IDEA AND PERSPECTIVE

Do biotic interactions shape both sides of the humped-back model of species richness in plant communities?

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Abstract

A humped-back relationship between species richness and community biomass has frequently been observed in plant communities, at both local and regional scales, although often improperly called a productivity–diversity relationship. Explanations for this relationship have emphasized the role of competitive exclusion, probably because at the time when the relationship was first examined, competition was considered to be the significant biotic filter structuring plant communities. However, over the last 15 years there has been a renewed interest in facilitation and this research has shown a clear link between the role of facilitation in structuring communities and both community biomass and the severity of the environment. Although facilitation may enlarge the realized niche of species and increase community richness in stressful environments, there has only been one previous attempt to revisit the humped-back model of species richness and to include facilitative processes. However, to date, no model has explored whether biotic interactions can potentially shape both sides of the humped-back model for species richness commonly detected in plant communities. Here, we propose a revision of Grime's original model that incorporates a new understanding of the role of facilitative interactions in plant communities. In this revised model, facilitation promotes diversity at medium to high environmental severity levels, by expanding the realized niche of stress-intolerant competitive species into harsh physical conditions. However, when environmental conditions become extremely severe the positive effects of the benefactors wane (as supported by recent research on facilitative interactions in extremely severe environments) and diversity is reduced. Conversely, with decreasing stress along the biomass gradient, facilitation decreases because stress-intolerant species become able to exist away from the canopy of the stress-tolerant species (as proposed by facilitation theory). At the same time competition increases for stress-tolerant species, reducing diversity in the most benign conditions (as proposed by models of competition theory). In this way our inclusion of facilitation into the classic model of plant species diversity and community biomass generates a more powerful and richer predictive framework for understanding the role of plant interactions in changing diversity. We then use our revised model to explain both the observed discrepancies between natural patterns of species richness and community biomass and the results of experimental studies of the impact of biodiversity on the productivity of herbaceous communities. It is clear that explicit consideration of concurrent changes in stress-tolerant and competitive species enhances our capacity to explain and interpret patterns in plant community diversity with respect to environmental severity.

INTRODUCTION

The relationship between diversity and productivity is a central component of community ecology, and has direct applicability to many issues such as the effective conservation of biodiversity and the maintenance of ecosystem function. In general, diversity is low in the least productive environments, highest at moderate levels of productivity, and then low again at very high levels of productivity; creating the so-called 'humped-back' or unimodal relationship. Recent meta-analyses (Mittelbach *et al.* 2001, 2003) suggest that the humped-back shape of the productivity–diversity relationship is more common in plant communities than in animal communities, and is generally relevant to only local and regional scales. Mittelbach *et al.* (2001) also emphasized that humped-back shape curves were especially common (65%) in studies of plant diversity that used plant biomass as a measure of productivity. Grime (1973) was the first to propose a conceptual model for the 'humped-back' pattern (but also see Huston 1979) which was strongly supported in a variety of environments (e.g. Molino & Sabatier 2001 for forest communities; Michalet *et al.* 2002 for alpine grasslands). Grime (1973) used plant biomass or density as surrogates for productivity. Grime (and the following authors) often interpreted this biomass gradient as a productivity gradient, likely because his model was elaborated primarily for herbaceous communities where productivity and biomass are strongly related. However, for clarity and because biomass and productivity are not necessarily positively correlated, we will use the word biomass instead of productivity. In this model, Grime assigned plant–plant interactions a major role in generating the humped-back shape, but considered only competitive exclusion. This is not surprising, since at the time of the model's development competition was considered to be the significant biotic filter structuring plant communities at local scales, and negative interactions were prominent in a number of key ecological theories, in particular those concerned with community richness (Connell 1978; Huston 1979).

