfel, C. & Mahall, B.E. (1999) Bidirectional facilitation and interference
4 between shrubs and annuals in the Mojave Desert. *Ecology*, **80**, 1747-1761.

5 Holzapfel, C., Tielbörger, K., Parag, H.A., Kigel, J. & Sternberg, M. (2006) Annual
6 plant-shrub interactions along an aridity gradient. *Basic and Applied Ecology*, **7**,
7 268-279.

8 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton,
9 J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J.,
10 Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem
11 functioning: A consensus of current knowledge. *Ecological Monographs*, **75**, 3-
12 35.

13 Huisman, J., Johansson, A.M., Folmer, E.O. & Weissing, F.J. (2001) Towards a
14 solution of the plankton paradox: the importance of physiology and life history.
15 *Ecology Letters*, **4**, 408-411.

16 Huisman, J. & Weissing, F.J. (1999) Biodiversity of plankton by species oscillations
17 and chaos. *Nature*, **402**, 407-410.

18 Hunter, A.F. & Aarssen, L.W. (1988) Plants helping plants. *Bioscience*, **38**, 34-39.

19 Huston, M.A. (1979) A general hypothesis of species diversity. *American Naturalist*,
20 **113**, 81-101.

21 Jensen, E. S. (1996) Barley uptake of N deposited in the rhizosphere of associated
22 field pea. *Soil Biology and Biochemistry*, **28**, 159–168.

23 Kikvidze, Z., Pugnaire, F.I., Brooker, R.W., Choler, P., Lortie, C.J., Michalet, R. &
24 Callaway, R.M. (2005) Linking patterns and processes in alpine plant
25 communities: a global study. *Ecology*, **86**, 1395-1400.

- 1 Kikvidze, Z., Khetsuriani, L., Kikodze, D. & Callaway, R.M. (2006a) Seasonal shifts
2 in competition and facilitation in subalpine plant communities of the central
3 Caucasus. *Journal of Vegetation Science*, **17**, 77-82.
- 4 Kikvidze, Z., Armas, C. & Pugnaire, F.I. (2006b) The effect of initial biomass in
5 manipulative experiments on plants. *Functional Ecology*, **20**, 1-3.
- 6 Klanderud, K. (2005) Climate change effects on species interactions in an alpine plant
7 community. *Journal of Ecology*, **93**, 127-137.
- 8 Klanderud, K. & Totland, Ø. (2005) The relative importance of neighbours and
9 abiotic environmental conditions for population dynamic parameters of two alpine
10 plant species. *Journal of Ecology*, **93**, 493-501.
- 11 Kunstler, G., Curt, T., Bouchaud, M. & Lepart, J. (2006) Indirect facilitation and
12 competition in tree species colonization of sub-mediterranean grasslands. *Journal*
13 *of Vegetation Science*, **17**, 379–388.
- 14 Laird, R.A. & Schamp, B.S. (2006) Competitive intransitivity promotes species
15 coexistence. *American Naturalist*, **168**, 182-193.
- 16 Lenz, T.I. & Facelli, J.M. (2003) Shade facilitates an invasive stem succulent in a
17 chenopod shrubland in South Australia. *Austral Ecology*, **28**, 480-490.
- 18 Levine, J. (1999) Indirect facilitation: evidence and predictions from a riparian
19 community. *Ecology*, **80**, 1762-1769.
- 20 Levine, S.H. (1976) Competitive interactions in ecosystems. *American Naturalist*,
21 **110**, 903-910.
- 22 Liancourt, P., Callaway, R.M. & Michalet, R. (2005) Stress tolerance and
23 competitive-response ability determine the outcome of biotic interactions.
24 *Ecology*, **86**, 1611-1618.

1 Loreau M & Hector, A (2001) Partitioning selection and complementarity in
2 biodiversity experiments. *Nature*, **412**, 72-76

3 Lortie, C.J., Brooker, R.W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F.I. &
4 Callaway, R.M. (2004a) Rethinking plant community theory. *Oikos*, **107**, 433-
5 438.

