



Tansley review

Plant–plant interactions and environmental change

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Summary

Key words: climate change, competition, evolution, facilitation, ranges, severity gradients.

Natural systems are being subjected to unprecedented rates of change and unique pressures from a combination of anthropogenic environmental change drivers. Plant–plant interactions are an important part of the mechanisms governing the response of plant species and communities to these drivers. For example, competition plays a central role in mediating the impacts of atmospheric nitrogen deposition, increased atmospheric carbon dioxide concentrations, climate change and invasive nonnative species. Other plant–plant interaction processes are also being recognized as important factors in determining the impacts of environmental change, including facilitation and evolutionary processes associated with plant–plant interactions. However, plant–plant interactions are not the only factors determining the response of species and communities to environmental change drivers – their activity must be placed within the context of the wide range of factors that regulate species, communities and ecosystems. A major research challenge is to understand when plant–plant interactions play a key role in regulating the impact of environmental change drivers, and the type of role that plant–plant interactions play. Although this is a considerable challenge, some areas of current research may provide the starting point to achieving these goals, and should be pursued through large-scale, integrated, multisite experiments.

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I. Introduction

We are living in a changing world. In fact we have, as most ecologists readily acknowledge, always lived in a changing world, and its species and ecosystems have always had to cope with and adapt to change. However, the current situation is unusual for a number of reasons. Firstly, the rate of change of many environmental parameters is unusually high. Secondly, many of the changes in our environment are anthropogenic, and the combination of changes that humans are currently causing in the natural world (e.g. changes in climate in association with fragmentation of habitats and the long-distance transportation of organisms) represents a unique challenge to the survival of many species.

Environmental change phenomena, also commonly called global change phenomena, are diverse in origin and nature and have become particularly notable within the last few centuries. For example, emissions of nitrogenous atmospheric pollutants have increased markedly during the past 100 years, from an estimated background input of 1–5 kg nitrogen (N) ha⁻¹ year⁻¹ to N deposition levels of 20–60 kg N ha⁻¹ year⁻¹ at the end of the 20th century in some European ecosystems (Bobbink, 1998; Fowler *et al.*, 1998). Carbon dioxide concentrations have risen, mainly as a consequence of fossil fuel combustion and cement production (Houghton *et al.*, 2001), from a preindustrial level of approx. 270–280 parts per million (ppm) to the current concentration of over 374.9 ppm (Blasing & Jones, 2006). During the past 100 years the Earth's climate has experienced an average warming of approx. 0.8°C, with an increase of 0.6°C in the past three decades, the 1990s being the warmest decade in the observational record (Houghton *et al.*, 2001; Hansen *et al.*, 2006). Climate change is now accepted as one of the major threats to global biodiversity (Sala *et al.*, 2000). It has even been proposed as the main future biodiversity threat in many regions of the globe (Thomas *et al.*, 2004), although this more recent claim has been criticized for: (i) insufficient assessment of potential uncertainties (Thuiller *et al.*, 2004), (ii) incorrect application of species–area relationships (Buckley & Roughgarden, 2004) and (iii) an underestimate of the negative impacts of local species adaptation (Harte *et al.*, 2004). Irrespective of a changing climate, increased ease of travel and transport of goods, along with increased anthropogenic disturbance in natural systems, are leading to increased occurrences of aggressively invasive alien species (Cabin *et al.*, 2002). All of these phenomena, either alone or in combination, are acting as drivers of change in the composition and function of natural systems.

The conservation of biodiversity in spite of such drivers has been recognized as a major research and policy priority, not least because the conservation of biodiversity is acknowledged as the cornerstone of sustainable development (Secretariat of the Convention on Biological Diversity, 2003). It is clear that in some circumstances the composition of communities and

ecosystems can have considerable consequences for the provision of the ecosystem services upon which society is heavily dependent (Peterson *et al.*, 1998; Hooper *et al.*, 2005). Consequently there is now a very strong practical need to understand those processes that regulate biodiversity.

Plant–plant interactions play a key role in regulating the composition of communities and ecosystems. Not only do they control the composition of plant communities, but they also have impacts that spread throughout ecosystems, for example through their effects on resource availability and habitat structure. However, the impacts of plant–plant interactions can be altered themselves by external drivers (both natural and anthropogenic) such as climatic conditions or nutrient availability. Therefore, because of the important role of plant–plant interactions, and the current speed and impact of environmental change, it is extremely timely to consider how plant–plant interactions may be playing a role in mediating the response of natural systems to drivers of environmental change, and how that role might itself be influenced by environmental change processes. Furthermore, we should now be considering what areas of research we might pursue with respect to plant–plant interactions in order to improve our ability to understand and predict the impacts of environmental change drivers on biodiversity, and thus develop adaptation strategies to preserve biodiversity in a rapidly changing world.

In this paper I will discuss how plant–plant interactions play a role in mediating the impact of environmental change drivers on plant species and communities, focusing in particular on a number of key environmental change drivers. I will attempt to show that the underlying plant–plant interaction processes by which plant communities respond to these drivers are often very similar, and that by understanding these fundamental ecological processes we can gain a great deal of insight into the response of natural systems to environmental change. I will then consider some areas of research on plant–plant interactions that might prove particularly fruitful in terms of improving our ability to predict these responses.

In this paper I will take plant–plant interactions to be the effect of one individual plant on another individual of either the same or a different species. Such effects at the level of the individual can cascade upwards to alter community and ecosystem structure (see e.g. Körner, 2004). There are countless different types of plant–plant interactions. Some are extremely specific in terms of both the species involved and the mechanism by which the interaction operates. For example, some hemiparasitic plants target particular host species, and their interaction mechanism of invasive haustoria or similar connective tissue restricts the impact of the individual hemiparasite to that particular host (Press & Phoenix, 2005). However many plant–plant interactions are commonly diffuse in nature, i.e. there is no specific targeting of their effect directly on another individual or species (although certain species may be the common recipient). Competitive

or facilitative interactions are often diffuse, resulting from changes in resource availability and abiotic environmental conditions caused by one individual (e.g. changes in light, water, nutrient availability, space, pollinators or temperature) that subsequently have an impact on another individual (commonly a close neighbour but not always so; for example, in the case of competition for pollinators). In addition, some interactions are direct between plants, whilst others operate indirectly via an organismic intermediary (e.g. the effects of herbivores, pollinators or soil microorganisms). It would be almost impossible to comprehensively review all of the possible links between the spectrum of different interaction types and the full range of environmental change drivers. In general, therefore, I will concentrate on the more diffuse types of interactions, especially those occurring between vascular plants (but with a few cryptogamic examples), and I will consider some generalities (rather than many detailed specifics) of the links between plant–plant interactions and environmental change.