However, despite the historical primacy of competition, interest in facilitation has increased considerably over the last 15 years. The proposition that direct positive interactions increase in stressful or physically disturbed communities (Bertness & Callaway 1994; Brooker & Callaghan 1998) led to numerous field experimental studies (e.g. most notably Callaway *et al.* 2002; Gómez-Aparicio *et al.* 2004) which demonstrated that positive interactions play a fundamental role in plant communities, especially in severe environments (see reviews by Callaway 1995; Callaway & Walker 1997; Callaway *et al.* 2002; Gómez-Aparicio *et al.* 2004). A recent review by Bruno *et al.* (2003) concluded that 'the inclusion of facilitation into ecological theory may fundamentally change many basic predictions and challenge some cherished paradigms' (see also Callaway & Walker 1997; Lortie *et al.* 2004). Given the clear links between community biomass, plant interactions and biodiversity proposed both by Grime's original model and in more recently developed facilitation theory, it seems reasonable to suggest that this is an area of ecological theory in need of revisiting. To our knowledge, there has been only one attempt to include positive interactions within the humped-back model of the biomass–diversity relationship (Hacker & Gaines 1997). These authors proposed a model where facilitation increases community richness by enlarging the realized niche of species in highly constrained environments. However, their revised model did not propose that facilitation can drive the increase in species richness occurring from very high to intermediate environmental severity and thus that biotic interactions can shape both sides of the humped-back relationship between community biomass and diversity. We believe that a re-examination of the humped-back model incorporating recent advances in our understanding of positive interactions, and in particular at the extreme end of an environmental severity gradient, will lead us to a more comprehensive perspective on the relationship between facilitation, biodiversity, and the general processes potentially driving ecosystem functioning.

This revision has important implications for understanding how biological diversity affects ecosystem function. For example, the BIODEPTH project (Hector *et al.* 1999) that the positive effect of diversity on the productivity of herbaceous communities may be explained by a decrease in competitive interactions (niche complementarity) and an increase in facilitation in species-rich communities. This finding has generated much controversy among plant ecologists mainly because the patterns observed in nature were counter to this trend, where the most productive ecosystems (and with high community biomass) are known to be dominated by a small number of highly competitive species (Loreau *et al.* 2001). We suggest that the discrepancy observed between results of experiments and natural patterns of biodiversity may arise from this lack of knowledge of the relationship that exists between positive interactions and diversity in natural or managed ecosystems.

INCLUDING FACILITATION WITHIN GRIME'S HUMPED-BACK MODEL OF SPECIES RICHNESS

In the classic model of Grime (1973), species diversity decreases from sites with intermediate levels of stress and disturbance to very stressed and disturbed sites because fewer species are able to tolerate these conditions (parts B of the gradient, Fig. 1). Grime (1973, 1974) and others propose that this decrease is strictly driven by the species' physiological tolerances to either environmental stress or
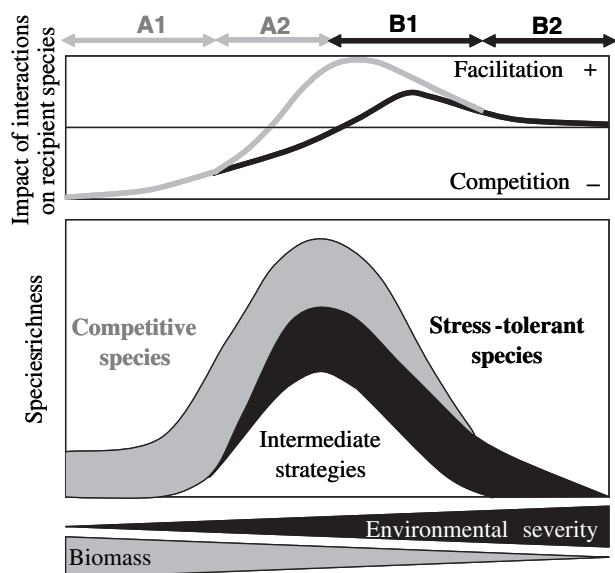
Figure 1 Schema showing the inclusion of facilitation into Grime's humped-back model of the relationship between species richness and both biomass and environmental severity (adapted from Grime 1973, Fig. 2a). Lower panel: species richness within the community of three strategy types, namely competitive species (grey), stress-tolerant species (black) and plants with intermediate strategies (white), e.g. C–S *sensu* Grime (1974). Ruderal species *sensu* Grime (1974) are not represented because their occurrence is limited along the gradient by either the effect of competition (left part of the gradient) or the effect of stress (right part of the gradient). In part A1 of the gradient (very high biomass and very low environmental severity) only competitive species occur in communities. In part A2 (high biomass and low environmental severity) the three strategy types are present but competitive species are more abundant than stress-tolerant species. In part B1 (medium to high environmental severity) the three strategy types are present but stress-tolerant species are more abundant than competitive species. In part B2 (very high environmental severity) only stress-tolerant species are present. Upper panel: the average type of net interactions (the sum of positive and negative interactions between neighbours) being received by competitive species (grey curve) and stress-tolerant species (black curve). In the parts A1 and B2 of the graph only one curve is drawn, because only one of these two types of strategies occurs in the communities (as is consistent with the lower panel).

