

FACILITATIVE MECHANISMS UNDERLYING THE  
EFFECTS OF BIODIVERSITY ON ECOSYSTEM FUNCTIONING

Essay Review

Are complementarity effects of species richness on  
productivity the strongest in species-rich communities?Richard Michalet<sup>1</sup>  | Florian Delerue<sup>2,3</sup>  | Pierre Liancourt<sup>4,5</sup>  |  
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## Abstract

1. How the relationship between species richness and productivity changes along environmental gradients remains poorly understood.
2. We examined the context dependency of complementarity processes underpinning this relationship (biotic feedbacks, resource partitioning and facilitation) using the framework of Grime's (1973) humped-back model. We considered several scenarios of variation in competition and facilitation along environmental gradients, either monotonic with the most common or intense facilitation at the most abiotically severe end of gradients or nonlinear with the strongest facilitation at intermediate positions along gradients.
3. How competition shifts to facilitation along environmental gradients is a key for determining where the effect of species richness on productivity occurs. Based on the literature, the original Stress Gradient Hypothesis would likely predict that complementarity effects should be the greatest, or the most important, in the most abiotically stressful environments. Alternatively, both the 'collapse of facilitation' and the 'shift back to competition' scenarios predict that the highest overall complementary effects on productivity, not biomass, would most likely occur at intermediate positions along environmental stress gradients, but this might vary depending on the source of stress. This latter prediction is consistent with a great deal of literature on natural gradients of productivity and species richness.
4. *Synthesis.* Our predictions illustrate the importance of better understanding the context dependency of complementarity processes and the key role of facilitation along environmental gradients to better focus conservation efforts where ecosystem functioning is more likely to be negatively affected by species loss, in particular in species-rich communities.

## KEYWORDS

biomass, competition, diversity, facilitation, natural patterns, niche complementarity, productivity