6 Lortie, C.J., Brooker, R.W., Kikvidze, Z. & Callaway, R.M. (2004b) The value of
7 stress and limitation in an imperfect world: A reply to Körner. *Journal of*
8 *Vegetation Science*, **15**, 577-580.

9 Lortie, C.J. & Callaway, R.M. (2006) Re-analysis of meta-analysis: support for the
10 stress-gradient hypothesis. *Journal of Ecology*, **94**, 7-16.

11 Maestre, F.T. (2002) *La restauración de la cubierta vegetal en zonas semiáridas en*
12 *función del patrón espacial de factores bióticos y abióticos*. PhD Thesis,
13 University of Alicante, Alicante.

14 Maestre, F.T., Bautista, S. & Cortina, J. (2003a) Positive, negative, and net effects in
15 grass-shrub interactions in Mediterranean semiarid grasslands. *Ecology*, **84**, 3186-
16 3197.

17 Maestre, F.T., Bautista, S., Cortina, J. & Bellot, J. (2001) Potential for using
18 facilitation by grasses to establish shrubs on a semiarid degraded steppe.
19 *Ecological Applications*, **11**, 1641-1655.

20 Maestre, F.T. & Cortina, J. (2004) Do positive interactions increase with abiotic
21 stress? A test from a semi-arid steppe. *Proceedings of the Royal Society of London*
22 *B (Supplement)*, **271**, S331-S333.

23 Maestre, F.T., Cortina, J. & Bautista, S. (2004) Mechanisms underlying the
24 interaction between *Pinus halepensis* and the native late-successional shrub
25 *Pistacia lentiscus* in a semi-arid plantation. *Ecography*, **27**, 776-786.

- 1 Maestre, F.T., Cortina, J., Bautista, S. & Bellot, J. (2003b) Does *Pinus halepensis*
2 facilitate the establishment of shrubs under semi-arid climate? *Forest Ecology and*
3 *Management*, **176**, 147-160.
- 4 Maestre, F.T. & Reynolds, J.F. (2006) Nutrient availability and atmospheric CO₂
5 partial pressure modulate the effects of nutrient heterogeneity on the size structure
6 of populations in grassland species. *Annals of Botany*, **98**, 227-235
- 7 Maestre, F.T. & Reynolds, J.F. (2007) Biomass responses to elevated CO₂, soil
8 heterogeneity and diversity: an experimental assessment with grassland
9 assemblages. *Oecologia* (in press). DOI 10.1007/s00442-006-0577-y
- 10 Maestre, F.T., Valladares, F. & Reynolds, J.F. (2005) Is the change of plant-plant
11 interactions with abiotic stress predictable? A meta-analysis of field results in arid
12 environments. *Journal of Ecology*, **93**, 748-757.
- 13 Maestre, F.T., Valladares, F. & Reynolds, J.F. (2006) The stress-gradient hypothesis
14 does not fit all relationships between plant-plant interactions and abiotic stress:
15 Further insights from arid environments. *Journal of Ecology*, **94**, 17-22.
- 16 Markham, J.H. (1997) Measuring and modelling plant neighbour effects: a reply to
17 Freckleton and Watkinson. *Functional Ecology*, **11**, 534-535.
- 18 Markham, J.H. & Chanway, C.P. (1996) Measuring plant neighbor effects. *Functional*
19 *Ecology*, **10**, 548-549.
- 20 Maron, J.L. & Connors, P.G. (1996) A native nitrogen-fixing shrub facilitates weed
21 invasion. *Oecologia*, **105**, 302-312.
- 22 Menge, B.A. (1976) Organization of the New England rocky intertidal community:
23 role of predation, competition and environmental heterogeneity. *Ecological*
24 *Monographs*, **46**, 355-369.
- 25 Michalet, R. (2006) Is facilitation in arid environments the result of direct or complex

1 interactions? *New Phytologist*, **169**, 3-6.

2 Michalet, R. (2007) Highlighting the multiple drivers of change in interactions along
3 stress gradients. *New Phytologist*, **173**, 3-6.

4 Michalet, R., Brooker, R.W., Cavieres, L.A., Kikvidze, Z., Lortie, C.J., Pugnaire, F.I.,
5 Valiente-Banuet, A. & Callaway, R.M. (2006) Do biotic interactions shape both
6 sides of the humped-back model of species richness in plant communities?
7 *Ecology Letters*, **9**, 767-773.