disturbance rather than by biotic processes. In sharp contrast, competitive exclusion is thought to regulate diversity in benign environmental conditions (parts A1 and A2 of the gradient, Fig. 1) whereas the effect of the abiotic environment is thought to be minimal. The initial premise we propose is that the net outcome of plant interactions and therefore of diversity is a product of both competition and facilitation, and their associated exclusion and inclusion of species, and depends upon the point at which a community sits along gradients of severity and the relative intensity of each interaction type (Lortie *et al.* 2004).

Recent research has convincingly demonstrated that direct facilitation plays a role in regulating community composition in severe environments (Bertness & Shumway 1993; Greenlee & Callaway 1996; Choler *et al.* 2001; Pugnaire & Luque 2001; Tewksbury & Lloyd 2001; Callaway *et al.* 2002; Gómez-Aparicio *et al.* 2004; Brooker *et al.* 2005; Lortie & Callaway 2006). Because positive interactions alleviate stress or physical disturbance (i.e. environmental severity), the realized niche of a species (*sensu* Elton 1958) can be expanded by facilitation (Hacker & Gaines 1997; Choler *et al.* 2001; Bruno *et al.* 2003; Baumeister & Callaway in press), which in turn might increase species richness in stressful and/or physically disturbed environments, as shown in salt marshes (Hacker & Gaines 1997) or in alpine grasslands from the Caucasus (Kikvidze & Nakhutsrishvili 1998) and the Andes (Cavieres *et al.* 2002, 2006). A number of authors have shown that stress-intolerant competitive species (*sensu* Grime 1974) would benefit the most from these facilitative processes (Hacker & Gaines 1997; Choler *et al.* 2001; Gómez-Aparicio *et al.* 2004; Liancourt *et al.* 2005; Pages & Michalet in press), and high species richness in sites with intermediate levels of stress or disturbance (*sensu* Grime 1973; Connell 1978; Huston 1979) may be due in part to the facilitative effect of dominant stress-tolerant species on subordinate stress-intolerant competitive species (parts A2 and B1 of the gradient, Fig. 1).

However, and as mentioned above, despite clearly relevant recent advances in understanding the role of facilitation, there has been only one previous attempt to include facilitation within the humped-back model of the biodiversity–biomass relationship (Hacker & Gaines 1997). These authors proposed that positive interactions increase species diversity by: (i) directly facilitating species that might not normally survive under very high physical disturbance, stress or predation; and (ii) indirectly creating new interaction webs under intermediate environmental severity or predation. They proposed a conceptual scheme, consistent with Bertness & Callaway (1994), in which the positive effects on biodiversity are shown to increase from intermediate to very high environmental severity. As a result, their inclusion of facilitation within the humped-back model did not fundamentally explain the decrease in species richness occurring in the right part of the gradient (parts B1 and B2, Fig. 1). In contrast to the effect of competition proposed by Grime (1973) for the left side of the model, facilitation is only assumed to skew the curve to the right, but not to drive its direction. This is not surprising, because, at the time when Hacker & Gaines (1997) proposed their model, facilitation was assumed to infinitely increase with environmental severity (Bertness & Callaway 1994) and thus was negatively correlated with community richness in the humped-back model.