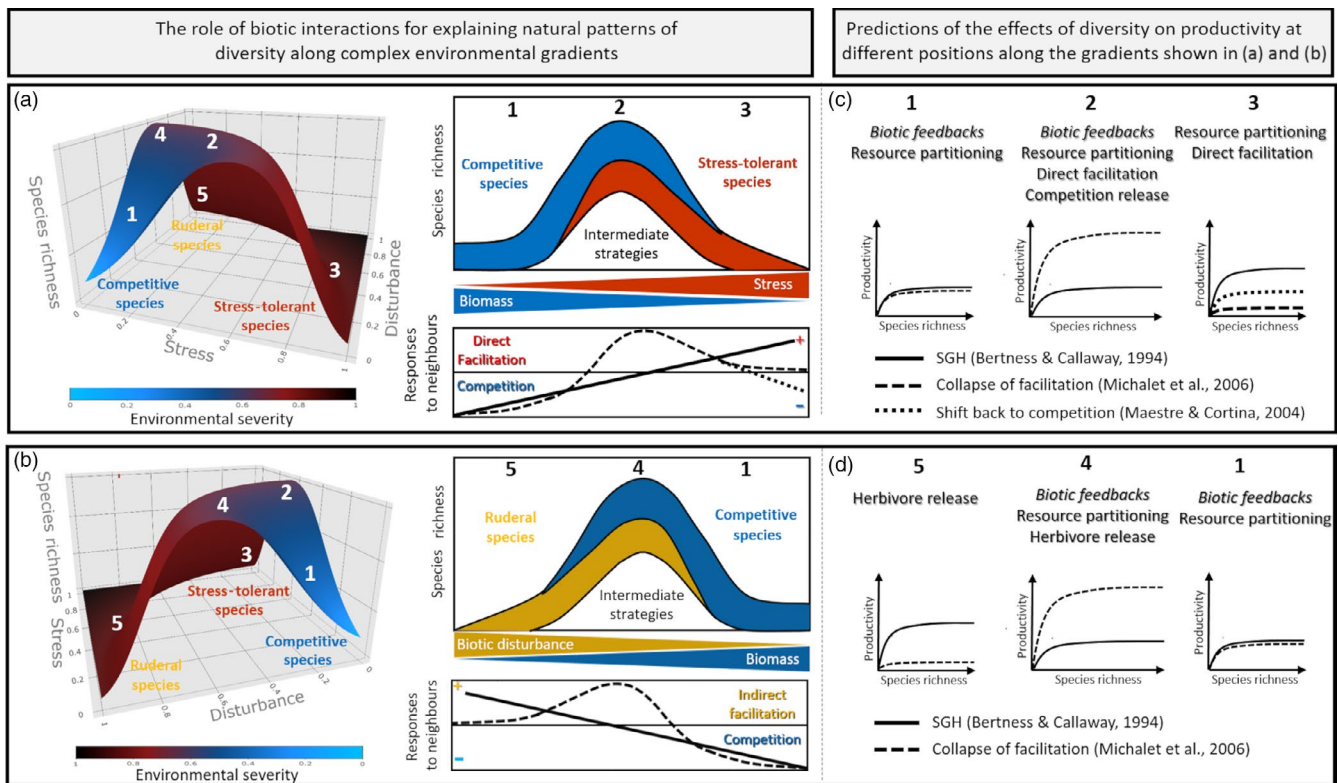
# 1 | INTRODUCTION

An intense interest on the effects of biological diversity on ecosystem functioning emerged in the 1990s with profound effects on the ecological sciences (Hooper & Vitousek, 1997; Naeem et al., 1994; Tilman et al., 1996; Wardle et al., 1997). In less than 5 years, this 'revolution' drove progress in experimental methods, statistical analyses and modelling, and contributed to the societal outreach of environmental sciences (Cardinale et al., 2012; Huston, 1997; Loreau & Hector, 2001; Tilman et al., 1997). At the same time, in particular after the global BIODEPTH experiments (Hector et al., 1999), there was a debate over statistical analysis and causality in these experiments (Huston, 1997; Huston et al., 2000; Loreau & Hector, 2001; Wardle, 2016).

This debate was in part due to inconsistency between the increase in productivity with species richness observed in BEF experiments (conducted mostly in grasslands), and the low species

richness of most presumed productive, natural herbaceous communities (Grime, 1973; Huston, 1979). The debate involved the role of competition in plant communities, and its change along environmental gradients, another source of controversy among ecologists (Grime, 1979; Liancourt, Corcket, et al., 2005; Tilman, 1982). This debate was resolved to a large degree by Loreau et al. (2001), who proposed that natural patterns reveal correlations between diversity and productivity driven by environmental factors, whereas small-scale experiments reveal the effect of species properties and diversity on productivity when other environmental factors are removed. In this resolution, scale (regional versus local) was crucial for understanding the effects of competition and diversity in biomass-diversity and diversity-productivity relationships (Figure 1, a and b vs. c and d).

However, two inconsistencies with other bodies of literature remained in Loreau et al.'s resolution (Michalet & Touzard, 2010). First, at the neighbourhood scale (i.e. in BEF experiments), diversity



**FIGURE 1** Left panels (a) and (b) show the role of plant interactions for explaining natural patterns of diversity along environmental severity and biomass gradients and right panels (c and d), and the effects on productivity of complementarity effects induced by increasing species richness at different positions along natural environmental gradients shown in left panels. Following Grime (1973), upper panels (a and c) focus on stress gradients in undisturbed conditions and lower panels (b and d) on biotic disturbance gradients in conditions of low stress, while 3D diagrams in the left panels show how the two direct gradients interact along complex gradients of environmental severity. Note that the two 3D diagrams are different views of the same diagram that has been rotated from (a) to (b), in order to highlight the stress or disturbance effects, respectively. 2D diagrams in (a) and (b) show the trade-offs between competitive (blue) and stress-tolerant species (red) and ruderals (yellow) along stress and disturbance gradients, respectively, following Grime (1973), while curves below them show variation in competition and direct and indirect facilitation along stress and biotic disturbance gradients following Grime (1973) for mild environmental conditions and Bertness and Callaway (1994), Maestre and Cortina (2004), Michalet et al. (2006) and Le Bagousse-Pinguet, Xiao, et al. (2014) for severe environmental conditions. Effects of species richness on productivity through complementarity effects in right panels are represented with different curves depending on the scenario of variation in plant interactions proposed in the literature and shown in left panels, and our knowledge from BEF experiments (Barry et al., 2019). Numbers in black letters in the right panels are positions along environmental gradients, also represented on the top of 2D diagrams and with white letters in the 3D diagrams

