*Journal of Ecology* 2008, **96**, 18–34 doi: 10.1111/j.1365-2745.2007.01295.x

ESSAY REVIEW

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

**Rob W. Brooker[1]*, Fernando T. Maestre[2], Ragan M. Callaway[3], Christopher L. Lortie[4], Lohengrin A. Cavieres[5], Georges Kunstler[6], Pierre Liancourt[7], Katja Tielbörger[7], Justin M. J. Travis[8], Fabien Anthelme[9], Cristina Armas[10], Lluis Coll[11], Emmanuel Corcket[12], Sylvain Delzon[12], Estelle Forey[12], Zaal Kikvidze[13], Johan Olofsson[14], Francisco Pugnaire[13], Constanza L. Quiroz[5], Patrick Saccone[6], Katja Schiffers[15], Merav Seifan[7], Blaise Touzard[12] and Richard Michalet[12]**

*[1]The Macaulay Land Use Research Institute, Craigiebuckler, Aberdeenshire AB15 8QH, UK, [2]Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Universidad Rey Juan Carlos, ESCET, C/ Tulipán s/n, 28933 Móstoles, Spain, [3]Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA, [4]Biology Department, York University, Toronto, ON M3J 1P3, Canada, [5]Departamento de Botánica, Universidad de Concepción and Instituto de Ecología y Biodiversidad (IEB), Concepción, Chile, [6]Cemagref – Unité de Recherche Ecosystèmes Montagnards, 2, rue de la Papeterie, B.P. 76, 38402 St-Martin-D'Heres cedex, France, [7]University of Tübingen, Institute for Botany, Plant Ecology Department, Auf der Morgenstelle 1 72076 Tübingen, Germany, [8]School of Biological Sciences, Zoology Building, Tillydrone Avenue, University of Aberdeen, Aberdeen AB24 2TZ, UK, [9]IRD, UMR 1097, 911 avenue Agropolis, 34394 Montpellier cedex 5, France, [10]Department of Biology, Box 90338, FFSC, Room 3304, Duke University, Durham, NC 27708, USA, [11]Centre Tecnològic Forestal de Catalunya / Forest Technology Centre of Catalonia, Pujada del Seminari s/n, 25280-Solsona, Spain, [12]University Bordeaux 1, Community Ecology Group, UMR INRA 1202 BIOGECO, 33405 Talence, France, [13]Estacion Experimental de Zonas Aridas, Consejo Superior de Investigaciones Cientificas, 04001 Almeria, Spain, [14]Department of Ecology and Environmental Science, Umeå University, Sweden, [15]Department of Plant Ecology and Nature Conservation, University of Potsdam, Maulbeerallee 2, 14469 Potsdam, Germany*

## Summary

**1.** Once neglected, the role of facilitative interactions in plant communities has received considerable attention in the last two decades, and is now widely recognized. It is timely to consider the progress made by research in this field.

**2.** We review the development of plant facilitation research, focusing on the history of the field, the relationship between plant–plant interactions and environmental severity gradients, and attempts to integrate facilitation into mainstream ecological theory. We then consider future directions for facilitation research.

**3.** With respect to our fundamental understanding of plant facilitation, clarification of the relationship between interactions and environmental gradients is central for further progress, and necessitates the design and implementation of experiments that move beyond the clear limitations of previous studies.

**4.** There is substantial scope for exploring indirect facilitative effects in plant communities, including their impacts on diversity and evolution, and future studies should connect the degree of non-transitivity in plant competitive networks to community diversity and facilitative promotion of species coexistence, and explore how the role of indirect facilitation varies with environmental severity.

**5.** Certain ecological modelling approaches (e.g. individual-based modelling), although thus far largely neglected, provide highly useful tools for exploring these fundamental processes.

**6.** Evolutionary responses might result from facilitative interactions, and consideration of facilitation might lead to re-assessment of the evolution of plant growth forms.

---

*Correspondence author. E-mail: r.brooker@macaulay.ac.uk.

© 2007 The Authors. Journal compilation © 2007 British Ecological Society

**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 environmental change drivers.

**8.** Attempts to apply 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.** Synthesis: Plant facilitation research provides new insights into classic ecological theory and pressing environmental issues. Awareness and understanding of facilitation should be part of the basic ecological knowledge of all plant ecologists.

**Key-words:** competition, disturbance, ecological theory, environmental change, environmental gradients, facilitation, plant communities, positive plant interactions, review, stress

## Introduction

> 'He grew low palms, for their spreading leaves shaded his plants from the sun which otherwise might in that stark valley wither them.'
>
> – T. E. Lawrence

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.

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

It is perhaps a suitable time for reviewing progress. Has the recent research effort taken this field forward? Given our current understanding, what gaps in our knowledge of facilitative interactions most urgently need to be addressed? Can we understand their role in mediating the impact of environmental change drivers or use this knowledge to mitigate such impacts? This paper will attempt to answer these questions.

As a necessary starting point we provide a brief overview of some key papers (several of which are themselves reviews) that helped to revitalize interest in plant facilitation. We also discuss how their conclusions have been the impetus for recent developments in facilitation research (examples in Table 1; see also Table S1 in Supplementary Material). We then suggest areas where we consider there to be substantial opportunities for future research, and the approaches that might be used. We focus our review in particular on interactions between vascular plants, as they have been the focus of the bulk of plant facilitation studies.

## Recent developments in plant facilitation research

Until recently, many ecologists only encountered facilitative plant–plant interactions within a particular context: facilitation of one successional stage by the preceding stage was a recognized, albeit underestimated, component of some theories of succession (Clements 1916; Connell & Slatyer 1977) and had been demonstrated in a number of ecosystems, for example in the classic studies of plant succession in Glacier Bay (Crocker & Major 1955; Chapin *et al.* 1994; for a review of the role of facilitation in primary succession see Walker & del Moral 2003).

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

From these papers some common themes emerged. Evidence of facilitative effects between plants tended to come from severe environments, such as deserts, arctic or alpine

**Table 1.** Advances in facilitation research since the publication of Bertness & Callaway (1994) and Callaway (1995), and examples of papers that have addressed these issues including their author(s), topics, and key development or finding. For a more extensive list of studies see Table S1

| Author(s) | Topic of paper | Key development or finding |
|---|---|---|
| *Integrating facilitation into mainstream ecological theory* | | |
| Bruno *et al*. (2003) | The need to include facilitation into mainstream ecological theory and the proposition that this process will 'challenge some of our most cherished paradigms'. | Revision of theory to include: potential for expansion of the realized niche by facilitation, positive density-dependence at high population densities, inclusion of facilitation in the diversity–invasibility paradigm, the role of dominant species in regulating local diversity. |
| Michalet *et al*. (2006) | Revision of Grime's (1973) model to incorporate facilitative interactions in plant communities. | Explicit consideration of facilitation in one of the central theories of plant community ecology. |
| *Facilitation and environmental gradients* | | |
| Tielbörger & Kadmon (2000a) | Temporal environmental variation between competition and facilitation in desert plants. | Increasing annual rainfall produced varying responses in impact of desert shrubs on annuals. Increased rainfall changed the effect of shrubs from negative to neutral, or neutral to positive depending on the species. Findings contradict prediction of increased facilitation with increased environmental severity. |
| Choler *et al*. (2001) | Examination of the relative importance of competitive and facilitative interactions along elevational and topographical gradients in alpine environments. | Facilitation increases with increasing altitude or exposure, but particularly strong for species at their upper altitudinal or physiological limit. Facilitation may therefore be promoting niche expansion into severe environments. |
| Callaway *et al*. (2002) | Multi-site examination of relationship between environmental severity and plant–plant interactions in arctic–alpine environments. | General shift from competition to facilitation as average community interaction with increasing altitude, and demonstration of large-scale relationship between dominant type of interaction and environmental severity. |
| Maestre & Cortina (2004) | Test of stress gradient hypothesis in semi-arid steppe environment. | Hump-backed relationship between interactions and accumulated rainfall (environmental severity) – competitive interactions dominate at both extremes of the severity gradient. |
| Maestre *et al*. (2005) | Meta-analysis of field and common garden experiments evaluating the effect of abiotic stress on the net outcome of plant–plant interactions in arid and semi-arid environments. | The measure of plant performance and experimental approach strongly influence the observed relationship between stress and net plant–plant interactions. Conclude that the role of facilitation does not increase with abiotic stress. |
| Cavieres *et al*. (2006) | Examination of the relative frequency of facilitative interactions at the community level along elevational gradients in Mediterranean-type alpine environments | Facilitative interactions did not increase with elevation. They were more frequent at lower elevations where environmental stress is higher due to water limitation, thus supporting the SGH. Stress-tolerant species (e.g. annuals, shrubs) were not facilitated. |
| Lortie & Callaway (2006) | Critique of Maestre *et al*.'s (2005) meta-analysis. | Conclude that study selection for Maestre *et al*.'s analysis was not rigorous, and that differences in stress gradient lengths between studies could have a considerable impact on results. |
| *Indirect interactions and facilitation* | | |
| Levine (1999) | Experimental study of indirect facilitation in a riparian community. | Experimental demonstration of indirect facilitation. Proposition of a general hypothesis that indirect facilitation among competitors will be important in assemblages where species vary in competitive mechanism. |