We suggest that this shortcoming occurs because early facilitation models did not consider extremely severe environments (see Bertness & Callaway 1994; Brooker & Callaghan 1998). Cropping the gradients limited the explanatory power of facilitation at the low-biomass end of the humped-back biomass–diversity relationship. However, recent experimental studies indicate that the role of facilitation may actually decrease in exceptionally severe environments (part B2 of the gradient shown, Fig. 1; Belcher *et al*. 1995; Kitzberger *et al*. 2000; see also Bruno *et al*. 2003). Although Callaway *et al*. (2002) found an overall increased role of facilitation with increasing stress and/or physical disturbance in their intercontinental study of biotic interactions along altitudinal gradients in alpine and arctic communities, facilitation was much more intense at temperate high elevation sites than at the most severe sites in high elevation arctic environments. This suggests that the importance or intensity of facilitation may actually decrease with increasing stress or physical disturbance in the most severe conditions. Admittedly, not all studies support this interpretation. For example, under some conditions in arid environments increasing water stress may increase competition (e.g. Tielbörger & Kadmon 2000; Maestre & Cortina 2004). However, the outcome of experiments on biotic interactions is strongly scale-dependent (Dickie *et al*. 2005; Michalet 2006), and even if competition has been shown to increase with water stress 'at the patch scale' (Pugnaire & Luque 2001; Maestre *et al*. 2003), the net effect of neighbours 'at the community scale' in dry environments tends to be positive, as demonstrated by empirical studies and meta-analyses (Pugnaire *et al*. 2004; Gómez-Aparicio *et al*. 2004; Lortie & Callaway 2006). Furthermore, the sign of net interactions has also been shown to change even within a single community with subtle changes in scale (from within patch negative to between patches positive) in a desert grassland (Lortie *et al*. 2005). In general, arid and semi-arid ecosystems are organized in mosaics of vegetated patches and areas of bare ground (Aguiar & Sala 1999), and positive interactions that may drive species richness at the community scale in these arid environments (Cavieres *et al*. 2006) have been shown to disappear in some exceptionally stressful and physically disturbed conditions (Belcher *et al*. 1995; Kitzberger *et al*. 2000) as in extreme arctic-alpine environments. To return to Grime's classic model, if the role of positive interactions actually decreases from environments of intermediate severity to the most severe environments (parts B1 and B2, respectively, of the gradient, Fig. 1), and if facilitation expands ecological niches of stress-intolerant competitive species (Hacker & Gaines 1997; Choler *et al*. 2001; Bruno *et al*. 2003), we would then predict that facilitation may promote species diversity in communities of intermediate to high environmental severity. Hence, the decline in species diversity is a combined effect of waning facilitation and a reduced number of species that still can tolerate those environmental conditions. The humped-back diversity model of Grime including the propositions of Hacker & Gaines (1997) should therefore be revised to incorporate this new knowledge on the decreasing role of facilitative interactions in extremely severe environments.