is thought to increase productivity primarily through niche partitioning and thus, reduced competition (see Hector et al., 1999; Naeem et al., 1994). This niche partitioning was thought to operate at similar intensities at all levels of productivity (see fig. 4b in Loreau et al., 2001). However, this is not consistent with Grime's (1973, 1979) ideas about competition being more important and intense in productive communities (also see Brooker et al., 2005; Pennings & Callaway, 1992). In other words, if niche partitioning reduces competitive exclusion, and competitive exclusion is more likely in productive communities, then the effects of niche partitioning (one component of complementarity) should be more important in highly productive communities. If the processes affecting coexistence change in importance along environmental gradients, then the processes involved in BEF should change as well. If competition is weak in harsh, unproductive environments, competition can only diminish so much with increasing species richness.

The second inconsistency with other literature derived from the assumption that in large-scale biomass–diversity relationships, the abiotic environment drives both diversity and productivity (see fig. 4a, Loreau et al., 2001). This conflicts with Grime (1973), who argued that decreases in species richness at high productivity are due to increased competition (see Brooker et al., 2005). This conceptual conflict may be due, in part, to some ecologists emphasizing the importance of stochastic environmental processes related to dispersal, and others emphasizing stress induced by climate and soil (Brooker et al., 2009; Lortie et al., 2004; Michalet, Maalouf, et al., 2015).

Michalet and Touzard (2010) proposed three arguments that might reconcile these conceptual inconsistencies. First, they argued that both points of view should integrate context-dependent effects of biodiversity on productivity while separating increases in productivity with diversity due to resource partitioning (i.e. a decrease in competition) and those due to facilitation (see Michalet et al., 2006; Mulder et al., 2001; Wright et al., 2017, 2021). These arguments were further developed by Wright et al. (2017) and Barry et al. (2019), who proposed that complementarity should not only separate resource partitioning and direct facilitative mechanisms (e.g. ambient VPD, this Special Feature, Aguirre et al., 2021) but also indirect facilitative mechanisms (e.g. Pugnaire et al., 2019; van der Putten et al., 2013; Zuppinger-Dingley et al., 2014). Second, Michalet and Touzard (2010) stressed that the refinement of the stress gradient hypothesis (SGH) of Bertness and Callaway (1994), proposing that facilitation increases with decreasing stress from conditions of high to intermediate environmental severity (Michalet et al., 2006), could reconcile BEF experiments with natural patterns, at least in stressful conditions. Indeed, in the Michalet et al. (2006) model, species richness, facilitation, biomass and productivity are positively correlated, consistent with BEF experiments conducted in abiotically stressful conditions (e.g. Mulder et al., 2001). However, no BEF experiment has been conducted in exceptionally stressful

conditions such as found at the ends of many stress gradients (e.g. Armas et al., 2011; Callaway, 1994; Callaway et al., 2002; Cavieres et al., 2014; Dohn et al., 2013; He et al., 2013; Molina-Montenegro et al., 2013; Pugnaire et al., 2015).

Michalet et al. (2006) also noted that explicitly distinguishing between productivity and biomass might help to resolve conceptual conflicts in the literature. Loreau et al. (2001) proposed that theoretical models (e.g. Grime, 1973; Huston, 1979) predicted a negative correlation between diversity and *productivity* under low abiotic stress conditions (also see Adler et al., 2012; Grace et al., 2016). However, most observational, or correlative, studies used final *biomass* as surrogate for productivity (Al-Mufti et al., 1977; Fraser et al., 2015). Furthermore, in the original humped-back model (HBM, Grime, 1973), the x-axis is a gradient of 'standing crop', that is, biomass, and not productivity as in Loreau et al. (2001; also, see Schmid, 2002). Productivity is the rate at which living biomass increases over time ( $\text{g g}^{-1} \text{year}^{-1}$ ), whereas biomass is a static metric of the accumulation of biomass over undefined periods of time ( $\text{g/m}^2$ ). Biomass and productivity can correlate in mesic grasslands dominated by herbaceous species that decay before the beginning of the next growing season, but the assumption of equivalence is problematic in communities that retain biomass over many growing seasons—those with larger proportions of woody plants or recalcitrant standing litter. Grace et al. (2016) analysed global grassland data (Nutnet; Adler et al., 2012) and explicitly distinguished between biomass and productivity. Doing so they identified a negative correlation between biomass and species richness, but a positive relationship between species richness and productivity. However, they used current year's biomass increment as proxy of productivity, since the sampling (Adler et al., 2012) was only conducted once, at the peak of biomass during the growing season. The sampling of only current-year leaves and green plant parts (Adler et al., 2012) can underestimate productivity since the yearly accumulated biomass can also be stored in woody stems and roots. Thus, our knowledge of the variation in productivity along natural environmental gradients driving community biomass and species richness is still approximate in grasslands and limited in most woodlands. The distinction between biomass and productivity is crucial, because if biomass, but not productivity, is high when competition decreases species richness, then the results of BEF experiments are not inconsistent with natural patterns of diversity (e.g. Grime, 1973), as suggested by Michalet and Touzard (2010).