**Table 1.** *continued*

| Author(s) | Topic of paper | Key development or finding |
|---|---|---|
| *Development of ecological models incorporating plant facilitation* | | |
| Travis *et al*. (2005, 2006) | Development of a simple patch occupancy model to simulate the dynamics of two species, a mutualist and cheater, along an imposed environmental gradient. | Use of simulation modelling to explore changes in the role of plant–plant interactions along environmental gradients and their impact on the spatial distribution of species. |
| Brooker *et al*. (2006) | Development of patch-occupancy model from Travis *et al*. (2005, 2006) to simulate impacts of climate change on a simple model system including two main plant strategies. | Demonstration that species distributions along environmental gradients, as determined by facilitative and competitive interactions, interact with dispersal ability to determine range shifting dynamics and species survival. |
| *Connecting facilitation to evolution* | | |
| Scheffer & van Nes (2006) | Examination of the evolutionary processes involved in self-organized similarity. | Indirect facilitation may be one of the processes driving the evolution of niche convergence. |
| Valiente-Banuet *et al*. (2006) | Facilitation of Tertiary plant lineages in Mediterranean-climate ecosystems by modern Quaternary species. | A large number of ancient Tertiary plant lineages, which evolved under wetter climatic conditions than found currently, are preserved by facilitative nurse plant effects from modern Quaternary species. Facilitation is a source of stabilizing selection for the regeneration niches of Tertiary species. |
| *Facilitation and ecosystem restoration* | | |
| Maestre *et al*. (2001) | Potential for using nurse plant effect of grasses to promote shrub establishment in degraded semiarid steppe ecosystems. | Facilitative effect of dominant grass on introduced shrubs, related to improved water potential. Evidence of potential use of facilitative interactions for the restoration of semi-arid steppes. |
| Castro *et al*. (2004) | Use of shrubs as nurse plants to promote reforestation in Mediterranean-type mountain ecosystems. | Technique proven – proposed to have the added advantage of utilizing natural successional processes, and thus reducing impact on the studied community. |
| Gómez-Aparicio *et al*. (2004) | Meta-analysis of the use of shrubs as nurse plants for reforestation. | Consistent evidence of facilitative effect but strength varied between environment and species. Pioneer shrubs can positively influence restoration efforts in Mediterranean mountains. |

tundra systems, or salt marshes. It was even suggested that 'fascination with competition has focused attention on communities where competition is conspicuous' (Bertness & Callaway 1994). These reviews also proposed that the severity of the environment influenced the balance of the numerous positive and negative interactions that occur between interacting plants. For example, plants that compete for nutrients can have simultaneous positive effects through the provision of shelter or protection from herbivory. Increased environmental severity appeared to increase either the potential for, or strength of, positive interactions, relative to negative interactions, thus shifting the observable net interactions toward facilitation in extreme environments (Hunter & Aarssen 1988; Bertness & Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998).

Competition still dominates consideration of plant–plant interactions within the ecological literature (Fig. 2). However, since these earlier papers, recent studies have helped to deal with 'the mistaken notion that positive interactions are not well demonstrated with field experiments' (Callaway 1995), and have explored the issues raised in detail (Table 1). One topic in particular has received considerable recent attention: the relationship between plant–plant interactions and environmental severity.

Although Hunter & Aarssen (1988) discussed the balance between positive and negative plant–plant interactions, they did not suggest any generic relationships between this balance and environmental gradients. Bertness & Callaway's (1994) paper took such a step, proposing that increases in either the degree of physical stress or consumer pressure would increase the frequency of positive interactions. Callaway & Walker (1997) discussed the possible regulatory effects of climatic conditions and life-history stage (see also Callaway 1995) on the balance between positive and negative interactions. Brooker & Callaghan (1998) explicitly framed their model within the context of Grime's (1974, 1977, 1979) definitions of stress and disturbance, concentrating on changes in interactions along gradients of disturbance because of unresolved

**Fig. 1.** Examples of mechanisms of plant–plant facilitation. (a) *Buffered substrate and air temperature, enhanced soil moisture and nutrient content.* Cushion of *Azorella monantha* harbouring native and invasive species (e.g. the Andean cauliflower *Nastanthus agglomeratus* and the field chickweed *Cerastium arvense*, respectively) at the upper limit of vegetation (3600 m a.s.l) in the high Andes of central Chile. Photo: Lohengrin A. Cavieres (see Cavieres *et al.* 2005, 2007). (b) *Protection from drought*. Adult individual of the tussock grass *Stipa tenacissima* facilitating a sapling of *Pinus halepensis* in a semi-arid steppe, south-east Spain. Photo: Fernando T. Maestre (see Maestre *et al.* 2001, 2003a). (c) *Protection from browsing*. *Quercus pubescens* seedling within unpalatable *Buxus sempervirens* shrubs, southern France. Photo: Georges Kunstler (see Kunstler *et al.* 2006). (d) *Protection from browsing and drought.* Facilitation by *Gymnocarpos decander* of annual vegetation in a semi-arid environment, Jordan. Photo: Pierre Liancourt.

debate concerning gradients of stress (Tilman 1988; Grace 1991, 1993; Reader *et al.* 1994; Brooker *et al.* 2005), although their approach was not without criticism (Bertness 1998).

Overall, an amalgam of these models has become known as the stress gradient hypothesis (SGH) – something of a misnomer considering that the commonly cited model of Bertness & Callaway (1994) included both stress and consumer pressure. Many recent studies have attempted to test the SGH, and have taken a 'high vs. low' approach, i.e. they consider two or perhaps three levels of environmental severity (disturbance and/or stress), and have frequently found that with increasing severity the beneficial impacts of neighbours increase (e.g. Greenlee & Callaway 1996; Pugnaire & Luque 2001; Maestre *et al.* 2003a; Gómez-Aparicio *et al.* 2004; Brooker *et al.* 2006; Kikvidze *et al.* 2006b; Callaway 2007). However, such studies often focus on interactions that are clearly facilitative, and examine one particular species pairing (but see Cavieres *et al.* 2002, 2006 for community-level studies).

A few studies have taken a broader approach, examining patterns across gradients. Choler *et al.* (2001) found that increasing altitude was associated with increasing frequency of facilitative interactions. They also found that facilitation depended on species identity – facilitated species were commonly at the extreme ends of their environmental tolerance (see also Liancourt *et al.* 2005) – and led to range expansion (as discussed by Bruno *et al.* (2003) with respect to niche theory). Callaway *et al.* (2002) found a generic shift in the average type of interaction along a large-scale climatic gradient, with facilitative interactions in colder environments and increasingly competitive interactions in warmer environments. In an aridity gradient study, Holzapfel *et al.* (2006) found a steady and consistent shift from net positive or neutral effects to net