Two key contemporary issues will now be reinterpreted using this new conceptual model. We first discuss the relationship between diversity and a gradient of environmental severity, including both stress and physical disturbance and then go on to consider the relationship between diversity and disturbance in general. First, on an environmental severity gradient the role of facilitation peaks for stress-intolerant competitive species (grey curve in Fig. 1) in conditions of intermediate severity, particularly at the point of highest species richness along the environmental gradient, i.e. the point where dominant stress-tolerant species have their maximum positive effect. When stress and/or physical disturbance increases from this intermediate point, the positive effects of the benefactors decrease (grey curve in part B1 of the gradient, Fig. 1), as demonstrated in field experiments, probably because they are less successful at ameliorating abiotic conditions and promoting the survival of beneficiary species in these very severe environments. In the most severe environmental conditions (part B2 of the gradient, Fig. 1), biotic interactions become unimportant relative to the effect of the environment, and only stress-tolerant species (*sensu* Grime 1974) can persist in these communities. With decreasing environmental severity from the intermediate position along the gradient (part A2, Fig. 1), diversity also decreases, but in this instance this decrease is due to the competitive exclusion of stress-tolerant species by the competitive stress-intolerant species (black curve in Fig. 1), as initially proposed by competition theory (Grime 1973). At the same time, the role of facilitation decreases for stress-intolerant competitive species (grey curve in part A2 of the gradient, Fig. 1), because these species can exist within the community without the help of a benefactor species, as initially proposed by facilitation theory (Bertness & Callaway 1994). Finally, in the most benign conditions (part A1 of the gradient, Fig. 1), only competitive species exist within the communities, as negative interactions are too high to allow the occurrence of slow-growing stress-tolerant species (*sensu* Grime 1974). Grime (1973) considered that most species in communities at the middle of the environmental gradient belong to intermediate strategies (e.g. C–S *sensu* Grime 1974). For simplicity and also because of the lack of precise knowledge about the average impact experienced by species with intermediate strategies, we did not draw an additional curve for these species, but these impacts are likely to be intermediate between those experienced by stress-tolerant and competitive species.

Hence, in this model the contrasting effects of competition and facilitation for species with different life-history traits combine to produce the hump-backed relationship, thereby changing average impact experienced by plants with different growth strategies (Fig. 1). In particular, the upper panel of the Fig. 1 shows how interactions change for different strategy groups along the environmental severity gradient. With these conceptual lines we try to depict the probable average effect (which is a sum of many positive and negative impacts that neighbouring plants have on each other) under given conditions. These average impacts change at different rates for different growth-forms along the severity gradient, so that at certain parts of the gradient competitive species can be facilitated whilst stress-tolerant species will suffer competition (Fig. 1, parts A2 and B1).

This co-occurrence within a given community of competitive and facilitative responses for stress-tolerant and competitive species respectively (as proposed in our revision) has been observed by several authors in a number of intermediate to high severity environments (Choler *et al.* 2001; Gómez-Aparicio *et al.* 2004; Liancourt *et al.* 2005). For instance, in the calcareous-soil grasslands of Europe Liancourt *et al.* (2005) quantified biotic interactions in two conditions of water availability for three dominant species of contrasted strategies. In the unwatered mesophilous and species-rich *Bromus erectus* community, the two competitive species, *Arrhenatherum elatius* and *Brachypodium rupestre*, were highly facilitated for survival, whereas the stress-tolerant *Bromus erectus* was only slightly negatively affected by neighbours. Conversely, in watered conditions simulating the species-poor *Brachypodium rupestre* community, there were no significant interactions for the survival of the two competitive species, whereas the stress-tolerant *Bromus erectus* experienced high competition. These experimental studies support our model in which facilitation is highest for competitive species at the peak of biodiversity within the humped-back model (see Fig. 1). This is also evident in the emblematic UK species-rich mesophilous *Bromus erectus* community (Grime 1973; Al-Mufti *et al.* 1977). Our revised model suggests that when increasing biomass and decreasing species richness towards the left side of the model, facilitation disappears for competitive species, while competition increases for stress-tolerant species (part A2 of the gradient, Fig. 1). Choler *et al.* (2001) quantified biotic interactions along an elevation gradient (from 2000 to 2800 m a.s.l.) in subalpine and alpine communities of the French Alps. In dry and species-rich subalpine communities (> 30 species per m^2), they found competitive responses for stress-tolerant species and facilitative responses for stress-intolerant species, whereas in species-poor high alpine communities (< 20 species per m^2) all species were facilitated. Choler *et al.* (2001) also quantified variation in biotic interactions along topographic gradients within each eleva-