II. Plant–plant interactions mediate the impacts of environmental change

There is substantial evidence that plant–plant interactions are an important part of the mechanism by which environmental change drivers affect plant species and communities. In this section, I discuss some of the different roles of plant–plant interactions in mediating the effects of a number of key environmental change drivers.

1. Competition

Competition is a central component of many of the fundamental ecological theories that have guided plant ecologists (e.g. Connell & Slatyer, 1977; Grime, 1979; Tilman, 1982), and is widely acknowledged as a principal factor determining the diversity and relative dominance of species within plant communities. Competition is commonly cited as one of the processes determining the response of plant communities to environmental change drivers such as N deposition, invasive alien species and climate change.

For example, nutrient availability can be a critical factor in determining the composition of plant communities (e.g. Gough *et al.*, 2000; Crawley *et al.*, 2005), and changes in nutrient availability have been shown to have radical effects on the species composition of vegetation (Bobbink *et al.*, 1998), not least because of their impact on the relative competitive abilities of plants. Several environmental change drivers act to alter the nutrient status of plants and therefore their relative competitive abilities. Low N availability, in particular, frequently limits plant growth and the competitive ability of potentially dominant species, especially in oligotrophic or mesotrophic ecosystems (Bobbink *et al.*, 1998), or cold systems such as arctic or alpine environments where low

temperatures restrict soil decomposition processes (Jonasson, 1983; Chapin & Shaver, 1985; Nadelhoffer *et al.*, 1991; Robinson *et al.*, 1995).

Atmospheric N deposition can lead to increased N availability in the soil (Bobbink, 1998; Lee & Caporn, 1998) and increased dominance of competitive plant species. This in turn can lead to species loss, with plants of higher growth rate and taller stature shading other plants out of a system (Bobbink, 1998; Lee & Caporn, 1998; Van den Berg *et al.*, 2005) or reducing the availability of water during critical stages of the growing season (Zavaleta *et al.*, 2003). Similar responses have been found in experimental warming and nutrient addition studies of arctic and alpine environments. The more competitive growth forms, for example graminoids, are particularly responsive to enhanced temperatures or nutrient addition treatments (Zhang & Welker, 1996; Dormann & Woodin, 2002; Brooker & Van der Wal, 2003; Bret-Harte *et al.*, 2004), probably as a consequence of both enhanced soil nutrient availability and enhanced nutrient uptake capacity in tissues (Semikhatova *et al.*, 1992; BassiriRad, 2000). For example, after five seasons of fertilization at a subarctic dwarf shrub heath site there was an 18-fold increase in the abundance of *Calamagrostis lapponica* (Parsons *et al.*, 1995; Press *et al.*, 1998). The enhanced growth of particular vascular plants, and associated increased levels of competition, have been proposed as a cause for changes in the composition of communities (Harte & Shaw, 1995), such as the loss of cryptogam species (Cornelissen *et al.*, 2001).

In the case of atmospheric N deposition, the impact on diversity can depend upon the initial availability of N. In systems where N availability is particularly low, increased availability can lead to increased diversity, whereas in systems where N availability is already at intermediate levels increased N can lead to the competitive dominance of particular species (e.g. *Brachypodium pinnatum* in chalk grasslands; Bobbink, 1991) and thus a loss of diversity from the community (as proposed in some diversity-productivity hypotheses; Grime, 1973; Huston, 1979). Similarly, in arctic and alpine environments increased temperature, whether acting directly or through changes in soil nutrient availability, can lead to increased diversity (at least within the vascular plant community) if new species from warmer environments are capable of migrating into a region (ACIA, 2004). One of the clearest impacts of increased global temperatures has been altered phenology in many species. (Root *et al.*, 2003). This has been particularly evident in those biological events that occur at the start of the growing season, for example bud burst and flowering in plants, which now occur earlier in the year for many species (Sparks & Menzel, 2002). However, the response of species is not uniform, i.e. changes in phenology are species-specific (Peñuelas & Filella, 2001; Walther, 2003). For example, Fitter & Fitter (2002) found a particularly large acceleration in the phenology of early flowering species, and that phenological responses were dependent on the position of individuals

within their species' range (with individuals at range margins responding less markedly). Species-specific phenological changes have important implications for the interactions between plants. Early season variation in the capacity to acquire resources (which will be influenced by phenology) may, as a consequence of the subsequent impacts of competition, strongly influence the relative abundance of species within communities. Dunnett & Grime (1999) proposed that this effect of competition would be stronger in productive environments, for example grassland systems (for reasons explained in section IV of this review). They demonstrated that, when grown in monocultures, five common UK roadside species all responded positively to increased spring warming. However, when grown in mixtures the benefits of warming were only observable in a subset of species, indicating that interspecific competition had regulated the response of plant community composition to climatic fluctuations.

Although commonly thought of in the context of being a major driver of global warming, elevated CO₂ concentrations can also have direct impacts on relative competitive abilities. When there are adequate supplies of other resources, increased CO₂ concentrations can enhance photosynthesis in C₃ plants and increase plant water use efficiency, thereby stimulating plant growth (Bazzaz, 1990). However, as with the response of phenology to climate change, these effects vary among species (and even among different populations of the same species; Bazzaz, 1990), and this differential stimulation of growth may alter the balance of plant–plant interactions. For example, Hättenschwiler & Körner (2003) found species-specific responses to elevated CO₂ in the tree species of Swiss temperate forests: nonnative *Prunus laurocerasus* was found to respond positively to elevated CO₂ concentrations, whereas some native species did not. This may alter the competitive relationships among tree species and promote the invasion of *Prunus*. That changes in interactions can scale up to substantial changes in community and ecosystem properties is demonstrated by the enhanced growth and biomass of lianas in tropical forests under elevated CO₂, which could promote faster tree turnover and a general shift in the demographic structure of tropical forests from late to early successional stages (Körner, 2004; Phillips *et al.*, 2004).