8 Miller, T.E. (1994) Direct and indirect species interactions in an early old-field plant
9 community. *American Naturalist*, **143**, 1007-1025

10 Miriti, M.N. (2006) Ontogenetic shift from facilitation to competition in a desert
11 shrub. *Journal of Ecology*, **94**, 973-979.

12 Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A.,
13 Klironomos, J.N., Maron, J.L., Morris, W.F., Parker, I.M., Power, A.G.,
14 Seabloom, E.W., Torchin, M.E. & Vázquez, D.P. (2006) Biotic interactions and
15 plant invasions. *Ecology Letters*, **9**, 726-740.

16 Odum, E.P. (1968) *Fundamentals of Ecology*. 2nd ed. W.B.Saunders, London.

17 Ormerod, S.J., Marshall, E.J.P., Kerby, G. & Rushton, S.P. (2003) Meeting the
18 ecological challenges of agricultural change: editors' introduction *Journal of*
19 *Applied Ecology*, **40**, 939-946.

20 Padilla, F. M. & Pugnaire, F.I (2006) The role of nurse plants in the restoration of
21 degraded environments. *Frontiers in Ecology and the Environment*, **4**, 196-202.

22 Pagès, J.P. & Michalet, R. (2003) A test of the indirect facilitation model in a
23 temperate hardwood forest of the northern French Alps. *Journal of Ecology*, **91**,
24 932-940.

- 1 Pagès, J.P., Pache, G., Joud, D., Magnan, N. & Michalet, R. (2003) Direct and
2 indirect effects of shade on four forest tree seedlings in the French Alps. *Ecology*,
3 **84**, 2741-2750.
- 4 Pate, J.S. & Dawson, T.E. (1999) Assessing the performance of woody plants in
5 uptake and utilisation of carbon, water and nutrients - Implications for designing
6 agricultural mimic systems. *Agroforestry Systems*, **45**, 245-275.
- 7 Pennings, S.C., Selig, E.R., Houser, L.T. & Bertness, M.D. (2003) Geographic
8 variation in positive and negative interactions among salt marsh plants. *Ecology*,
9 **84**, 1527-1538.
- 10 Pugnaire, F.I., Haase, P. & Puigdefábregas, J. (1996) Facilitation between higher plant
11 species in a semiarid environment. *Ecology*, **77**, 1420-1426.
- 12 Pugnaire, F.I. & Luque, M.T. (2001) Changes in plant interactions along a gradient of
13 environmental stress. *Oikos*, **93**, 42-49.
- 14 Reader, R.J., Wilson, S.D., Belcher, J.W., Wisheu, I., Keddy, P.A., Tilman, D.,
15 Morris, E.C., McGraw, J.B., Olff, H., Turkington, R., Klein, E., Leung, Y.,
16 Shipley, B., van Hulst, R., Johansson, M.E., Nilsson, C., Gurevitch, J., Grigulis,
17 K., & Beisner, B.E. (1994) Plant competition in relation to neighbor biomass: an
18 intercontinental study with *Poa pratensis*. *Ecology*, **75**, 1753-1760.
- 19 Reinhart, K. O., Maestre, F. T. & Callaway, R. M. (2006) Facilitation and inhibition
20 of seedlings of an invasive tree (*Acer platanoides*) by different tree species in a
21 mountain ecosystem. *Biological Invasions*, **8**, 231-240.
- 22 Richardson, D.M., Allsop, N., D'Antonio, C.M., Milton, S.J. & Rejmánek, M., (2000)
23 Plant invasions-the role of mutualisms. *Biological Reviews*, **75**, 65-93.

1 Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Michener, C.D. (2004). Economic value
2 of tropical forest to coffee production. *Proceedings of the National Academy of*
3 *Sciences*, **101**, 12579-12582.

4 Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse
5 habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **43**,
6 95-124.

7 Rousset, O. & Lepart, J. (2000) Positive and negative interactions at different life
8 stages of a colonizing species (*Quercus humilis*). *Journal of Ecology*, **88**, 401-412.