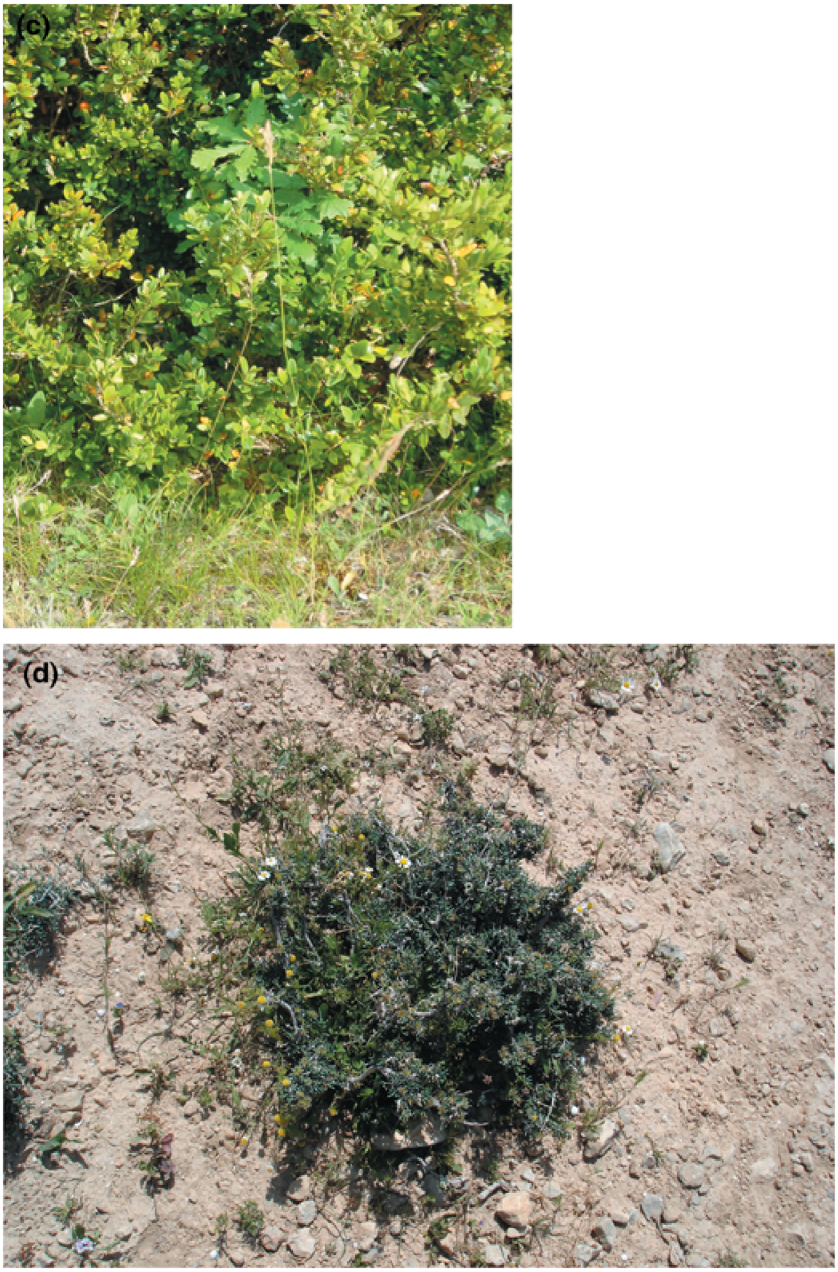

**Fig. 1.** *continued*

negative effects of desert shrubs on annual species with increasing water availability. In contrast, but in a study conducted on only one species pair, Maestre & Cortina (2004) found a switch from competition to facilitation and back to competition along a gradient of decreasing rainfall in a semi-arid steppe system. Similarly, Tielbörger & Kadmon (2000a) found that the effect of desert shrubs on annuals shifted from negative to neutral or neutral to positive (depending on the species) with increasing annual rainfall. Pennings *et al.* (2003) failed to find support for predictions from the SGH in a study conducted over a large-scale geographical gradient in salt marshes.

Simple individual-based models have also been used to examine the SGH. Travis *et al.* (2005) found that facilitative interactions were restricted to the most severe environmental conditions when the stress gradient acted upon reproduction, but competitive interactions were again prevalent in severe conditions when it acted upon mortality (Travis *et al.* 2006). These results match the conclusions of Goldberg *et al.*'s (1999) review of field studies that the observed relationship between environmental severity and success depends on the measure of plant performance used. However, 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).

A number of factors have been proposed to influence the outcome of studies testing predictions from the SGH. These include relatively short-term experiments, a lack of adequate control for the occurrence of multiple stress factors or ontogenetic effects (but see Armas & Pugnaire 2005; Miriti 2006; Schiffers & Tielbörger 2006), or the effects of resource vs. non-resource stress factors (Michalet 2007). Maestre *et al.*

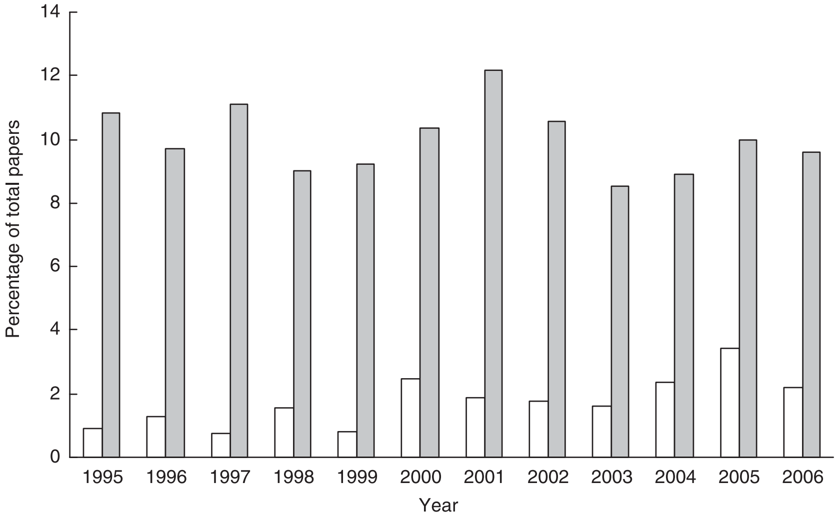

**Fig. 2.** The number of papers examining facilitation (open bars) and competition (closed bars) as a percentage of the total number of papers published in five leading plant ecology journals (*American Naturalist*, *Ecology*, *Journal of Ecology*, *Oikos* and *Oecologia*) between 1995 and 2006. Data obtained from ISI Web of Knowledge (http://portal.isiknowledge.com/; 1 March 2007) using the search strings [('positive interaction*' OR facilitation) AND plant*] or alternatively [('negative interaction*' OR competition) AND plant*], specifying English language articles only. After Dormann & Brooker (2002).

(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 gradient used (resource vs. non-resource or temporal vs. spatial).

Progress in understanding this relationship is crucial as it underlies key theories within plant ecology and is central to integrating facilitation into mainstream ecological theory. When interactions have been addressed in theories of plant community or population ecology (e.g. Grime 1977; Tilman 1988) they have tended to be negative, competitive interactions (except for the handful of well-recognized examples mentioned above). However, given that facilitative interactions are widespread and can regulate the success of individuals and the composition of communities, there is a clear need to explore how facilitation might fit within or modify these classic theories. Bruno *et al.* (2003) discussed revision of niche theory to include the potential for expansion of the realized niche by facilitation (as empirically demonstrated by Hacker & Gaines 1997; Choler *et al.* 2001), positive density-dependence at high population densities, inclusion of facilitation in the diversity–invasibility paradigm, and the role of dominant species in regulating local diversity.

However, Bruno *et al.* (2003) did not discuss in detail one of the classic theories of plant community ecology to which the SGH is directly relevant – the hump-backed diversity model (Grime 1973; Huston 1979). One of the first attempts to explore the relevance of facilitation to this model was that of Hacker & Gaines (1997), who suggested a conceptual scheme in which the positive effects of facilitation on biodiversity (species richness) increase from intermediate to very high environmental severity, in line with predictions from the SGH. Hacker & Bertness (1999) demonstrated the importance of facilitation for increasing diversity at intermediate levels of environmental severity. Michalet *et al.* (2006) further developed these ideas, suggesting that facilitation promotes diversity at medium to high environmental severity by expanding the range of stress-intolerant competitive species into harsh physical conditions (as discussed by Bruno *et al.* 2003 and demonstrated by Choler *et al.* 2001), but that when environmental conditions become extremely severe the positive effects of the benefactors wane and diversity is reduced, indicating that biotic interactions shape both sides of the humped-back curve of diversity. Perhaps one of the most striking examples of the potential importance of facilitation for the maintenance of biodiversity is that described by Valiente-Banuet *et al.* (2006). They found that a large number of ancient Tertiary plant lineages, which evolved under much wetter climatic conditions than found in the Mediterranean-climate ecosystems where they now live, have been preserved by facilitative nurse plant effects from modern Quaternary species. In the absence of such interactions the flora of these regions would be significantly altered, and facilitative interactions have therefore played 'a central role in the preservation of global biodiversity' (Valiente-Banuet *et al.* 2006).

## Looking to the future

Recent research has clearly built upon the synthesis papers that reignited interest in plant facilitation. This research, as well as continuing to explore in detail the mechanisms of individual facilitative interactions (see Table S1), has attempted to test the broader scale synthetic predictions and models derived from these classic papers. The accuracy of these broader syntheses has become a topic of considerable debate, but it has also become clear that resolving such debate is directly relevant to a number of ecological issues, not least the integration of facilitation into mainstream ecological theory. Our review therefore highlights the significant potential for future research into plant facilitation. In addition, there are a number of research fields that have, perhaps surprisingly, so far failed to make links to facilitation research, despite their clear relevance. In this section we thus discuss what we consider to be some of the most interesting topics for future research and, where possible, the approaches by which they could be taken forward.

## IMPROVING OUR UNDERSTANDING

### *Facilitation and environmental gradients*

One important step to understanding the shifting balance between positive and negative interactions along environmental gradients is the design and implementation of experiments that move beyond the limitations of previous studies. These should, whenever possible, include at least one of the following aspects: (i) several co-occurring stress factors (e.g. temperature and water availability in arid areas and Mediterranean mountains), (ii) several levels within each stress factor, ideally accounting for a wide range in the variation of each factor, and (iii) an appropriate control of 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 in situations where benefactors may themselves be limited, such as at the extreme end of severity gradients. Experiments should also attempt to isolate the environmental factors affected by potential benefactors (to provide a mechanistic understanding of severity interaction relationships, e.g. Holmgren *et al.* (1997), Holmgren (2000)), evaluate different performance variables (e.g. survival, growth, physiological status and fitness), attempt to account for factors such as initial biomass effects (Gibson *et al.* 1999; Goldberg *et al.* 1999; Kikvidze *et al.* 2006a), 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). Taking into account these issues will be challenging and (comparatively) costly. However, we also 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 with this rejuvenated research effort, we must also address the issue of the importance of facilitative interactions. A detectable process may not necessarily play a predominant role. Community composition is commonly seen as being regulated by filters, including chance biogeographical events, local abiotic conditions and interactions with other species (Grime 1998; Diaz *et al.* 1999; Lortie *et al.* 2004). The relative impact of each filter is not fixed, and there is a general assumption that filters operate to regulate distribution at different scales, e.g. chance biogeographical events and biotic interactions are considered most important for regulating distributions at the regional and local scales, respectively (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 may remain unaltered along an environmental gradient, their impact relative to other processes (i.e. their importance) may vary. When and where, therefore, are facilitative interactions not only detectable but playing a key role, and does the importance of their role vary depending upon whether we are considering (for example) community composition or evolutionary processes?