Hättenschwiler & Körner's (2003) study of Swiss temperate forests demonstrates the potential interacting effects of environmental change drivers. In this instance, elevated CO₂ concentrations promote the success of an alien species, and alien species are themselves considered a driver of environmental change. Changes in the relative competitive abilities of native and alien species may also result from enhanced N availability, and the impact of N deposition on interactions may promote the influx of alien species into communities (Brooks, 2003). Even in the absence of altered nutrient availability or elevated CO₂ concentrations, competition is an important part of the processes associated with the influx of alien species into communities. In many instances, the influx

of alien species has negative effects on the existing plant community, leading to reduced diversity and the loss of native species (Levine *et al.*, 2003). Competitive plant–plant interactions commonly play a central role in these impacts. In the native dry forest ecosystems of Hawaii, the dense roots and shoots of invading grass species negatively affect nutrient and water acquisition and germination of native woodland species (D'Antonio & Vitousek, 1992; Cabin *et al.*, 2002), whilst in Californian coastal chaparral communities the invasive *Carpobrotus edulis* reduces soil water availability to native shrubs, negatively affecting their growth and reproduction (D'Antonio & Mahall, 1991). In both these cases the type of interaction is one that the native species will have experienced before, i.e. diffuse competition for resources such as water or nutrients. However, in some instances the interaction mechanism is entirely novel. For example, *Centaurea diffusa* (the Eurasian forb, diffuse knapweed) invades and dominates native bunchgrass communities of North America through the allelopathic effects of root exudates. These have a far greater effect on grass species from North America than on those from the native European range of *C. diffusa* (Callaway & Aschehoug, 2000; Callaway & Ridenour, 2004; Vivanco *et al.*, 2004). These allelopathic effects are not competitive interactions in the commonly used sense of the term, yet they enable one species to actively dominate a community and monopolize its resources – to all intents and purposes *C. diffusa* is a competitive 'winner'.

In general, experimental studies demonstrate strong competitive effects of invasive alien species on native species (Levine *et al.*, 2003). However, it is important to realize that very few plant species introduced to communities away from their native ranges actually establish and go on to become aggressively invasive. There is now a considerable body of research examining the processes that restrict or promote invasibility in native communities, and although the nature of the relationship between species diversity and invasibility of ecosystems is still unclear (see e.g. Davis *et al.*, 2005a; Herben, 2005), it is widely accepted that competitive plant–plant interactions can be an important component of the mechanisms that exclude potentially invasive species from communities (Shea & Chesson, 2002; Fargione *et al.*, 2003; Davis *et al.*, 2005a).

2. Facilitation

It is clear that competition plays an important role in mediating the impacts of a wide range of environmental change drivers (e.g. climate, N deposition and CO₂ concentrations) on natural systems, and the ready evocation of competition as a mediating mechanism may reflect how well the concept of competition is imbedded in the minds of plant ecologists. More recently, however, the role of facilitative interactions in regulating the composition of communities has received increasing attention (Bertness & Callaway, 1994;

Callaway, 1995; Brooker & Callaghan, 1998; Dormann & Brooker, 2002; Bruno *et al.*, 2003). Although in some cases they can be very specific (e.g. through increased ectomycorrhizal infection of tree seedlings by conspecifics; Dickie *et al.*, 2005), facilitative interactions are commonly diffuse. Other than with respect to a small set of commonly recognized phenomena, for example the nurse-plant effect where a mature plant provides protection and shelter for establishing seedlings in desert ecosystems (e.g. Holzapfel & Mahall, 1999; Schenk & Mahall, 2002), such processes have undergone a considerable period of neglect. However, following recent renewed interest it now appears to be generally accepted that facilitative interactions (between plants at all life-history stages) can play an important role in regulating the composition of some plant communities, and that the outcome of interactions is the net effect of both positive and negative plant–plant interactions (Holzapfel & Mahall, 1999; Pugnaire & Luque, 2001; Schenk & Mahall, 2002).

Despite the recognition of their role in regulating the success of individuals and shaping communities, there is much less evidence for facilitative plant interactions mediating the impacts of environmental change drivers. However, there are a few interesting examples and more may come to light as interest in facilitative interactions increases. For example, plant–plant interactions associated with invasive species need not necessarily be negative, nor is it always the native species that receives the impact of an interaction. Facilitative interactions can promote the survival of plant species in environmental conditions that would otherwise be too stressful (Choler *et al.*, 2001; Cavieres *et al.*, 2002), thus effectively expanding their realized niche (Bruno *et al.*, 2003), and in some cases the facilitated species can be an invasive species. Cavieres *et al.* (2005) demonstrated how the nonnative *Taraxacum officinale* was facilitated at high-altitude sites in the central Chilean Andes by the cushion plant *Azorella monantha*. *Taraxacum officinale* seedling survival, net photosynthetic rates and stomatal conductance were all higher for seedlings growing within cushions than outside them, suggesting that the microclimatic modifications of the cushion facilitate the establishment and survival of *T. officinale*. In Brooks's (2003) investigation of the impact of N deposition on invasives in the Mojave Desert, one of the invasive species examined appeared to be facilitated by the *Larrea tridentata* bushes under which it grew. The positive effects of nitrogen addition were highest for *Bromus madritensis* beneath *L. tridentata* canopies, whilst they were greatest in interbush spaces for *Schismus arabicus*, *Schismus barbatus* and *Erodium cicutarium*. In a study of alpine treelines, Germino *et al.* (2002) demonstrated that improved environmental conditions as a consequence of ground-layer vegetation facilitated the establishment of tree seedlings, thus promoting the upwards shift of treeline species in response to climate change, and neighbour removal experiments (where neighbouring plants around a target

individual are removed, and the response of the target is compared with that of untreated individuals to assess the net effect of neighbours on the target) in conjunction with experimental warming have indicated that both competitive and facilitative interactions play a role in the response of species to enhanced temperatures in alpine *Dryas octopetala* heath in southern Norway (Klanderud, 2005).