9 Sala, O.E., Chapin, F.S. III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R.,
10 Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R.,
11 Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker,
12 B.H., Walker M. & Wall, D.H. (2000). Global biodiversity scenarios for the year
13 2100. *Science*, **287**, 1770–1774.

14 Scheffer, M. & van Nes, E.H. (2006) Self-organized similarity, the evolutionary
15 emergence of groups of similar species. *Proceedings of the National Academy of*
16 *Sciences*, **103**, 6230-6235.

17 Schiffers, K. & Tielbörger, K. (2006) Ontogenetic shifts in interactions among annual
18 plants. *Journal of Ecology*, **94**, 336-341.

19 Seifan, M. & Kadmon, R. (2006) Indirect effects of cattle grazing on shrub spatial
20 pattern in a mediterranean scrub community. *Basic and Applied Ecology*, **7**, 496-
21 506.

22 Sekiya, N. & Yano, K. (2004) Do pigeon pea and sesbania supply groundwater to
23 intercropped maize through hydraulic lift? Hydrogen stable isotope investigation
24 of xylem waters. *Field Crops Research*, **86**, 167-173.

- 1 Shevtsova, A., Haukioja, E. & Ojala, A. (1997) Growth response of subarctic dwarf
2 shrubs, *Empetrum nigrum* and *Vaccinium vitis-idaea*, to manipulated
3 environmental conditions and species removal. *Oikos*, **78**, 440-458.
- 4 Siemann, E. & Rogers, W.E. (2003) Changes in light and nitrogen availability under
5 pioneer trees may indirectly facilitate tree invasions of grasslands. *Journal of*
6 *Ecology*, **91**, 923-931.
- 7 Simberloff, D., Rejmanek, M.A. & Nuñez, M. (2003) Introduced species and management
8 of a *Nothofagus/Austrocedrus* forest. *Environmental Management*, **31**, 263-275.
- 9 Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous
10 species: invasional meltdown? *Biological Invasions*, **1**, 21-32.
- 11 Stoll, P. & Weiner, J. (2000). A Neighborhood View of Interactions among Individual
12 Plants. *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*
13 (eds U. Dieckmann, R. Law & J.A.J. Metz), pp. 11–27. Cambridge University
14 Press, Cambridge.
- 15 Suding, K.N., Gross, K.L. & Houseman, G.R. (2004) Alternative states and positive
16 feedbacks in restoration ecology. *Trends in Ecology & Evolution*, **19**, 46-53.
- 17 Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004) The need for
18 evidence-based conservation. *Trends in Ecology and Evolution*, **19**, 305-308.
- 19 Thomson, J.D. (1978) Effects of stand composition on insect visitation in two-species
20 mixtures of *Hieracium*. *American Midland Naturalist*, **100**, 431-440.
- 21 Tielbörger, K. & Kadmon, R. (1995) Effect of shrubs on emergence, survival and
22 fecundity of four coexisting annual species in a sandy desert ecosystem.
23 *Ecoscience*, **2**, 141-147.

- 1 Tielbörger, K. & Kadmon, R. (2000a) Temporal environmental variation tips the
2 balance between facilitation and interference in desert plants. *Ecology*, **81**, 1544–
3 53.
- 4 Tielbörger, K. & Kadmon, R. (2000b) Indirect effects in a desert plant community: is
5 competition among annuals more intense under shrub canopies? *Plant Ecology*,
6 **150**, 53-63.
- 7 Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant*
8 *Communities*. Princeton University Press, Princeton, New Jersey, USA.
- 9 Tirado, R. & Pugnaire, F.I. (2003) Shrub spatial aggregation and consequences for
10 reproductive success. *Oecologia*, **136**, 296–301.
- 11 Travis, J.M.J. (2002) Climate change and habitat destruction: a deadly anthropogenic
12 cocktail. *Proceedings of the Royal Society of London Series B-Biological*
13 *Sciences*, **270**, 467-473.
- 14 Travis, J.M.J., Brooker, R.W., Clark, E.J. & Dytham, C. (2006) The distribution of
15 positive and negative species interactions across environmental gradients on a
16 dual-lattice model. *Journal of Theoretical Biology*, **241**, 896-902.
- 17 Travis, J.M.J., Brooker, R.W., & Dytham, C. (2005) The interplay of positive and
18 negative interactions across an environmental gradient: insights from an
19 individual-based simulation model. *Biology Letters*, **1**, 5-8.
- 20 Travis, J.M.J. & Dytham, C. (1999) Habitat persistence, habitat availability and the
21 evolution of dispersal. *Proceedings of the Royal Society of London Series B*, **266**,
22 723-728.
- 23 Valiente-Banuet, A., Rumebe, A.V., Verdú, M. & Callaway, R.M. (2006) Quaternary
24 Plant lineages sustain global diversity by facilitating Tertiary lineages.
25 *Proceedings of the National Academy of Sciences*, **103**, 16812–16817.