tion level. When soil depth and community biomass increased along this gradient at the subalpine level, they found competitive interactions for all species, which was related with a drop in species richness from > 30 to 25 species per m^2 (see Michalet *et al.* 2002 for more precise data). These results from high-elevation communities also support our model, in which facilitative and competitive responses are observed at the peak of community richness, depending on the species' strategies. As for calcareous-soil grasslands, when increasing biomass and decreasing species richness towards the left side of the model (mesic subalpine grasslands), facilitation disappears for stress-intolerant species, while competition increases for stress-tolerant species (part A2 of the gradient, Fig. 1). In contrast, when decreasing biomass and decreasing species richness towards the right side of the model (alpine grasslands), facilitation occurs for all species (part B1 of the gradient, Fig. 1). However, Choler *et al.* (2001) did not observe in their study a decrease in facilitation in the most severe environment (i.e. the B2 segment, Fig. 1), likely because they did not experiment in the nival communities (> 3000 m a.s.l.), where species richness has been described to be much lower (< 15 species per m^2, Grabherr *et al.* 1994).

Our model was proposed to include the role of facilitation in the explanation of the humped-back shape of the biodiversity–biomass relationship along gradients of environmental severity involving competitive and stress-tolerant species. For simplicity, we have not considered ruderal species (*sensu* Grime 1974). Furthermore, ruderals can be expected to be rare along most stress gradients due to limitation by either the effect of competition (left part of the gradient) or the effect of stress (right part of the gradient). This gradient of environmental severity was defined *sensu* Bertness & Callaway (1994, right side of the model) and corresponds to the gradient of environmental stress of Grime (1973). Grime (1973) initially proposed a similar relationship along a gradient of management intensity, involving competitive species and ruderal species. Stress-tolerant species are rare along this gradient due to a limitation by either the effect of competition (left part of the gradient) or the effect of disturbance (right part of the gradient). This gradient of management intensity corresponds to the gradient of biotic disturbance occurring in productive communities in the left side of the model of Bertness & Callaway (1994). These authors proposed that indirect positive interactions increased along this gradient due to the occurrence of associational defences (protection against herbivores). To our knowledge, there are no experimental studies suggesting that a decrease in indirect positive interactions may occur at the low biomass end of this gradient, similar to what has been observed along gradients of environmental severity. Further studies are needed along gradients of biotic disturbances in productive

communities to understand if ruderal species *sensu* Grime (1974) are drivers of community richness changes in intermediate to highly disturbed conditions.

Patterns of species richness are also highly dependent on the scale at which they are measured. Mittelbach *et al.* (2001, 2003) have shown that the humped-back shape observed at local and regional scales commonly disappears at a scale larger than a continent (see also Kikvidze *et al.* 2005). Huston (1999) argued that species interactions are likely to play a strong role in determining richness at local scale, whereas other mechanisms (including speciation and extinction) are more likely to affect species richness at larger scales. The humped-back model was primarily proposed by Grime (1973) to explain local and regional diversity patterns by competitive interactions, and so inclusion of positive interactions into this model does not propose that facilitation is a mechanism explaining species richness patterns at larger scales.

Reassessment of Grime's humped-back model and the general inclusion of facilitation into ecological theory is not simply of academic interest. Environments in which facilitation appears to be a key process (e.g. arctic, alpine, coastal and arid systems) are particularly sensitive to major anthropogenic drivers of ecosystem change, including climate change, land use change and introduced species. In order to manage and conserve these environments it is vital to understand the ecological processes that regulate their biodiversity. It is clear that facilitation is such a process, and an improved understanding of the relationship between facilitation and biodiversity will enhance our ability to protect these threatened ecosystems. Our inclusion of facilitation within Grime's humped-back model of species richness may be particularly helpful for explaining some of the discrepancies observed between natural patterns of species richness and the results of experiments analysing the role of biodiversity for the productivity (and biomass) of herbaceous communities (Hector *et al.* 1999; Loreau *et al.* 2001). If facilitation, biodiversity and both biomass and productivity are all positively correlated along a part of the gradient of environmental severity, we can then explain why some experimental studies conducted in stressful conditions found that diversity enhanced productivity (e.g. Mulder *et al.* 2001). Specifically, diversity is very likely to increase productivity when facilitation is present, but not when it is absent from an assemblage of species, which itself depends on the position of the community along the environmental gradient.

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