3. Evolutionary processes

When discussing the role of competition and facilitation, we are considering how plant–plant interactions regulate the diversity of existing species. However, a key process determining community composition is species evolution which, along with species extinction, sets the overall size of the global species pool from which a community is constructed. An important recent realization with respect to understanding the response of species and communities to environmental change is that species are not static entities, and can evolve rapidly in response to environmental change drivers. For example, Thomas *et al.* (2001) have demonstrated how insect species are evolving at range margins in such a way as to promote range expansion, and Davis *et al.* (2005b) have argued that the concept of rapid evolutionary responses (on the time-scale of decades to centuries depending upon the plant species involved) should be included in the analysis of paleoecological data on species range shifting in response to past climate change.

The concept of plant growth strategies, in particular the existence of a competitive strategy (as in the classic C-S-R theory, which proposed three main plant strategies – competitors, stress-tolerators and ruderals; Grime, 1974), implicitly accepts that plant–plant interactions can act as a selective force on plants. Recent studies of the impacts of environmental change drivers are also bringing to light more evidence of selective impacts of plant–plant interactions, and the possibility of coevolution in plant communities. Above, in the section on competition, I discussed the comparatively low impact of root exudates from *C. diffusa* on grass species from its native range, which suggests these native-range grasses have an evolved resistance to the chemicals of *C. diffusa* (Callaway & Aschehoug, 2002; Callaway & Ridenour, 2004; Lortie *et al.*, 2004). Other studies have also discussed the potential for interactions to act as a selective force during the processes of environmental change. The Allee effect, the positive relationship between fitness and population size (or density) in small populations (Allee, 1931), is a mechanism by which plant–plant interactions might have a selective impact. At low densities, reduced seed set and recruitment can occur as a consequence of pollen limitation (Antonovics & Levin, 1980; Davis *et al.*, 2004). Pollen sharing is a form of interaction between plants. The physiological characteristics of plants from an invasion front have been shown to differ from those in the source population in such a way as to overcome the

negative consequences of these Allee effects, i.e. they have a greater degree of self-compatibility, indicating that changes in the strength of interactions may have acted as a selective force, although it is difficult to determine whether this is the consequence of selection or founder effects (Davis, 2005).

Plant–plant interactions might also be the target rather than the driver of selection. It has been hypothesized that the release from enemies (herbivores and parasites) that a plant species experiences when transported to a new environment could lead to the evolution of increased competitive ability (the EICA hypothesis) as the selective force diverting resources to mechanisms protecting the plant from herbivory, for example phenolic compounds in leaves, would be reduced or removed (Blossey & Nötzold, 1995). However, there is currently conflicting evidence as to whether or not this process operates (Vilà *et al.*, 2003; Maron *et al.*, 2004b). For example, although Maron *et al.* (2004a) found reduced levels of foliar defence compounds from North American as opposed to native European populations of *Hypericum perforatum*, there was no corresponding increase in plant size or fecundity.

Overall, and in comparison to our understanding of the role of interactions in the structuring of communities, our understanding of the relationships between plant–plant interactions and evolutionary processes (with respect to environmental change drivers or otherwise) is limited. However, given increasing evidence in support of the potential for rapid evolutionary change during environmental change, the selective role of plant–plant interactions is likely to become an increasingly important research topic.

To briefly summarize, it is clear that competitive plant–plant interactions play an important role in mediating environmental change impacts, and that we are now also starting to see evidence of a similar role for facilitative plant–plant interactions and the evolutionary consequences of plant–plant interactions during environmental change. It would seem, therefore, that it is worth pursuing the research area of plant–plant interactions in relation to understanding and predicting the impacts of environmental change. Furthermore, although the environmental change drivers discussed vary widely in nature, the responses of plants to many of these drivers are governed by the same underlying, fundamental ecological processes (competition, facilitation and local adaptation). This would suggest a great deal of potential synergy between research fields dealing with environmental change drivers; for example, understanding the processes that regulate community invasibility and the expansion of invasive species could also help us to understand the phenomenon of range shifting under climate change. However, although some authors, for example Davis *et al.* (2005a; with respect to community assembly theory and invasion biology), have discussed the links between different fields, these research areas have not yet been well integrated.

III. Plant–plant interactions in context

Although I have highlighted the important role of plant interactions, including their possible role in evolutionary processes, I am not suggesting that plant–plant interactions are the only factor regulating the response of plants to environmental change. Many of the studies discussed in the previous sections also point to the role of other factors in determining the response of individual plants or plant communities. For example, herbivory, rather than plant–plant interactions, is the dominant driving force leading to the influx of aggressive grass species in Hawaiian dry woodlands (Cabin *et al.*, 2002). Soil organisms can also play a considerable role in determining the composition of plant communities, exerting both direct and indirect species-specific effects on the growth of plant species (Bever, 2003). The presence of mycorrhizal fungi has been shown to regulate the outcome of competition between neighbouring plants (Fitter, 1977), and negative feedback from soil organisms can lead to diversification in plant communities through limitation of the abundance of potentially dominant species (Reynolds *et al.*, 2003).

Simple physiological intolerance of conditions or a complex combination of factors can lead to the loss of species as a result of N deposition (Bobbink *et al.*, 1998; Lee & Caporne, 1998). Van der Wal *et al.* (2003) found that direct negative impacts of N (physiological intolerance), negative competitive effects from increased graminoid cover, and enhanced herbivore activity were all involved in the decline of the moss *Racomitrium lanuginosum* in response to enhanced N deposition in a Scottish montane plant community. These processes also interacted: enhanced graminoid cover attracted grazers, leading to a faster rate of N turnover within the system and promoting further competition from graminoids (Fig. 1).

In terms of species evolution, many more processes can be acting upon the local adaptation of species than just the interactions to which it is subjected, for example genetic effects in small populations (Galeuchet *et al.*, 2005) or the selective force of abiotic environmental conditions (Maron *et al.*, 2004b).