- 1 Vilà. M., Williamson, M. & Lonsdale, M. (2004) Competition experiments on alien
2 weeds with crops: lessons for measuring plant invasion impact? *Biological*
3 *Invasions*, **6**, 59-69.
- 4 Welden, C.W. & Slauson, W.L. (1986) The intensity of competition versus its
5 importance: an overlooked distinction and some implications. *The Quarterly*
6 *Review of Biology*, **61**, 23-44.
- 7 Went, F.W. (1942) The dependence of certain annual plants on shrubs in southern
8 California deserts. *Bulletin of the Torrey Botanical Club*, **69**, 100-114.
- 9 Wipf, S., Rixen, C. & Mulder, C.P.H. (2006) Advanced snowmelt causes shift toward
10 positive neighbour interactions in a subarctic tundra community. *Global Change*
11 *Biology*, **12**, 1-11.
- 12 Wootton, J.T. (1994) The nature and consequences of indirect effects in ecological
13 communities. *Annual Review of Ecology and Systematics*, **25**, 443-466.
- 14 Yamamura, N., Higashi, M., Behera, N. & Wakano, J.Y. (2004) Evolution of
15 mutualism through spatial effects. *Journal of Theoretical Biology*, **226**, 421-428.
- 16 Zavaleta, E.S. & Hulvey, K.B. (2004). Realistic species losses disproportionately
17 reduce grassland resistance to biological invaders. *Science*, **306**, 1175- 1177.

1 **Figure 1.** Examples of the nurse plant effect in extreme environments. (a) Cushion of
2 *Azorella monantha* harbouring native and invasive species (e.g. the Andean
3 cauliflower *Nastanthus agglomeratus* and the field chickweed *Cerastium arvense*
4 respectively) at the upper limit of vegetation (3600 m a.s.l.) in the high-Andes of
5 central Chile. Photo: Lohengrin A. Cavieres. (b) Adult individual of the tussock grass
6 *Stipa tenacissima* facilitating a sapling of *Pinus halepensis* in a semiarid steppe, SE
7 Spain. Photo: Fernando T. Maestre.

9 **Figure 2.** The number of papers examining facilitation and competition as a
10 percentage of the total number of papers published in 5 leading plant ecology journals
11 (American Naturalist, Ecology, Journal of Ecology, Oikos, Oecologia) between 1995
12 and 2006. Data obtained from ISI Web of Knowledge
13 (<http://portal.isiknowledge.com/>; 1st March 2007) using the search strings [(“positive
14 interaction*” OR facilitation) AND plant*] or alternatively [(“negative interaction*”
15 OR competition) AND plant*], specifying English language articles only. After
16 Dormann and Brooker (2002).