The few studies to have considered the response of both the importance and the intensity of interactions demonstrate that they might not change in parallel along environmental gradients (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). Evaluating the effects of facilitation on the survival and fitness of individuals is therefore crucial if we want to understand when and where facilitation acts as a filtering process in plant communities. We predict that facilitation is likely to be important relative to other filters when 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 when growing *adjacent to the benefactor species* (see *Development of models incorporating plant facilitation* for discussion of the related concept of a plant's interaction 'kernel'). Low or extremely high environmental severity would prevent facilitation from having a significant role, either in regulating the composition of the community or as a selective force. Field studies need to 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; Wooton 1994; Rousset & Lepart 2000; Corcket *et al.* 2003b; Seifan & Kadmon 2006). However, complex indirect interactions *within* a trophic level, or among competitors (Aarssen 1992; Miller 1994; Levine 1999; Callaway & Pennings 2000;

Tielbörger & Kadmon 2000b; Callaway 2007) 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 linear, with each species out-competing all those that are lower in the hierarchy. From this we might conclude that the only outcome of strong competition in communities at equilibrium is the exclusion of some or most members. However, this overlooks potential positive effects that occur in multi-species communities due to non-transitive 'networks' of interactions (Aarssen 1992). When interactions take place among many species at the same time, the competitive suppression of one species (B) by another (A) can decrease the latter's competitive effect on a third species (C) (Fig. 3a), thus leading to the phenomenon of indirect facilitation.

Few studies have considered that the occurrence of indirect facilitation may depend on complementarities in the interactions between species and therefore the identities or traits of the organisms involved (Huisman & Weissing 1999; Huisman *et al.* 2001). For example, in our model system (Fig. 3) indirect facilitation is most likely when pairs of plants (A–B, B–C) compete for different resources, for example light for the first species pair, and water or nutrients for the second (Levine 1999; Pagès & Michalet 2003; Siemann & Rogers 2003; Kunstler *et al.* 2006). Plant characteristics other than resource uptake ability (such as the production of allelopathic chemicals) may create such species-specific interactions, and thus non-transitive interaction networks and indirect interactions (Pagès *et al.* 2003; Callaway & Howard 2006; Kunstler *et al.* 2006; Callaway 2007). If the existence of multiple interaction mechanisms among coexisting species increases the potential for strong indirect interactions, indirect facilitation should be more common in communities where several limiting factors co-occur with similar strengths. In contrast, in environments with one dominant limiting factor, such as xeric, N-poor or low light conditions, indirect facilitation should be less important.

Surprisingly few studies have analysed how gradients of diversity will influence, and be influenced by, indirect facilitative interactions. Indirect facilitation should be more common in species-rich communities (Miller 1994; Dodds 1997). Indeed, it may have the potential to sustain the coexistence of high species diversity by reducing the potential for competitive exclusion (Czaran *et al.* 2002; Laird & Schamp 2006) and may be the dominant facilitative process in more productive environments (given the predicted reduction in direct facilitative effects). Indirect facilitation among competitors therefore challenges assumptions about competition consistently leading to exclusion.

There is therefore a notable dearth of studies exploring the role of indirect facilitative effects in plant communities, including their impacts on diversity and evolution. Future studies, using artificial manipulations of diversity or modelling approaches (see *Development of models incorporating plant facilitation*), should: (i) attempt to assess the conditions under which we might expect the greatest level of non-transitivity within plant communities; (ii) connect the degree of non-transitivity in plant competitive networks to community diversity and facilitative promotion of species coexistence; (iii) explore how the role of non-transitivity and indirect facilitation varies along gradients both of diversity and of system productivity, and in relation to direct facilitative effects; and (iv) explore, through multi-species evolutionary modelling, the potential for indirect facilitative effects to drive or limit niche differentiation.

### *Development of ecological models incorporating plant facilitation*

Although a broad suite of modelling approaches is available, and despite their likely relevance and utility, they have not yet been widely employed in furthering our understanding of the role of facilitative plant interactions. This represents a significant missed opportunity for promoting the development of theory in this field.

Recent work illustrates the potential for relatively simple models to provide generic insights into the dynamics of communities structured with a mixture of positive and negative interactions. For example, Yamamura *et al.* (2004) used a

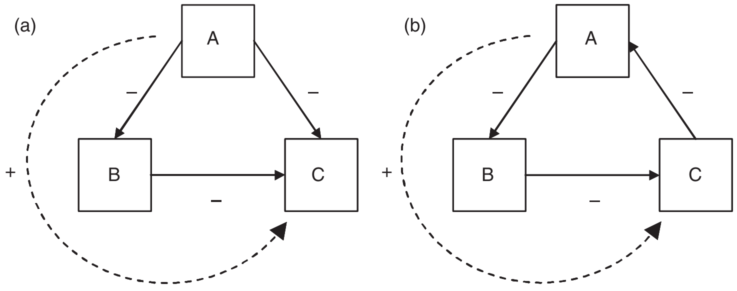

**Fig. 3.** Indirect (dotted line) and direct (solid line) interactions in a complex system. (a) Species A suppresses species B, which affects the potential negative effect of species B on C. As suggested by Levine (1976), if the benefit from suppression is higher than the direct negative effects, indirect facilitation occurs in the community. However, the benefit from suppression can be outweighed by direct negative effects, resulting in no net indirect facilitation (Levine 1999; Pagès *et al.* 2003). (b) Non-transitive interactions (A > B, B > C, C > A). The suppression of species B by A causes an indirect facilitation of species C, which increases its negative effect on A. In such a system the species ameliorate each other's effects and contribute to long-term coexistence (Czaran *et al.* 2002; Callaway & Howard 2006).

spatially explicit patch occupancy model to study the evolution of mutualisms, highlighting the importance of local spatial structure in determining the outcome of interactions. Their modelling approach represented space as a regular grid, each cell of which can be in one of two states, occupied or unoccupied. Rules determine the way in which neighbouring plants interact, reproduce, disperse their propagules, evolve and die. Yamamura *et al.* highlighted the importance of local spatial structure in determining the outcome of interactions among a mutualistic and a cheater species. Although having great potential, spatially explicit simulation models of this type have only recently been applied to facilitation.

Travis *et al.* (2005) extended the model of Yamamura *et al.* to consider plant facilitation specifically, demonstrating that positive interactions are most likely towards the harsh end of environmental gradients (although this depends on whether the gradient primarily influences reproduction or survival; Travis *et al.* 2006). Such models can therefore readily provide hypotheses suitable for testing with field experiments. In addition they can also be used to run experiments. Brooker *et al.* (2007) used the spatial model of Travis *et al.* (2005, 2006) to explore the impact of interactions on the capacity of species to track a moving 'climate envelope'. They found that the spatial arrangement of species with particular traits (as determined initially by interactions), along with the rate of climate change and level of long-distance dispersal, interacted to regulate the capacity of species to track their climate envelope.

Such developments in facilitation modelling are at an early stage. Although these spatially explicit models are a move in the right direction, they do not yet properly represent facilitation as most empirical plant ecologists have described it. In the mutualism models adapted for facilitation research the interaction term is commonly +/+ (Odum 1968), i.e. reciprocal benefit. However, although mutualistic interactions between neighbouring plants are possible, and may be more common than currently expected (Pugnaire *et al.* 1996), the impact of the beneficiary on the benefactor may range from positive to zero (+/0 commensalism), and some interactions might even be classified as parasitic (+/–). Future modelling should therefore start to distinguish clearly between mutualism and facilitation. Such a distinction would, for example, be important in determining the outcome of evolutionary modelling studies – facilitative interactions may have very different evolutionary impacts from mutualistic interactions, and may also evolve under different circumstances.

There is also a need for modelling approaches that accommodate variation in the role of facilitative interactions along environmental gradients, both in space and time, and at a local as well as landscape scale. If the spatial extents of positive and negative effects differ, the net outcome of interactions will be highly dependent on the spatial relation of the individual plants. Appropriate models would include the key elements of neighbourhood models (currently used to examine competitive plant interactions), i.e. individuals with an explicit location and basal extension where no other plant can exist, and a zone of competitive influence in which negative interactions occur (Stoll & Weiner 2000). Facilitation could be included through a zone of facilitation, although such zones of influence typically assume that all neighbours within a certain distance of a focal plant experience the same negative impact from competition. This is clearly unrealistic. More sophisticated approaches using interaction kernels, which describe the relationship between the distance of a neighbour from a focal individual and the competitive impact of that individual, have recently been developed (e.g. Murrell & Law 2003). However, few, if any, experiments in the literature provide the parameters necessary for such models.

Models thus extended to incorporate facilitation have the potential for a wide range of applications. For example, by allowing evolution of competition and facilitation kernels we may systematically test under which circumstances (frequency of interactions, gene flow, etc.) facilitation might evolve as an evolutionary stable strategy. Modelling could also explore the potential for different life-history characteristics (such as dispersal, dormancy, time to first reproduction, self-compatibility) to evolve in response to the balance between facilitation and competition present within a local community. Furthermore, the need to investigate interactions in multi-species assemblages is increasingly being recognized (e.g. Weigelt *et al.* 2007) and two-species models (Travis *et al.* 2006; Brooker *et al.* 2007) could readily be extended to multi-species models. This would enable, for example, the dynamics of indirect interactions to be examined in detail, including predicting the conditions under which this type of effect is likely to be observed in natural systems, and how its community and evolutionary impacts might compare with those of direct facilitative effects.