Some factors can limit interaction-mediated impacts of environmental change drivers. For example, Brooks (2003) showed that the negative impact of N addition and enhanced growth of nonnatives on native annuals in the Mojave desert only occurred in the year of highest abundance of annual plants, which in turn was regulated by winter rainfall. Lee & Caporn (1998) suggested that the slow rate of change in community composition in response to N addition in some grasslands may be partly caused by phosphorus limitation, and pointed out that, although enhanced N addition initially promoted *Calluna vulgaris* growth in moorland systems in northern England, after several years of treatment enhanced winter frost damage started to place a check on growth of *C. vulgaris*. Similarly, Körner (2003) discussed how the

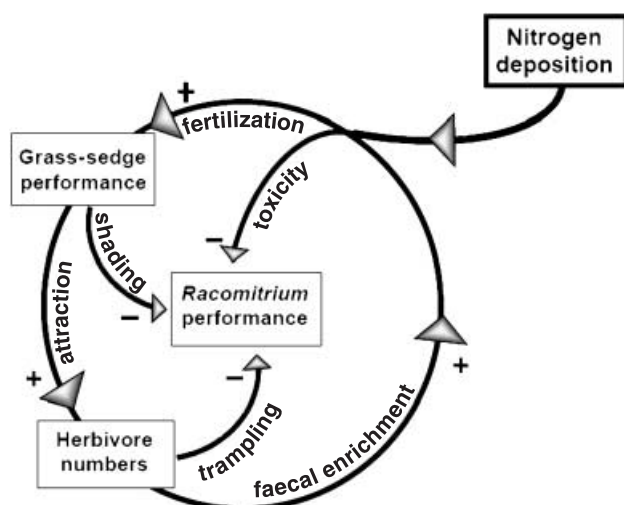


Fig. 1 A conceptual model integrating the impacts of nitrogen deposition and grazing on montane *Racomitrium* moss heath in Scotland (UK), and illustrating the complex interactions of processes (including plant–plant interactions) that can determine the response of a plant species to an environmental change driver. In the cyclical feedback loop, atmospheric nitrogen deposition is directly toxic to the moss *Racomitrium lanuginosum*, and also leads to competitive replacement of the moss by graminoids. Stimulation of graminoids in turn attracts sheep that trample the moss and deposit nutrient-rich faeces, further enhancing graminoid performance, and continuing the feedback cycle (reproduced with permission from Van der Wal *et al.* (2003) and Blackwell Publishing).

promotion of growth and competitive dominance under enhanced atmospheric CO₂ concentrations may depend upon both soil pH and the availability of soil nutrients.

When we consider the type of schema often given for the factors that structure communities, presenting these factors as a series of filters regulating community composition (e.g. Grime, 1998; Lortie *et al.*, 2004), we see that a broad and complex suite of processes is involved. These include the size of the potential species pool from which a community can be constructed, the ability of a species to reach a particular site (the dispersal ability often discussed with respect to range shifting), the physiological tolerances of a species, and the role of consumers (herbivores or parasites in the case of plant communities). Plant–plant interactions are only one component of these filtering processes. Therefore, when trying to predict the important processes associated with environmental change, and their consequences for species and communities, determining when and where we should consider the role of plant–plant interactions is essential and perhaps one of the major challenges for plant ecologists.

I will use climate envelope modelling to illustrate this point. Climate envelope models (a type of species distribution model) are commonly used to predict the response of species to climate change scenarios, thus producing scenarios of biodiversity responses (e.g. Berry *et al.*, 2002). To simplify the modelling approach, a range of climate parameters are fitted to the existing distribution of a species and, using future

climate scenarios produced by global circulation models (GCMs), the possible future distribution of the species is then calculated. This modelling approach has been criticized for ignoring important biological processes such as evolution, dispersal ability and biotic interactions (Davis *et al.*, 1998; Pearson & Dawson, 2003, 2004; Hampe, 2004), all components of the series of filters that act to structure communities. However, the difficulty comes in including these processes within large-scale (rather than detailed mechanistic) modelling approaches. It has even been argued that the role of interactions in determining species distributions is relatively trivial (e.g. Guisan & Thuiller, 2005), *ergo* they can be ignored in the modelling approach, echoing the rebuttal of interactions as important processes in structuring communities that is found in neutral theory (Hubbell, 2001).

But, as we have seen, in *some cases* this is clearly not true. If we look specifically at species ranges (the focus of climate envelope modelling) there is excellent evidence to suggest that plant–plant interactions can have a considerable modifying effect (far more than simply ‘tinkering around the edges’ of an envelope set predominantly by climate). In an excellent study, Leathwick & Austin (2001) demonstrated the sizeable modification by *Nothofagus* species of the distributions of other tree genera in New Zealand old-growth forests. One of the major factors determining the ranges of these other species was the presence of *Nothofagus*, and the presence or absence of *Nothofagus* changed the climate–distribution fit of the other tree species. Vetaas (2002) demonstrated how interactions played an important role in constraining the ranges of Himalayan *Rhododendron* species in their native habitats – when removed from these habitats and grown in ornamental gardens and arboreta they grew under a far wider range of climatic conditions than when growing with neighbours in their native environments (Fig. 2). However, as well as demonstrating the impact of interactions on range size, these studies suggest spatial variation in the dominant processes that regulate the ranges of species. For example, it is notable that in the study of Vetaas (2002) the expansion of the niche for rhododendrons outside of their native habitat occurs at the more productive (i.e. warmer) range margin, suggesting that other processes, perhaps limitations imposed by abiotic environmental conditions (such as low temperature), regulate rhododendron success at the cooler range margin. Evidence for this shift in the dominant processes that regulate range margins across species ranges can also be found in alpine environments. Competition has been proposed as a mechanism that sets the lower altitudinal limit of many alpine species. Halloy & Mark (2003) have shown that removal of competitors at lower altitudes (through burning and grazing) has enabled alpine and subalpine species in New Zealand to increase their distributions downslope, and competition has been proposed as a key mechanism causing the retraction of low-altitude range limits during recent upwards shifts of alpine plant species in response to climate change (Grabherr