18 **Figure 3.** Summary of field experiments evaluating the net effect of either *Pinus*
19 *halepensis* (white symbols) or *Stipa tenacissima* (black symbols) on the post-summer
20 survival (between eight and ten months after planting) of seedlings of different
21 Mediterranean shrub species, demonstrating the importance of setting up wide abiotic
22 stress gradients when evaluating the response of plant-plant interactions to them, and
23 the fact that the relationship between these gradients and plant-plant interactions is
24 more complicated than set out in the original stress-gradient hypothesis (Bertness &
25 Callaway 1994). Positive and negative values of the RII index indicate net facilitative

1 and competitive interactions, respectively. As suggested by Lortie & Callaway (2006),
 2 seedling survival in the open areas without vegetation was used as a surrogate of
 3 abiotic stress. RII was calculated as $(S_N - S_O)/(S_N + S_O)$, where S_N and S_O are the
 4 survival of seedlings planted under the canopy of either *Pinus* or *Stipa* and in open
 5 areas without vegetation, respectively (Armas *et al.* 2004). All the experiments were
 6 conducted with one-year old seedlings planted with the same methodology (manually-
 7 dig holes) in semiarid *Stipa* steppes and *Pinus* plantations of Alicante (SE Spain).
 8 Original data come from Maestre (2002), Maestre *et al.* (2001, 2003a, 2003b, 2004)
 9 and Maestre & Cortina (2004).

10

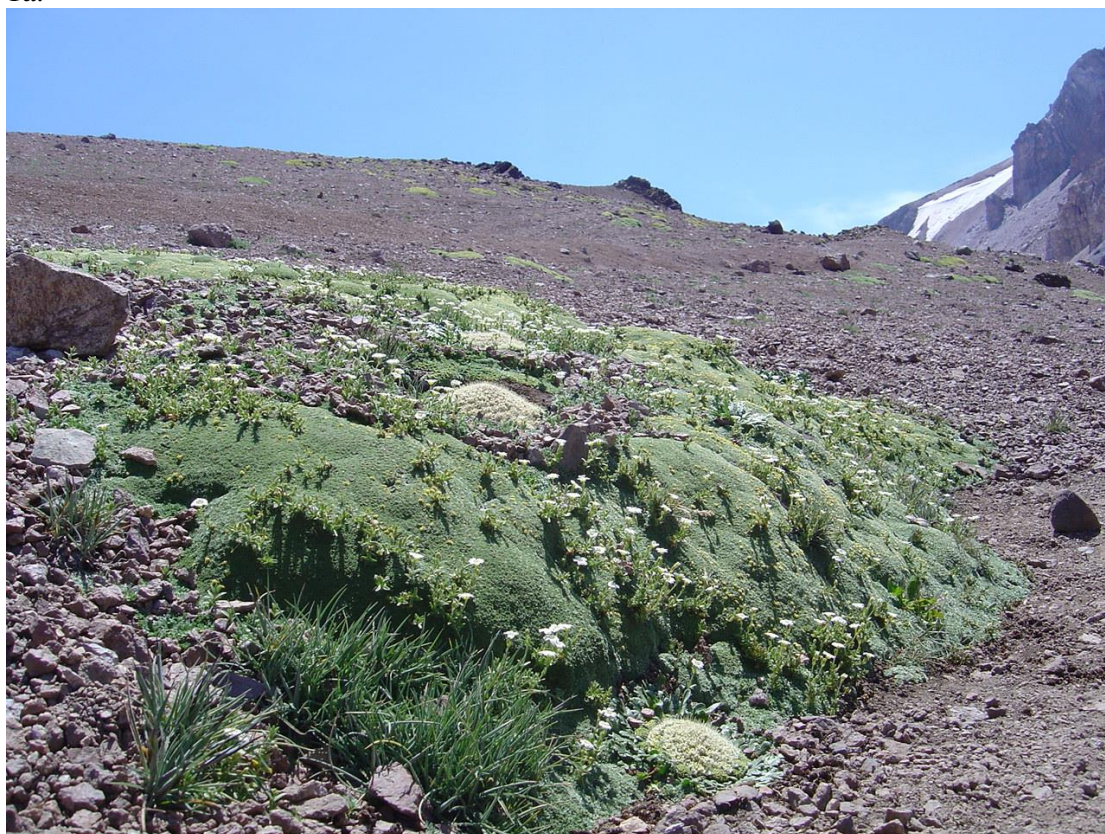
11 **Figure 4.** Indirect (dotted line) and direct (solid line) interactions in a complex
 12 system: (a) Species A suppresses species B, which affects the potential negative effect
 13 of species B on C. As suggested by Levine (1976), if the benefit from suppression is
 14 higher than the direct negative effects, indirect facilitation occurs in the community.
 15 However, the benefit from suppression can be outweighed by direct negative effects,
 16 resulting in no net indirect facilitation (Levine 1999; Pagès *et al.* 2003), (b) non-
 17 transitive interactions ($A > B$, $B > C$, $C > A$). The suppression of species B by A causes
 18 an indirect facilitation of species C, which increases its negative effect on A. In such a
 19 system the species ameliorate each other's effects and contribute to long-term
 20 coexistence (Czaran *et al.* 2002; Callaway & Howard 2006).