### *Connecting facilitation to evolution*

Recent studies indicate that facilitation may act as an evolutionary force: Scheffer & van Nes (2006) predicted that indirect facilitation may drive convergence of species' niches, and Valiente-Banuet *et al.* (2006) suggested that facilitation is a source of stabilizing selection for the regeneration niches of ancient Tertiary species within Mediterranean-climate ecosystems. However, although the possible relationships between facilitation and evolution have been discussed previously (Hunter & Aarssen 1988; Brooker & Callaghan 1998; Callaway 2007), an evolutionary focus is absent from almost all recent work in the facilitation field.

We can readily visualize the 'competitor' syndrome that might evolve in response to strong and consistent negative interactions in productive environments: a high, dense canopy of wide-spreading leaves, rapid potential RGR (relative growth rate), high morphological plasticity, etc. (a classic C-strategy species; Grime 1977). However, it may not be straightforward to predict the evolutionary response to facilitative interactions, as both facilitative and competitive mechanisms may evolve in response to facilitation. For example, if species A is facilitated by species B, any negative effects of species A could select for those B individuals that are weaker facilitators (either by selecting against the key facilitation trait or in favour of an avoidance mechanism in species B). However, an alternative second selective force might favour individuals of species A with lower negative impacts on their benefactor.

One key trait that may come under such selection within the context of an assemblage comprising facilitators and facilitated is dispersal. Selection might favour dispersal kernels in the facilitated species that map onto those of the facilitator, for example through the convergence of dispersal agents. Conversely, selection of the facilitator might favour dispersal kernels enabling escape from the negative consequences of competition (unless the level of competition is itself reduced). Similarly, selection acting on characteristics such as the balance between reproduction by clones and seed may vary depending on the nature or balance of interactions – reproduction by seed may aid dispersal and be favoured by avoidance of competition, whereas clonal growth may be selected for by facilitation in the immediate vicinity of the parent plant. It is interesting to speculate that the reduced competitive effect or enhanced clonality of stress-tolerant species may in part result from selection in favour of enhanced facilitation. As stated by Brooker & Callaghan (1998) 'It may be the case that we already have evidence of the evolutionary impact of positive plant–plant interactions, but have never examined it in the light of this possible interpretation'.

The outcome of the selective process will depend not only upon the frequency and relative strength of the interactions, but also upon evolutionary constraints on specific traits – is evolution of an avoidance mechanism more likely than reduced competitive impact? The evolution of life-history traits will play an important role in determining the spatial dynamics of an assemblage, resulting in a continuous interaction between evolutionary dynamics related to the interactions and the spatial ecology of the system. The extension of relatively simple evolutionary models (e.g. Travis & Dytham 1999; Travis 2003), similar to the individual-based models discussed above, could explore the interplay between ecological and evolutionary dynamics that might result from these types of effects. However, given the potential complexity involved, including variability in the two-way nature of facilitation, a simple starting point for evolutionary studies might be to ask whether all facilitative interactions provide common selective forces, from this predicting patterns of traits, and then to explore whether traits vary in the expected manner along environmental gradients in association with quantification of the importance and intensity of interactions. With current rapid technological advances in genetic methodologies capable of looking at quantitative traits (e.g. Barton & Keightley 2002), we should ultimately aim to develop evolutionary models that explicitly incorporate the genetic architectures involved and are able to separate out the heritable from the environmental components of the traits concerned. An improved understanding of their genetic basis would also permit robust estimation of the strength and direction of selection on the suites of traits involved, and would provide insights into correlations and potential pleiotropic effects between these traits.

## APPLYING OUR UNDERSTANDING

### *Facilitation and ecosystem restoration*

In the face of current rapid degradation of terrestrial ecosystems worldwide, there is an increasing need for the development of novel, low-cost and efficient restoration techniques for maintaining ecosystem function and services (e.g. Ormerod *et al.* 2003; Hobbs *et al.* 2006). Because facilitation has been recognized as an important structuring force in natural plant communities, it is being increasingly discussed as an ecological mechanism which could be exploited for developing vegetation restoration tools, particularly for severe and highly disturbed environments (see reviews by Young *et al.* 2005; Padilla & Pugnaire 2006; Halpern *et al.* 2007).

Yet, except for arid environments, the role of positive plant interactions in terrestrial restoration is almost always overlooked. This is despite studies reporting strong facilitative effects during restoration in high mountain environments (Walker & Powell 1999; Aerts *et al.* 2007), tropical forests (Parrotta *et al.* 1997) or highly disturbed sites such as mine spoils (Densmore 2005; Frérot *et al.* 2006), and a range of examples from aquatic and intertidal ecosystems (reviewed by Bruno *et al.* 2003; Halpern *et al.* 2007).

Studies examining plant facilitation in terrestrial ecosystem restoration usually focus on the positive effects of nurse plants. Water-limited ecosystems offer one of the best opportunities for exploring these effects, as well illustrated by the study of Gómez-Aparicio *et al.* (2004). They investigated the use of naturally occurring shrubs as nurse plants for reforestation in a Mediterranean environment, and found that shrubs had a consistent beneficial effect on tree seedling survival and growth during four consecutive years. Such results directly contradict traditional reforestation management practice, where shrubs are removed prior to tree planting due to their presumed competitive effects on tree seedlings (see also Castro *et al.* 2004). Unfortunately, most studies addressing the use of nurse plants for restoration in arid systems have usually been conducted over shorter time frames, i.e. fewer than three growing seasons (e.g. Maestre *et al.* 2001, 2003b, 2004; Barchuk *et al.* 2005). Given the temporal variability in facilitative interactions in these systems (Tielbörger & Kadmon 2000a; Miriti 2006), this may be an insufficient period over which to assess whether nurse plants have a net beneficial effect, and longer-term studies are clearly needed. Furthermore, these studies commonly plant beneficiary species under existing nurse plants. However, in extremely degraded ecosystems nurse plants may themselves be lost (Gibson & Brown 1991). In such cases management for nurse plant re-establishment may be necessary as a first step, although it is also important to consider whether the restoration of nurse plant cover would be the most effective way of driving beneficiary re-establishment.

Novel techniques currently being developed in agroecosystems and polluted areas demonstrate the wide range of possible uses of facilitative interactions for environmental management. Facilitation can operate via increased pollinator visits, which lead to greater crop yields (Ricketts *et al.* 2004), enhanced water status of crops growing with species capable of hydraulic lift (Pate & Dawson 1999; Sekiya & Yano 2004), the transfer of symbiotically fixed nitrogen from legume to non-legume species (Jensen 1996; see also Hauggaard-Nielsen & Jensen 2005 for a review of facilitative root interactions in agro-ecosystems), or phytostabilization by metallicolous nurse plants in heavy-metal-polluted environments (Frérot *et al.* 2006). Transgressive over-yielding has been reported for multi-species mixtures in intensively managed grassland systems, although the precise mechanism is unclear (Kirwan *et al.* 2007). There may therefore be a wide range of facilitative mechanisms, in addition to the classic nurse plant effect, that could act as the basis for restoration tools.

As strikingly illustrated by the work of Gómez-Aparicio *et al.* (2004) discussed above, Sutherland *et al.* (2004) proposed that 'Much of current conservation practice is based upon anecdote and myth'. The acknowledgement of facilitation in studies of restoration, particularly within environments that are difficult to restore, would help to raise facilitation's profile as a tool for natural resource conservation and management. Furthermore, applied facilitation research also has significant unexploited potential for advancing the science of restoration ecology in general. The explicit consideration of facilitation when exploring key topics in this research area, such as stable alternative states (Suding *et al.* 2004), succession (Walker *et al.* 2007) or the links between ecosystem structure/function and restoration success (Young *et al.* 2005; Cortina *et al.* 2006), are likely further to help managers and practitioners to develop effective tools to achieve the desired restoration targets.

### *Facilitation and global change*

Climate change, nitrogen deposition, biological invasions and land-use change have been suggested as the current major threats to global biodiversity (Sala *et al.* 2000; CBD 2003), and significant evidence is accumulating that interactions, including facilitative ones, play a role in mediating the impact on natural communities of these environmental change drivers (Brooker 2006; Maestre & Reynolds 2006, 2007). However, the exact nature of that role, and how it will alter in response to environmental change, remains unclear.