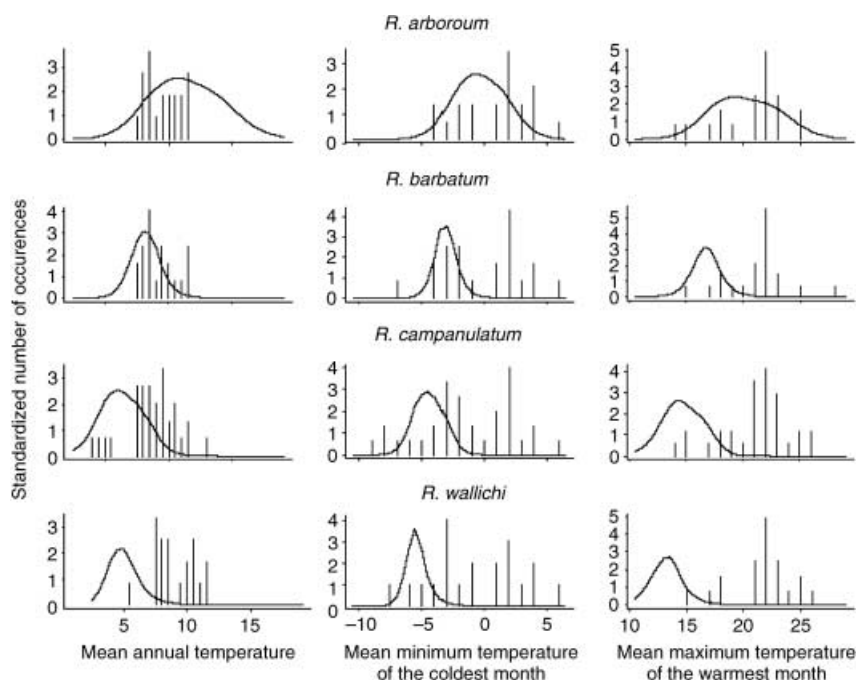


Fig. 2 The natural realized niches (solid lines; estimated by generalized additive models) of four rhododendron species (*Rhododendron arbororum* Sm., *Rhododendron barbatum* Wall., *Rhododendron campanulatum* D. Don., and *Rhododendron wallichii* Sm.), as illustrated by their response curves for mean annual temperature (MAT), mean minimum temperature of coldest month and mean maximum temperature of warmest month. The standardized number of *ex situ* occurrences (i.e. occurrences of the plant when growing in sites outside its native habitat, for example when growing in botanical gardens or herbaria) is superimposed on the graph as vertical lines. The number of *ex situ* locations and the realized response are both calculated as the number of occurrences for each 0.5°C interval divided by the standard deviation for each species. Vertical line length is not directly comparable with the realized response curve (reproduced with permission from Vetaas (2002) and Blackwell Publishing).

et al., 1994). However, intolerance of abiotic environmental conditions limits the upper altitudinal ranges of many alpine species (Körner, 1999; Choler *et al.*, 2001).

These examples illustrate, firstly, that the suite of processes that determine the range of a species, and therefore its distribution–climate fit, includes its interactions. If these interactions are disrupted then you may have a zero-analogue situation (Walther, 2003) where the combination of factors determining the original range, including the interactions that occurred in a particular time and space, no longer exist. Secondly, they demonstrate that even for a single species the role of plant–plant interactions may vary across its range. Therefore, it is necessary both to explicitly consider plant–plant interactions in activities such as climate envelope modelling, and to understand spatial and temporal variation in the role of plant–plant interactions.

IV. Understanding variation in the role of plant–plant interactions

It is true that it might be difficult to include the impact of some plant–plant interactions in predictive modelling approaches. How, for example, could the impact of *C. diffusa*, with its novel allelopathic abilities, have been predicted? However, it may be possible to start developing some simple but generic rules for determining when and where plant–plant interactions are key processes, as well as the types of effects that they have. If we can develop such rules then we might, for example, be able to refine predictive modelling approaches to include the role of interactions, to understand why we see spatial variation in evolutionary responses to

plant–plant interactions (i.e. spatial variation in the validity of the EICA), or to predict when plant–plant interactions might be an important part of the processes that should be considered in the development of management activities. Importantly, some research is already exploring whether such generic patterns exist, but as of yet the implications of this work for understanding and managing environmental change impacts have not been explored. Here I will outline two key themes within this research that have direct relevance to understanding the ecological consequences of environmental change.

1. Plant–plant interactions and gradients of environmental severity

As noted, there has been a recent surge in interest in facilitative (positive) plant–plant interactions (Dormann & Brooker, 2002). Many recent papers have highlighted the fact that facilitative plant–plant interactions seem to be common in severe environments, for example arctic, alpine, desert and saltmarsh systems (Bertness & Callaway, 1994; Callaway, 1995; Brooker & Callaghan, 1998; Bruno *et al.*, 2003). It has been proposed that this is a consequence of the mechanisms by which many facilitative interactions operate, i.e. amelioration of the abiotic environmental conditions (e.g. extremes of temperature or low soil water availability), and that increasing environmental severity leads to a change from the dominance of net competitive interactions to the dominance of facilitative interactions. This is not to say that facilitative interactions are the only type to be found in severe environments (see e.g. Moen, 1993; Maestre & Cortina, 2004) but rather that

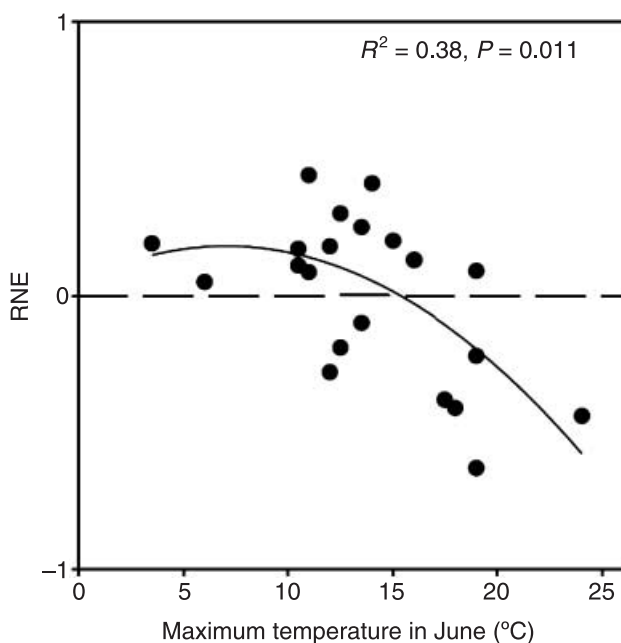


Fig. 3 The relationship between the estimated maximum temperature in early summer at each of 22 alpine meadow sites (11 mountain areas, each with a low- and high-altitude site) and the mean relative neighbour effect (RNE; the impact of neighbours on target individuals, measured with neighbour removal experiments) at that location (reproduced with permission from Callaway *et al.* (2002)). RNE is calculated as $(P_{T+N} - P_{T-N})/x$, where P_{T+N} and P_{T-N} are the performance (e.g. biomass) of target plants (P_T) in the presence (+N) and absence (-N) of neighbours, and x is the greater of the two; either P_{T+N} or P_{T-N} . RNE values greater than zero indicate facilitation, whereas those less than zero indicate competition (modified by Brooker *et al.* (2005) from Markham & Chanway (1996)).

facilitative interactions are on average more common in severe environments, certainly between vascular plant species.