In light of advances over the last 20 years (Eisenhauer, 2012; Isbell et al., 2017; Reich et al., 2012; Zuppinger-Dingley et al., 2014) and the clarification of different processes in complementarity (Barry et al., 2019; Wright et al., 2017), we now elaborate on predictions for the effects of species richness on the productivity of natural plant communities. We integrate the results of BEF experiments with different scenarios for variation in competition and facilitation along environmental gradients.

## 2 | A FRAMEWORK FOR PREDICTING THE INFLUENCE OF SPECIES RICHNESS ON PRODUCTIVITY ALONG ENVIRONMENTAL GRADIENTS

To predict the effect of species richness on productivity along environmental gradients, we build on a framework inspired by fig. 4 in Loreau et al. (2001; Figure 1). In Figure 1, the left two panels show relationships among community biomass, environmental conditions and biotic interactions and species richness following Grime (1973). The two panels on the right show how complementarity effects might increase productivity with increasing diversity along environmental gradients following the results of BEF experiments. Many textbooks and authors, including Loreau et al. (2001), have simplified Grime's (1973) model to a single figure with productivity on the x-axis and species richness on the y-axis. However, Grime originally proposed two conceptual diagrams—reproduced in Figure 1a,b. One diagram (Figure 1a) represented changes in species richness along gradients of stress in undisturbed communities. The other (Figure 1b) showed changes in species richness along disturbance gradients in productive environments with no variation in abiotic stress. These two diagrams allowed Grime to illustrate the switch from competitive to stress-tolerant species, or ruderals, along gradients of abiotic stress or disturbance, respectively. In both diagrams, standing crop (i.e. biomass, not productivity) decreased with increasing abiotic stress or disturbance, and there were no direct measurements of productivity on the x-axis (e.g. Al-Mufti et al., 1977). Likely, because of the similarity between the two curves, many authors (including Grime, 1979) simplified the figure into a single conceptual diagram. Additionally, standing crop (i.e. biomass) was (wrongly) replaced by productivity, as in Loreau et al. (2001) and several textbooks. If we put the two original diagrams into a 3D diagram, we see how stress and disturbance interact along complex environmental gradients to shape biomass and species richness (left panel of Figure 1a,b with two views of the same 3D diagram).

Using this framework, we include the different scenarios of variation in competition and facilitation along stress and disturbance gradients (Figure 1) proposed in the literature (Bertness & Callaway, 1994; Grime, 1973; Le Bagousse-Pinguet, Xiao, et al., 2014; Maestre & Cortina, 2004; Michalet et al., 2006; Pugnaire & Luque, 2001). From these, it is evident that, in conditions of low stress and disturbance (i.e. from positions 1 to 2 or 4 in Figure 1a and b, respectively), competition should decrease—and species richness increase—when biomass decreases. These changes have empirical support (e.g. Michalet et al., 2002; Fraser et al., 2015, but see Adler et al., 2012). The stress gradient hypothesis (SGH) further proposed that, at mid-point along the two gradients (i.e. at position 2 or 4), the frequency of competition should gradually shift to facilitation through habitat amelioration (Figure 1a) or through herbivore release (Figure 1b), respectively (Bertness & Callaway, 1994). The SGH model suggested that direct and indirect facilitation should increase monotonically with increasing stress or herbivory towards the severe end of each gradient (i.e. until position 3 or 5,