Several studies have demonstrated the importance of facilitation for the maintenance of biodiversity in arctic and alpine habitats (e.g. Choler *et al.* 2001; Callaway *et al.* 2002), and these habitats are predicted to be amongst the most sensitive to global warming (Guisan & Theurillat 2000; ACIA 2004). Based on the original SGH, some authors have predicted a general shift in species interactions from more strongly positive to more strongly negative as these environments warm (e.g. Klanderud & Totland 2005; Klanderud 2005). In support, experiments that evaluated the impact of enhanced nitrogen availability in these ecosystems (simulating the expected effect of climate change on nutrient mineralization rates) mostly reported increased competitive interactions (e.g. Chapin *et al.* 1995; Bret-Harte *et al.* 2004; Klanderud & Totland 2005). Similarly, in a North American arctic tundra system, where artificially advanced snowmelt (a phenomenon expected under global warming) created a more severe environment through increased early-season frost events, neighbours increasingly facilitated the survival, growth and reproduction of *Empetrum nigrum* (Wipf *et al.* 2006). However, Shevtsova *et al.* (1997) reported that the positive effects of elevated temperature on the growth and reproduction of *Vaccinium vitis-idaea* and *Empetrum nigrum* in subarctic Finland were amplified by the presence of neighbours – in this instance a reduced level of environmental severity (warming) led to an increased impact of facilitative interactions.

These findings support the argument that the relationship between gradients of environmental severity and the relative role of interactions is more complicated than set out in the original SGH (e.g. Bertness & Ewanchuk 2002). At first glance we might conclude that such a pattern supports the recently proposed humped-back relationship (Michalet *et al.* 2006). However, it is notable that the increased role of facilitation with decreasing severity found by Shevtsova *et al.* (1997) occurs within an environment that is apparently less severe than, for example, the open tundra systems studied by Chapin *et al.* (1995) and Wipf *et al.* (2006), and in which the opposite pattern was observed. Such apparently contradictory findings indicate that the perception of environmental severity is to some extent species-specific, and that the response of interactions at the individual species level may not reflect the trend of average interactions within a community. Improving our knowledge of the variation in interactions under different environmental conditions between different species, growth-forms or strategies (e.g. competitive vs. stress-tolerant strategies), and how these differ from trends at the community level, will help in the development of general theory and in explaining such apparently contradictory results.

Invasive species are another critical global change driver. In the study of biological invasions, interactions are considered crucial in determining the success of exotics (e.g. Daehler 2003; Simberloff *et al.* 2003; Vilà *et al.* 2004). Although most studies have focused on negative interactions as the main drivers of invasive success (e.g. Callaway & Aschehoug 2000; Colautti *et al.* 2004; Mitchell *et al.* 2006), a sizable number have also reported that facilitation by other exotics (Simberloff & Von Holle 1999) or by natives (Maron & Connors 1996; Richardson *et al.* 2000; Lenz & Facelli 2003; Cavieres *et al.* 2005, 2007) can promote exotic invasion. For instance, Maron & Connors (1996) reported that the nitrogen-fixing native shrub *Lupinus arboreus* facilitates the establishment of exotic species by ameliorating soil nutrient shortage. Cavieres *et al.* (2005) found that the cushion plant *Azorella monantha* facilitates the establishment of the exotic species *Taraxacum officinale* in the high-alpine zone of the Andes of central Chile by providing microsites with milder microclimatic conditions (see also Cavieres *et al.* 2007). Reinhart *et al.* (2006) showed how seedlings of the invasive tree *Acer platanoides* had higher densities, recruitment and survival, and less photoinhibition and water stress when beneath conspecific canopies than when growing under adjacent native *Pseudotsuga menziesii* trees; they related these differences to the environmental modification created by the invaders. When exotic species facilitate the establishment of other exotics, accelerated invasion can occur. Simberloff & Von Holle (1999) coined the term 'invasional meltdown' to describe such a process. Invasional meltdown demonstrates that facilitation can be an important driver of plant invasion (Simberloff 2006) but, interestingly, invasion can also be 'resisted' by greater diversity of native species (e.g. Zavaleta & Hulvey 2004; Fargione & Tilman 2005), a mechanism by which facilitation of natives may help limit the influx of invasives.

Improving our understanding of facilitative interactions is therefore of direct relevance to understanding the impacts of environmental change drivers on biodiversity (Callaway 2007). Resolving the debate concerning the SGH (difficult though this may be) may, for example, enable us more accurately to predict changes in the role of interactions in response to environmental change, or the conditions under which interactions might restrict or enhance biodiversity change, for example through the influx of invasives. However, it is not necessarily the case that radical new experiments are needed to explore these issues. As with restoration ecology, simply recognizing the potential role of facilitation, and including it within both experimental designs and the interpretation of ecosystem responses, could provide us with valuable insights into facilitation both as a mediator of global change and as a fundamental ecological process.

## Conclusions

Our coverage cannot hope to be fully comprehensive in an essay review such as this. Other relevant topics which we have touched upon at best only briefly include: the possible impacts of facilitation on ecosystem function (Hector *et al.* 1999); the concept of ecosystem engineering (Jones *et al.* 1997; Crain & Bertness 2006; Hastings *et al.* 2007); the use of indices in plant interaction studies (as hotly debated with respect to competition indices; Markham & Chanway 1996; Freckleton & Watkinson 1997a,b, 1999; Markham 1997; Weigelt & Jolliffe 2003; Armas *et al.* 2004; Wilson 2007); and the possible contrasting consequences of diffuse and species-specific facilitation (e.g. the general facilitative effects of neighbours compared with the specific one-on-one facilitative impacts of nurse plants). However, we have covered what are widely recognized as some of the central current issues for plant facilitation research, as well as highlighting what we believe to be some novel future directions for this field and a number of testable hypotheses (Table 2).

We should perhaps now answer the questions posed at the outset of this review. First, has the recent substantial research effort taken this field forward? Yes, undoubtedly, both in terms of developing general models and in exploring some of their underlying complexity, and also in raising general awareness of the widespread and important role of facilitative interactions in plant communities.

Secondly, what gaps in our knowledge of facilitative interactions need to be addressed? Clarification of the relationship between interactions and environmental gradients is central for further progress, and necessitates implementation of experiments specifically designed to address this issue. There is also substantial scope for exploring indirect facilitative effects, including their impacts on diversity and evolution, and future studies should attempt to connect the degree of non-transitivity in plant competitive networks to community diversity and facilitative promotion of species coexistence, perhaps exploring how the role of indirect facilitation varies with community productivity and the number of limiting resources. Certain ecological modelling approaches could provide highly useful tools for exploring these fundamental processes, and also clearly lend themselves to studying the evolutionary responses that might result from facilitative

**Table 2.** Some testable hypotheses that might be addressed by future plant facilitation research projects, organized by research theme (as used in this paper)

| Research theme | Hypothesis |
|---|---|
| Facilitation and environmental gradients | Facilitation will be important when environmental severity is high but not extreme.<br>High importance will be indicated by the dependence of a large proportion of species within a community on facilitative interactions. |
| Indirect facilitation | Indirect facilitative interactions will be more likely when the cause of competition varies between species pairs within a community.<br>Indirect facilitation will be more likely in communities where there are several co-occurring limiting factors.<br>Indirect facilitation will be more frequent in species-rich communities.<br>Indirect facilitation may be the principal mode of facilitation in productive environments. |
| Ecological modelling | The relationship between environmental severity and positive or negative plant interactions depends upon the factor being influenced by the environment (e.g. reproduction or survival).<br>Facultative positive interactions may not lead to the same evolutionary responses as obligate mutualistic interactions |

interactions, including possible re-assessment of the evolution of plant growth forms.

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

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

## Acknowledgements

This review was an outcome of the conference 'Facilitation, Biodiversity, Invasibility in a Changing World', held from 4 to 7 September 2006 at the University of Bordeaux's Marine Biological Station, Arcachon, France. We gratefully acknowledge the financial support provided for this meeting by the European Science Foundation, and thank Pierre Chardy and Xavier de Montaudouin for hosting the meeting. We thank all conference participants for stimulating discussions. R.W.B. would like to acknowledge support for writing this paper from the Scottish Executive Environment and Rural Affairs Department, and the use of Ray Callaway's reference data base for production of the supplementary material. F.T.M. acknowledges support from a Ramón y Cajal contract awarded by the Spanish Ministerio de Educación y Ciencia and from the British Ecological Society (ECPG 231/607).

## References

Aarssen, L.W. (1992) Causes and consequences of variation in competitive ability in plant communities. *Journal of Vegetation Science*, **3**, 165–174.

ACIA (2004) *Arctic Climate Impact Assessment*. Cambridge University Press, Cambridge.

Aerts, R., Negussie, A., Maes, W., November, E., Hermy, M. & Muys, B. (2007) Restoration of dry Afromontane forest using pioneer shrubs as nurse-plants for *Olea europaea ssp. cuspidata. Restoration Ecology*, **15**, 129–138.

Armas, C., Ordiales, R. & Pugnaire, F.I. (2004) Measuring plant interactions: a new comparative index. *Ecology*, **85**, 2682–2686.

Armas, C. & Pugnaire, F.I. (2005) Plant interactions govern population dynamics in a semi-arid plant community. *Journal of Ecology*, **93**, 978–989.

Barchuk, A.H., Valiente-Banuet, A. & Díaz, M.P. (2005) Effect of shrubs and seasonal variability of rainfall on the establishment of *Aspidosperma quebracho-blanco* in two edaphically contrasting environments. *Austral Ecology*, **30**, 695–705.

Barton, N.H. & Keightley, P.D. (2002) Understanding quantitative genetic variation. *Nature Reviews Genetics*, **3**, 11–21.