21

22 **Figure 5.** Simple scenarios for the evolutionary impact of facilitation. Solid lines
 23 show direct interactions, dotted lines show evolutionary responses. Species B
 24 facilitates species A, while species A has some negative effect on species B (thick and
 25 thin solid lines respectively). (a) The negative effects of species A cause selection to

1 favour those species B individuals with lower facilitative impacts. Evolution would
2 act to weaken the facilitatory effect. (b) Within species A, individuals with lower
3 negative features will be selected, since they maximise the advantages of the presence
4 of species B, thus decreasing the negative effects of A and maintaining the neutral
5 features of species B that benefit species A.

Figure 1. *Brooker et al.*
1a.



1b.



Figure 2. Brooker *et al.*

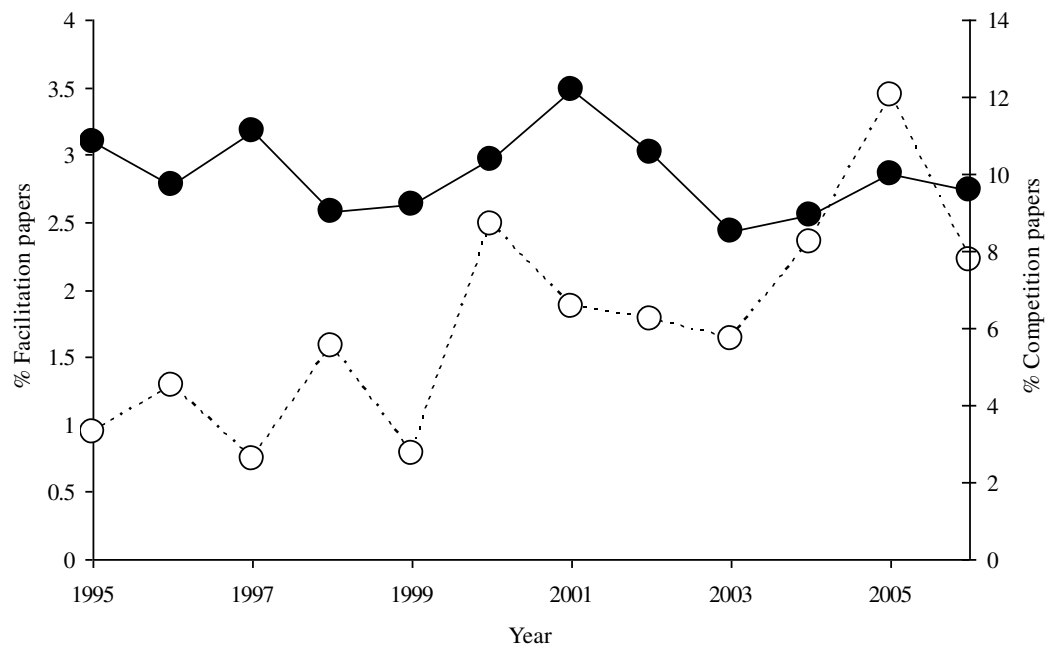


Figure 3. Brooker *et al.*

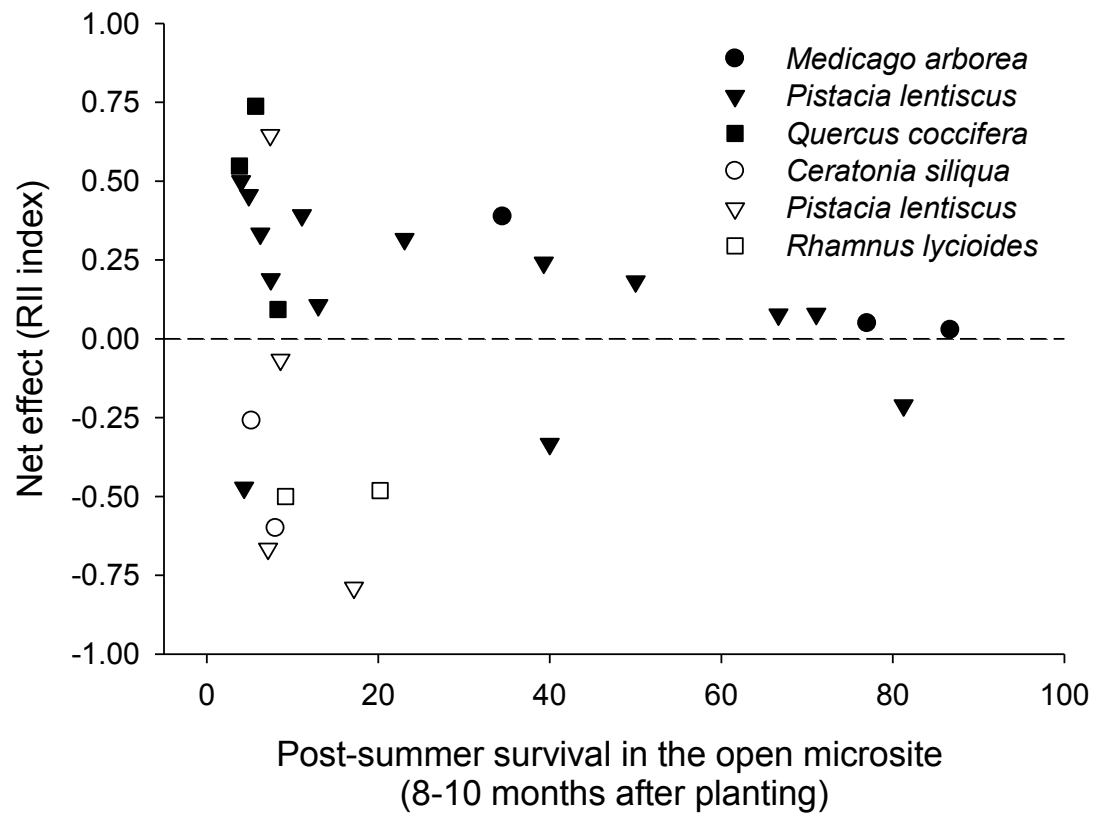


Figure 4. Brooker *et al.*

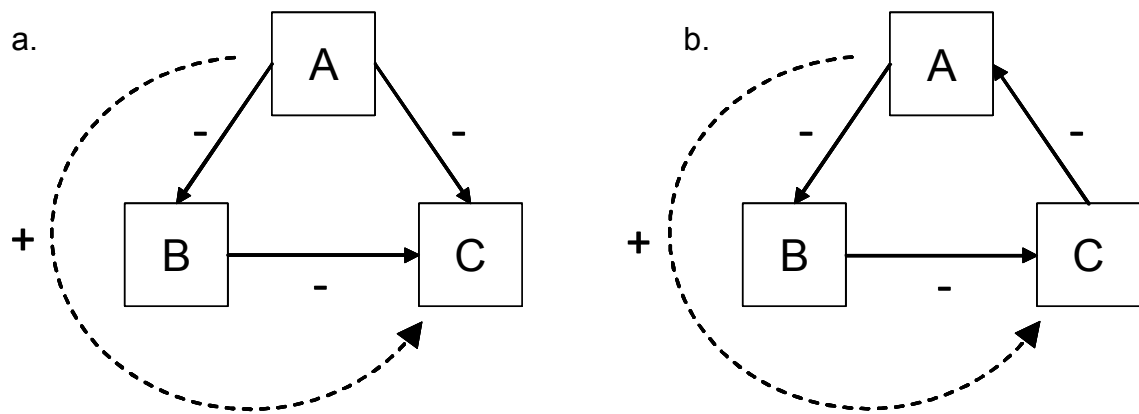


Figure 5. Brooker *et al.*