respectively, Figure 1a,b). This model has been supported by the results of a number of experiments, in particular along gradients of cold stress (e.g. Callaway et al., 2002; Cavieres et al., 2014; Michalet, Schöb, et al., 2014). However, more complex results have been found along drought gradients (Maestre et al., 2005), either supporting the SGH (e.g. Armas et al., 2011; Callaway, 1994; Dohn et al., 2013; Gomez-Aparicio et al., 2004; Greenlee & Callaway, 1996; Holzapfel et al., 2006; Liancourt, Corcket, et al., 2005; Pugnaire & Luque, 2001; see reviews by Blaser et al., 2013; He et al., 2013), a few reporting an increase in competition with increasing drought (e.g. Davis et al., 1998; Maestre & Cortina, 2004; Tielbörger & Kadmon, 2000; but see fig. 4.25, Callaway, 2007) and other finding an absence of interaction at the most stressed end of the gradient (e.g. Chaieb et al., 2020; Kitzberger et al., 2000; Le Bagousse-Pinguet, Maalouf, et al., 2014). Facilitation has also been shown to wane in conditions of extreme biotic or physical disturbance (Brooker et al., 2006; Forey et al., 2010; Smit et al., 2007). Thus, Michalet et al. (2006), Maestre et al. (2009), Holmgren and Scheffer (2010), Malkinson and Tielbörger (2010) and Verwijmeren et al. (2013) have proposed several alternatives to monotonic changes in competition and facilitation with increase abiotic stress, but always with a peak of facilitation at intermediate position along environmental severity gradients. Michalet, Le Bagousse-Pinguet, et al. (2014) distinguished between the collapse of facilitation described by Michalet et al. (2006) from a shift back to competition. This was because the former is generally due to a decrease in the positive effect of the nurse, more likely to occur on a non-resource gradient (e.g. disturbance or temperature), whereas the latter may be due to increasing competition for resources. The left panels in Figure 1 show different scenarios of variation in competition and facilitation along stress and disturbance gradients. The first scenario corresponds to the original SGH, describing a monotonic increase in facilitation, the second considers that facilitation wanes at high level of stress ('collapse' hereafter), and the third considers that facilitation could shift back to competition at high level of stress ('shift back' hereafter). We examine the influence of species richness on productivity for these three scenarios along a stress gradient, and for the two first only along a disturbance gradient since disturbance is not a resource and, thus, unlikely to induce a shift back to competition.

## 3 | THE CONTEXT DEPENDENCY OF COMPLEMENTARY EFFECTS AND IMPLICATIONS FOR PRODUCTIVITY

We selected five key environmental positions for predicting the effects of species richness on productivity in natural environments (Figure 1c,d). Position 1 shows the least constrained environmental conditions with high biomass and low diversity (due to both low stress and disturbance) but with high competition. Positions 2 and 4 are intermediate positions along the stress and disturbance gradients where species richness is highest due to intermediate levels of stress and disturbance, low competition and either weak facilitation

(see Bertness & Callaway, 1994) or high direct or indirect facilitation following other SGH-ideas (Le Bagousse-Pinguet, Xiao, et al., 2014; Maestre & Cortina, 2004; Michalet et al., 2006). Finally, positions 3 and 5 point to the severe end of a gradient where species richness is low, with either high or low facilitation, or even competition, depending on the three models of potential interactions described in Figure 1a,b (left panels).

Barry et al. (2019) noted that the relative contribution of complementarity processes to increases in productivity with increasing species richness is highly context dependent. Negative biotic feedbacks from other trophic levels should dominate in monocultures, whereas resource partitioning and indirect facilitation dominate in mixtures under low stress, and direct facilitation under high stress (Barry et al., 2019). Direct facilitation through microclimate amelioration has been shown to be crucial in driving complementarity effects in BEF experiments conducted under moderately stressful conditions (Caldeira et al., 2001; Klaus et al., 2016; Mulder et al., 2001; Steudel et al., 2012; Wright et al., 2017; this Special Feature, Aguirre et al., 2021). For example, Mulder et al. (2001) experimented with bryophyte communities at two levels of water availability, and diversity increased productivity only under dry conditions. This result was due to increasing survival of drought-intolerant species below the canopy of more tolerant species. Thus, following Wright et al. (2017) and Barry et al. (2019), we argue that facilitation is most likely the dominant process explaining complementarity effects in stressful conditions versus resource partitioning or negative biotic feedbacks in milder environmental conditions.