Bertness, M.D. (1998) Searching for the role of positive interactions in plant communities. *Trends in Ecology and Evolution*, **13**, 133–134.

Bertness, M. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.

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

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

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

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

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

Brooker, R.W., Scott, D., Palmer, S.C.F. & Swaine, E. (2006) Transient facilitative effects of heather on Scots pine along a grazing disturbance gradient in Scottish moorland. *Journal of Ecology*, **94**, 637–645.

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

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

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

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

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

Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht.

Callaway, R.M. & Aschehoug, E.T. (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science*, **290**, 521–523.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D. & Cook, B.J. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Callaway, R.M. & Howard, T.G. (2006) Competitive networks, indirect interactions, and allelopathy: a microbial viewpoint on plant communities. *Progress in Botany*, **68**, 317–335.

Callaway, R.M. & Pennings, S.C. (2000) Facilitation may buffer competitive effects: indirect and diffuse interactions among salt marsh plants. *American Naturalist*, **156**, 416–424.

Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and Evolution*, **2**, 436–443.

Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M. & Gómez-Aparicio, L. (2004) Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. *Restoration Ecology*, **12**, 352–358.

Cavieres, L., Arroyo, M.T.K., Penaloza, A., Molina-Montenegro, M. & Torres, C. (2002) Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *Journal of Vegetation Science*, **13**, 547–554.

Cavieres, L., Badano, E.I., Sierra-Almeida, A., Gómez-González, S. & Molina-Montenegro, M.A. (2006) Positive interactions between alpine plant species and the nurse cushion *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytologist*, **169**, 59–69.

Cavieres, L.A., Badano, E.I., Sierra-Almeida, A. & Molina-Montenegro, M.A. (2007) Microclimatic modifications of cushion plants and their consequences for seedlings survival of native and non-native plants in the high-Andes of central Chile. *Arctic, Antarctic and Alpine Research*, **39**, 229–236.

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

CBD (2003) *Interlinkages Between Biological Diversity and Climate Change. Advice on the Integration of Biodiversity Considerations Into the Implementation of the United Nations Framework Convention on Climate Change and its Kyoto Protocol*. Secretariat of the Convention on Biological Diversity, Montreal.

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

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

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

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

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

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

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119–1144.

Connolly, J., Wayne, P. & Bazzaz, F.A. (2001) Interspecific competition in plants: How well do current methods answer fundamental questions? *American Naturalist*, **157**, 107–125.

Corcket, E., Callaway, R.M. & Michalet, R. (2003b) Insect herbivory and grass competition in a calcareous grassland: results from a plant removal experiment. *Acta Oecologica*, **24**, 139–146.

Corcket, E., Liancourt, P., Callaway, R. & Michalet, R. (2003a) The relative importance of competition for two dominant grass species as affected by environmental manipulations in the field. *Ecoscience*, **10**, 186–194.

Cortina, J., Maestre, F.T., Vallejo, V.R., Baeza, J., Valdecantos, A. & Pérez-Devesa, M. (2006) Ecosystem function and restoration success: are they related? *Journal for Nature Conservation*, **14**, 152–160.

Crain, C.M. & Bertness, M.D. (2006) Ecosystem engineering across environmental gradients: Implications for conservation and management. *Bioscience*, **56**, 211–218.

Crocker, R.L. & Major, J. (1955) Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *Journal of Ecology*, **43**, 427–448.

Czaran, T.L., Hoekstra, R.F. & Pagie, L. (2002) Chemical warfare between microbes promotes biodiversity. *Proceedings of the National Academy of Sciences USA*, **99**, 786–790.

Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology and Systematics*, **34**, 183–211.

Densmore, R.V. (2005) Succession on subalpine placer mine spoil: Effects of revegetation with Alnus viridis, Alaska, USA. *Arctic, Antarctic and Alpine Research*, **37**, 297–303.

Diaz, S., Cabido, M. & Casonoves, F. (1999) Functional implications of trait-environment linkages in plant communities. *Ecological Assembly Rules: Perspectives, Advances, Retreats* (eds E. Weiher & J.P. Keddy), pp. 338–362. Cambridge University Press, Cambridge.

Dodds, W.K. (1997) Interspecific interactions: constructing a general neutral model for interaction type. *Oikos*, **78**, 377–383.

Dormann, C.F. & Brooker, R.W. (2002) Facilitation and competition in the high Arctic: the importance of the experimental approach. *Acta Oecologica*, **23**, 297–301.

Fargione, J.E. & Tilman, D. (2005) Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters*, **8**, 604–611.

Flores, J. & Jurado, E. (2003) Are nurse–protégé interactions more common among plants from arid environments? *Journal of Vegetation Science*, **14**, 911–916.

Freckleton, R.P. & Watkinson, A.R. (1997a) Measuring plant neighbour effects. *Functional Ecology*, **11**, 532–534.

Freckleton, R.P. & Watkinson, A.R. (1997b) Response to Markham. *Functional Ecology*, **11**, 536.

Freckleton, R.P. & Watkinson, A.R. (1999) The mis-measurement of plant competition. *Functional Ecology*, **13**, 285–287.

Frérot, H., Lefèbvre, C., Gruber, W., Collin, C., Dos Santos, A. & Escarré, J. (2006) Specific interactions between local metallicolous plants improve the phytostabilization of mine soils. *Plant and Soil*, **282**, 53–65.

García-Moya, E. & McKell, C. (1970) Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology*, **51**, 81–88.

Gaucherand, S., Liancourt, P. & Lavorel, S. (2006) Importance and intensity of competition along a fertility gradient and across species. *Journal of Vegetation Science*, **17**, 455–464.

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

Gibson, D.J., Connolly, J., Hartnett, D.C. & Weidenhamer, J.D. (1999) Designs for greenhouse studies of interactions between plants. *Journal of Ecology*, **87**, 1–16.

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

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

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

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

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

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

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

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

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. Wiley, Chichester.

Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.

Grime, J.P. (2007) Plant strategy theories: a comment on Craine (2005). *Journal of Ecology*, **95**, 227–230.

Guisan, A. & Theurillat, J.P. (2000) Assessing alpine vulnerability to climate change, a modelling perspective. *Integrated Assessment*, **1**, 307–320.

Hacker, S.D. & Bertness, M.D. (1999) Experimental evidence for factors maintaining species diversity in a New England salt marsh. *Ecology*, **80**, 2064–2073.

Hacker, S.D. & Gaines, S.D. (1997) Some implications of direct positive interactions for community species diversity. *Ecology*, **78**, 1990–2003.

Halpern, B.S., Silliman, B.R., Olden, J.D., Bruno, J.P. & Bertness, M.D. (2007) Incorporating positive interactions in aquatic restoration and conservation. *Frontiers in Ecology and the Environment*, **5**, 153–160.

Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.G., Lambrinos, J.G., Talley, T.S. & Wilson, W.G. (2007) Ecosystem engineering in space and time. *Ecology Letters*, **10**, 153–164.

Hauggaard-Nielsen, H. & Jensen, E.S. (2005) Facilitative root interactions in intercrops. *Plant and Soil*, **274**, 237–250.

Hay, M.E. (1986) Associational defenses and the maintenance of species diversity: turning competitors into accomplices. *American Naturalist*, **128**, 617–641.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., *et al.* (1999) Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123–1127.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., *et al.* (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.

Holmgren, M. (2000) Combined effects of shade and drought on tulip poplar seedlings: trade-off in tolerance of facilitation? *Oikos*, **90**, 67–78.

Holmgren, M., Scheffer, M. & Huston, M.A. (1997) The interplay of facilitation and competition in plant communities. *Ecology*, **78**, 1966–1975.

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

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

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

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

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

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

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

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

Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**, 1946–1957.

Kikvidze, Z., Armas, C. & Pugnaire, F.I. (2006a) The effect of initial biomass in manipulative experiments on plants. *Functional Ecology*, **20**, 1–3.

Kikvidze, Z., Khetsuriani, L., Kikodze, D. & Callaway, R.M. (2006b) Seasonal shifts in competition and facilitation in subalpine plant communities of the central Caucasus. *Journal of Vegetation Science*, **17**, 77–82.

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

Kirwan, L., Lüscher, A., Sebastia, M.T., Finn, J.A., Collins, R.P., Porqueddu, C., *et al*. (2007) Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. *Journal of Ecology*, **95**, 530–539.

Klanderud, K. (2005) Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, **93**, 127–137.

Klanderud, K. & Totland, Ø. (2005) The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology*, **93**, 493–501.

Kunstler, G., Curt, T., Bouchaud, M. & Lepart, J. (2006) Indirect facilitation and competition in tree species colonization of sub-mediterranean grasslands. *Journal of Vegetation Science*, **17**, 379–388.

Laird, R.A. & Schamp, B.S. (2006) Competitive intransitivity promotes species coexistence. *American Naturalist*, **168**, 182–193.

Lenz, T.I. & Facelli, J.M. (2003) Shade facilitates an invasive stem succulent in a chenopod shrubland in South Australia. *Austral Ecology*, **28**, 480–490.

Levine, S.H. (1976) Competitive interactions in ecosystems. *American Naturalist*, **110**, 903–910.

Levine, J. (1999) Indirect facilitation: evidence and predictions from a riparian community. *Ecology*, **80**, 1762–1769.