A number of papers have supported this conclusion. For example, Choler *et al.* (2001) found that in French alpine communities increased altitude was associated with an increased frequency of facilitative interactions. Bertness & Ewanchuk (2002) found that latitudinal and interannual variation in climate altered the type of interactions operating within saltmarsh ecosystems, with more competitive interactions in cooler (and more productive) latitudes and years. Perhaps the largest study of this kind was that conducted by Callaway *et al.* (2002), who examined the average type of interaction occurring in alpine meadow communities, and showed a consistent shift from competitive to facilitative interactions with increasing environmental severity (Fig. 3).

The generality of the pattern found by Callaway *et al.* has been disputed. Although individual-based modelling studies of interactions in relation to environmental gradients have shown a similar pattern to that of Callaway *et al.* (Travis *et al.*, 2005), Maestre & Cortina (2004) concluded that there was a humpbacked relationship between the dominant type of plant–plant interaction found in arid steppe communities

and environmental severity (with competition dominating at both ends of the severity gradient), and Maestre *et al.*'s (2005) meta-analysis of studies from arid environments concluded that there was no relationship between stress and the net effect of neighbours. However, the analytical approach used in this last study is currently the subject of debate. Lortie & Callaway (2006) concluded that, in Maestre *et al.*'s (2005) analysis, study selection was not rigorous and, consequently, analysed data were not suitable, and that differences in stress gradient lengths between studies could have a considerable impact on the results of the analysis, although these criticisms have been disputed by Maestre *et al.* (2006).

2. The importance and intensity of plant–plant interactions

The issue of the intensity compared with the importance of competition, and their relationships to environmental gradients, is one that has *specifically* received far less attention than the change in interaction type. I emphasize 'specifically' because a lot of work has been done that relates to this issue but has not been recognized as such. This distinction is likely to be important when considering the links between the different roles of plant–plant interactions and environmental change.

A long-running debate in plant ecology has been that concerning the relationship between the role of competition and the severity of the environment. On the one hand it has been argued that competition plays a significant role in both productive and severe environments, and that the switch in interactions along the severity gradient is from above- to below-ground competition (a switch from competition for light to competition for below-ground resources such as water and soil nutrients; Newman, 1973; Tilman, 1982, 1988), whilst on the other hand it is argued that competition plays a significant role in productive systems but that its role is reduced in unproductive environments because of the increasing role of abiotic environmental conditions in regulating biological processes (Grime, 1979; Huston, 1979; Keddy, 1989). Importantly, evidence has been provided that supports both sides of this argument, and so it would seem sensible (working on the assumption that this evidence is scientifically sound) to try to find some way of reconciling the two.

Grace (1991) attempted just such a reconciliation, pointing researchers to an important distinction made earlier by Welden & Slauson (1986) between the *intensity* and *importance* of competition. Throughout this paper I have, from necessity, discussed the importance of competition in very loose terms. However, in this context it has a very specific meaning, i.e. the impact of competition proportional to the impact of all other factors within an environment. This is compared with the intensity of competition, which is the proportional decrease in success attributable to competition alone (Fig. 4). Welden & Slauson pointed out that it is possible for competition to be as intense but less important in

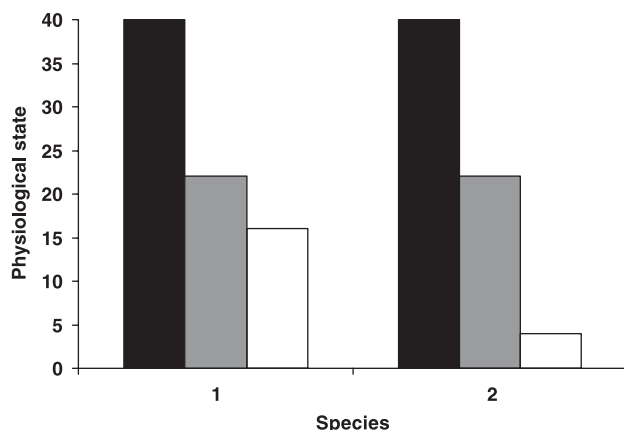


Fig. 4 Illustration of the difference between the intensity and importance of competition based on fig. 1 of Welden & Slauson (1986). The figure shows the hypothetical physiological states of two species under three different conditions: optimum growth (closed bar), the state resulting purely from competition (light grey bar) and the state resulting from the combined effect of competition and other environmental factors (open bar). For species 1, the total reduction in success attributable to all factors is 24 arbitrary units, of which competition accounts for 18; competition intensity is therefore 18 units whilst competition importance is $18/24 = 0.75$. For species 2, competition intensity is also 18 units, but the impact of other factors is far greater, and so the importance of competition is reduced to $18/36 = 0.5$ (reproduced with permission from Brooker *et al.* (2005), and Oikos).

one environment than another, and that they 'need not be correlated'. Therefore we can reconcile these opposing camps by considering that one is dealing with the intensity and the other with the importance of competition. Although Grace proposed this possible framework, his approach has been largely ignored, leading to confusion. A recent paper by Brooker *et al.* (2005) pointed out that even Grace failed to clearly make the distinction between the two measurements of competition (Grace, 1993). They also pointed out that the conclusions of one of the best-known large-scale experiments on this topic (Reader *et al.*, 1994) can be significantly altered by using the correct index to measure the role of competition. Reader *et al.* (1994) examined the impact of the presence of neighbours on the growth of a common phytometer, *Poa pratense*, along a multisite productivity gradient. If an index of competition intensity is calculated from the data (as in the original study) then no relationship between environmental severity (productivity) and the impact of competition is observed (Fig. 5a). However, if an index of competition importance is applied (as in the re-analysis by Brooker *et al.*, 2005) then a significant relationship is detectable, with the importance of competition declining with increasing environmental severity (Fig. 5b).