Liancourt, P., Callaway, R.M. & Michalet, R. (2005) Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology*, **86**, 1611–1618.

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

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

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

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

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

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

Maestre, F.T., Cortina, J., Bautista, S. & Bellot, J. (2003b) Does *Pinus halepensis* facilitate the establishment of shrubs under semi-arid climate? *Forest Ecology and Management*, **176**, 147–160.

Maestre, F.T. & Reynolds, J.F. (2006) Nutrient availability and atmospheric $CO_2$ partial pressure modulate the effects of nutrient heterogeneity on the size structure of populations in grassland species. *Annals of Botany*, **98**, 227–235.

Maestre, F.T. & Reynolds, J.F. (2007) Biomass responses to elevated $CO_2$, soil heterogeneity and diversity: an experimental assessment with grassland assemblages. *Oecologia*, **151**, 512–520.

Maestre, F.T., Valladares, F. & Reynolds, J.F. (2005) Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, **93**, 748–757.

Maestre, F.T., Valladares, F. & Reynolds, J.F. (2006) The stress-gradient hypothesis does not fit all relationships between plant–plant interactions and abiotic stress: further insights from arid environments. *Journal of Ecology*, **94**, 17–22.

Markham, J.H. (1997) Measuring and modelling plant neighbour effects: a reply to Freckleton and Watkinson. *Functional Ecology*, **11**, 534–535.

Markham, J.H. & Chanway, C.P. (1996) Measuring plant neighbor effects. *Functional Ecology*, **10**, 548–549.

Maron, J.L. & Connors, P.G. (1996) A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia*, **105**, 302–312.

Menge, B.A. (1976) Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs*, **46**, 355–369.

Michalet, R. (2006) Is facilitation in arid environments the result of direct or complex interactions? *New Phytologist*, **169**, 3–6.

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

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

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

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

Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N., *et al*. (2006) Biotic interactions and plant invasions. *Ecology Letters*, **9**, 726–740.

Murrell, D.J. & Law, R. (2003) Heteromyopia and the spatial coexistence of similar competitors. *Ecology Letters*, **6**, 48–59.

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

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

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

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

Pagès, J.P., Pache, G., Joud, D., Magnan, N. & Michalet, R. (2003) Direct and indirect effects of shade on four forest tree seedlings in the French Alps. *Ecology*, **84**, 2741–2750.

Parrotta, J.A., Turnbull, J.W. & Jones, N. (1997) Introduction – Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management*, **99**, 1–7.

Pate, J.S. & Dawson, T.E. (1999) Assessing the performance of woody plants in uptake and utilisation of carbon, water and nutrients – Implications for designing agricultural mimic systems. *Agroforestry Systems*, **45**, 245–275.

Pennings, S.C., Seling, E.R., Houser, L.T. & Bertness, M.D. (2003) Geographic variation in positive and negative interactions among salt marsh plants. *Ecology*, **84**, 1527–1538.

Pugnaire, F.I., Haase, P. & Puigdefábregas, J. (1996) Facilitation between higher plant species in a semiarid environment. *Ecology*, **77**, 1420–1426.

Pugnaire, F.I. & Luque, M.T. (2001) Changes in plant interactions along a gradient of environmental stress. *Oikos*, **93**, 42–49.

Reader, R.J., Wilson, S.D., Belcher, J.W., Wisheu, I., Keddy, P.A., Tilman, D., *et al*. (1994) Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. *Ecology*, **75**, 1753–1760.

Reinhart, K.O., Maestre, F.T. & Callaway, R.M. (2006) Facilitation and inhibition of seedlings of an invasive tree (*Acer platanoides*) by different tree species in a mountain ecosystem. *Biological Invasions*, **8**, 231–240.

Richardson, D.M., Allsop, N., D'Antonio, C.M., Milton, S.J. & Rejmánek, M. (2000) Plant invasions-the role of mutualisms. *Biological Reviews*, **75**, 65–93.

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

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

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

Sala, O.E., Chapin, F.S. III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., *et al*. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

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

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

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

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

Shevtsova, A., Haukioja, E. & Ojala, A. (1997) Growth response of subarctic dwarf shrubs, *Empetrum nigrum* and *Vaccinium vitis-idaea*, to manipulated environmental conditions and species renoval. *Oikos*, **78**, 440–458.

Siemann, E. & Rogers, W.E. (2003) Changes in light and nitrogen avaibility under pioneer trees may indirectly facilitate tree invasions of grasslands. *Journal of Ecology*, **91**, 923–931.

Simberloff, D. (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters*, **9**, 912–919.

Simberloff, D., Relva, M.A. & Nuñez, M. (2003) Introduced species and management of a *Nothofagus*/*Austrocedrus* forest. *Environmental Management*, **31**, 263–275.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Stoll, P. & Weiner, J. (2000) A neighborhood view of interactions among individual plants. *The Geometry of Ecological Interactions: Simplifying Spatial Complexity* (eds U. Dieckmann, R. Law & J.A.J. Metz), pp. 11–27. Cambridge University Press, Cambridge.

Suding, K.N., Gross, K.L. & Houseman, G.R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, **19**, 46–53.

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004) The need for evidence-based conservation. *Trends in Ecology and Evolution*, **19**, 305–308.

Thomson, J.D. (1978) Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. *American Midland Naturalist*, **100**, 431–440.

Tielbörger, K. & Kadmon, R. (1995) Effect of shrubs on emergence, survival and fecundity of four coexisting annual species in a sandy desert ecosystem. *Ecoscience*, **2**, 141–147.

Tielbörger, K. & Kadmon, R. (2000a) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, **81**, 1544–1553.

Tielbörger, K. & Kadmon, R. (2000b) Indirect effects in a desert plant community: is competition among annuals more intense under shrub canopies? *Plant Ecology*, **150**, 53–63.

Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.

Tirado, R. & Pugnaire, F.I. (2003) Shrub spatial aggregation and consequences for reproductive success. *Oecologia*, **136**, 296–301.

Travis, J.M.J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 467–473.

Travis, J.M.J., Brooker, R.W., Clark, E.J. & Dytham, C. (2006) The distribution of positive and negative species interactions across environmental gradients on a dual-lattice model. *Journal of Theoretical Biology*, **241**, 896–902.

Travis, J.M.J., Brooker, R.W. & Dytham, C. (2005) The interplay of positive and negative interactions across an environmental gradient: insights from an individual-based simulation model. *Biology Letters*, **1**, 5–8.

Travis, J.M.J. & Dytham, C. (1999) Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London Series B*, **266**, 723–728.

Valiente-Banuet, A., Rumebe, A.V., Verdú, M. & Callaway, R.M. (2006) Quaternary Plant lineages sustain global diversity by facilitating Tertiary lineages. *Proceedings of the National Academy of Sciences USA*, **103**, 16812–16817.

Vilà. M., Williamson, M. & Lonsdale, M. (2004) Competition experiments on alien weeds with crops: lessons for measuring plant invasion impact? *Biological Invasions*, **6**, 59–69.

Walker, L.R. & del Moral, R. (2003) *Primary Succession and Ecosystem Rehabilitation*. Cambridge University Press, Cambridge.

Walker, L.R. & Powell, E.A. (1999) Regeneration of the Mauna Kea silversword *Argyroxiphium sandwicense* (Asteraceae) in Hawaii. *Biological Conservation*, **89**, 61–70.

Walker, L.R., Walker, J. & Hobbs, R.J. (2007) *Linking Restoration and Ecological Succession*. Springer, New York.

Weigelt, A. & Jolliffe, P. (2003) Indices of plant competition. *Journal of Ecology*, **91**, 707–720.

Weigelt, A., Schumacher, J., Walther, T., Bartelheimer, M., Steinlein, T. & Beyschlag, W. (2007) Identifying mechanisms of competition in multi-species communities. *Journal of Ecology*, **95**, 53–64.

Welden, C.W. & Slauson, W.L. (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. *Quarterly Review of Biology*, **61**, 23–44.

Went, F.W. (1942) The dependence of certain annual plants on shrubs in southern California deserts. *Bulletin of the Torrey Botanical Club*, **69**, 100–114.

Wilson, M.V. (2007) Measuring the components of competition along productivity gradients. *Journal of Ecology*, **95**, 301–308.

Wipf, S., Rixen, C. & Mulder, C.P.H. (2006) Advanced snowmelt causes shift toward positive neighbour interactions in a subarctic tundra community. *Global Change Biology*, **12**, 1–11.

Wooton, J.T. (1994) The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics*, **25**, 443–466.

Yamamura, N., Higashi, M., Behera, N. & Wakano, J.Y. (2004) Evolution of mutualism through spatial effects. *Journal of Theoretical Biology*, **226**, 421–428.

Young, T.P., Petersen, D.A. & Clary, J.J. (2005) The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology Letters*, **8**, 662–673.

Zavaleta, E.S. & Hulvey, K.B. (2004) Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science*, **306**, 1175–1177.

*Received 20 March 2007; accepted 3 July 2007*
*Handling Editor: David Gibson*

## Supplementary material

The following supplementary material is available for this article:

**Table S1.** Survey of recent (1996–present) publications exploring positive interactions between vascular plants

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01295.x
(This link will take you to the article abstract).

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.