What have these issues to do with environmental change? The debate concerning plant–plant interactions and gradients of environmental severity, or the 'stress-gradient hypothesis' as it has become known, deals with trying to understand whether there are generic rules governing the *types* of

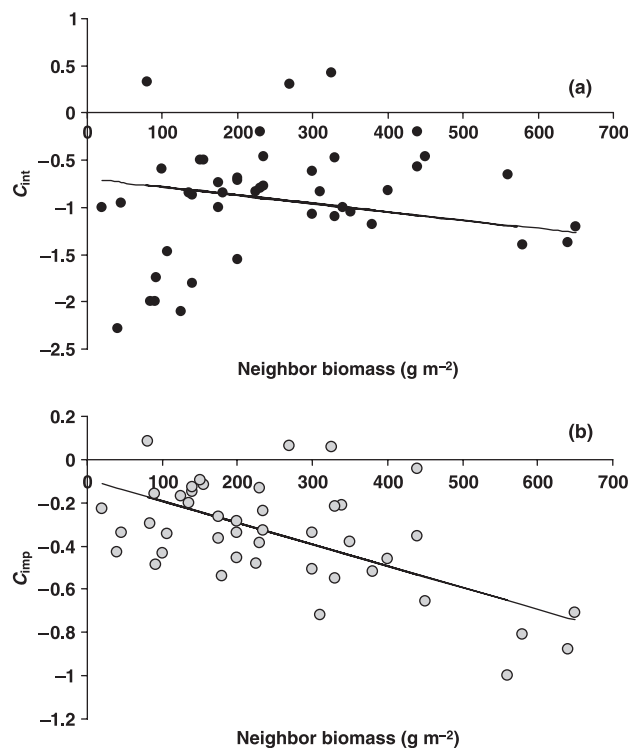


Fig. 5 The relationship between indices of (a) the intensity of competition (C_{int}) and (b) the importance of competition (C_{imp}) as calculated from the impact of neighbours on the biomass of *Poa pratensis* growing at 12 sites across a range of environmental severity (neighbour biomass; g m⁻²). The data shown are recalculated from the data of Reader *et al.* (1994). C_{int} is the same as relative neighbour effect (RNE) (see Fig. 3 for method of calculation) and C_{imp} is calculated as $(P_{T+N} - P_{T-N}) / (MaxP_{T-N} - y)$, where P_{T+N} and P_{T-N} are the performance (e.g. biomass) of target plants (P_T) in the presence (+N) and absence (-N) of neighbours, $MaxP_{T-N}$ is the maximum value of P_{T-N} along the gradient and y is the smaller of P_{T+N} and P_{T-N} (for a more detailed discussion of these indices, see Brooker *et al.*, 2005). Fitted lines show results of generalized linear mixed model analysis: $C_{int} = (-0.00088 \times \text{neighbour biomass}) - 0.6957$, $F_{1,39} = 2.76$, $P = 0.1047$; $C_{imp} = (-0.00100 \times \text{neighbour biomass}) - 0.09264$, $F_{1,42} = 27.32$, $P < 0.0001$ (reproduced with permission from Brooker *et al.* (2005) and Oikos).

plant–plant interaction that are operating, i.e. competition or facilitation, and how these might vary through space or time. As we have seen, these different types of interaction can have different consequences for community structure, for example promoting or preventing the influx of species. The debate concerning the intensity or importance of interactions is one that focuses on the *role* of interactions. The key point made by Grace (1991) was that the theory of Grime (1979) 'is one that is explicitly based on tradeoffs in the relative importance of selective forces'. Therefore the distinction between the importance and the intensity of interactions may be one between the selective force and the community structuring properties of plant–plant interactions. If we are interested in the selective impact of interactions, then we must understand spatiotemporal variation in the importance of competition.

In short, the research fields that I have outlined are attempting to discover whether there are the kind of generic patterns in the type and role of interactions that I have argued are necessary in developing the field of environmental change research. Furthermore, the drivers that are being proposed as important for changes in the type and role of interactions (i.e. changes in environmental severity or productivity) are a common consequence of the impacts of key environmental change drivers (e.g. climate change or N deposition).

If we can understand these fundamental relationships, we might be able to start to answer questions concerning when and where plant interactions need to be considered in order to accurately predict the impacts of environmental change. Where, for example, in a species range might we expect survival or local adaptation to be driven by interactions or by abiotic environmental conditions? Because we can detect facilitative interactions in severe environments, does this mean that they have the same selective impact as competitive interactions in productive environments, i.e. are they as important?

Current insights do not indicate a uniform response in the role of plant–plant interactions to environmental change, i.e. they do not become uniformly more or less important as a consequence of environmental change. Instead, research indicates that, although they can play a central role in regulating the impacts of environmental change, there will be large-scale spatial variation in changes in the role of interactions. For example, increasing productivity in arctic and alpine environments will probably lead to an increasing role for competitive interactions, and increasing severity in increasingly dry Mediterranean-type ecosystems to an increasing role for facilitation. Furthermore, competitive interactions are likely to be a major driver for range margins and local adaptation at the (comparatively) productive edges of a species range, whereas facilitation or abiotic environmental conditions would play a larger role at unproductive range margins. However, given the current uncertainties surrounding the models upon which such predictions are based, further research is clearly necessary to advance these fields and aid their integration into environmental change research.

V. Concluding remarks

I have shown that there is strong evidence of the role of competition in the impacts of environmental change, but also that there is increasing evidence of a role for facilitation, and of the selective evolutionary impacts of plant–plant interactions. However, plant–plant interactions must be placed within the context of the numerous processes that mediate the impacts of environmental change drivers. The role of interactions is clearly variable, and a major challenge for plant community ecology is to understand whether there are generic, large-scale (and predictable) patterns in this variability. Experimental evidence suggests that these large-scale patterns exist, but at

this time plant ecologists have only just started to consider these issues, and they are still subject to considerable debate. However, given the current rate of environmental change and the need for urgent action to conserve biodiversity, it seems vital to invest effort in understanding these processes. Multisite comparative experiments (e.g. Reader *et al.*, 1994; Callaway *et al.*, 2002) or well-conducted meta-analyses (e.g. Suding *et al.*, 2005) are now needed in order to address these issues, and to elucidate the exact nature of these large-scale generic patterns. Such research is likely to become more important as the fields of community ecology, population ecology and evolutionary ecology merge to address the problems posed by environmental change, and would enable us to utilize a large body of fundamental ecological knowledge to address a major issue for biodiversity conservation.

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