The relative contribution of each complementarity process in natural environments has been minimally documented (but see this Special Feature). Negative biotic feedbacks from other trophic levels are likely to operate on the high-biomass side of Grime's HBM (Figure 1a,b), corresponding with plant communities dominated by a few competitive species, due to low stress and low disturbance. Indeed, since its early formulation (Connell, 1971; Janzen, 1970), negative density-dependent effects have been suggested to be more important in tropical systems with low environmental constraints for plant growth that lead to high species diversity. Thus, negative biotic feedbacks from higher trophic levels should be important complementarity effects driving communities from positions 1 to 2 or 1 to 4 in HBM models, as proposed in Figure 1c,d.

The influence of the abiotic environment on the importance of resource partitioning is certainly an old and open question, for which Braun-Blanquet (1932) proposed a solution. He, like Grime later (1979), argued that competition among species is low in unfavourable environments and increases as environmental conditions improve (but see Tilman, 1982). If competition is less intense and less important in environments supporting less standing biomass (Grime, 1979, Figure 1), resource partitioning is less likely to explain species richness. With improving environmental conditions and increasing species richness (and therefore community complexity), we could expect resource partitioning to become more important (see Braun-Blanquet, 1932; Naeem et al., 1994) because the benefits of avoiding competitive exclusion increase. Considering covariation

between standing biomass and species richness (Fraser et al., 2015), and if resource partitioning is higher in 'highly organized communities' (i.e. more diverse sensu Braun-Blanquet, 1932), resource partitioning should peak at a middle point along severity gradients (i.e. positions 2 and 4 in Figure 1) and should be present but less important at position 1. Following the original SGH model (Bertness & Callaway, 1994), resource partitioning would be less important at positions 3 and 5, because competition is assumed to be less frequent. In contrast, resource partitioning would be still present at position 3 if there is a shift back to competition (Maestre & Cortina, 2004). Finally, the relative contribution of direct facilitation to increasing productivity with increasing species richness should be highest at position 3, following the SGH model, but at position 2 following the other two scenarios (Figure 1c). Additionally, consistent with Aschehoug and Callaway (2015) and Wright et al. (2017), indirect facilitation due to competitive release should promote complementarity effects at position 2 because of the higher number of species there (Figure 1c). Release from consumer pressure should be most important with increasing productivity concomitant with increasing species richness at position 5 with SGH (Bertness & Callaway, 1994), at position 4 with the 'collapse' scenario (Le Bagousse-Pinguet, Xiao, et al., 2014, Figure 1d).

The overall complementarity effect on productivity is dependent on both the importance of each complementarity process and the species richness at each position on a particular abiotic stress gradient. This overall complementarity effect on productivity is represented in Figure 1c,d. In the absence of facilitation, and with strong competition (position 1), important negative feedbacks and weak resource partitioning, the effect of increasing species richness on productivity should be low. An experimental test of this effect would be hard to carry out, since variation in species richness should ideally represent both the environmental and community characteristics, that is, low disturbance and low number of species. Alternatively, an experimental test might involve species removals in natural communities (e.g. Diaz et al., 2003).

At positions 2 and 4, the overall complementarity effect on productivity should largely depend on the scenario of variation in competition and facilitation along stress and disturbance gradients. It should be the highest in the case of a collapse of facilitation or a shift back to a relatively high frequency of competition (Le Bagousse-Pinguet, Xiao, et al., 2014; Maestre & Cortina, 2004; Michalet et al., 2006), both predicting a maximum of facilitation at these positions (Figure 1c,d), and because all complementarity processes are predicted to operate. The response of dependent species to dominant neighbours at intermediate environmental positions is highly variable and depends on their functional strategies (Bai et al., 2021; Michalet, Chen, et al., 2015; Wang et al., 2019), which is consistent with Choler et al. (2001), Liancourt, Callaway, et al. (2005) and Liancourt et al. (2017). Thus, species of different functional strategies (C, S and R; Grime, 1973) may contribute specific kinds of complementarity to increasing productivity. At positions 3 and 5, predictions also depend on the scenario, with higher effects expected in the original SGH scenario than in the other two scenarios,

in particular the collapse of facilitation, since the absence of competition precludes resource partitioning.

## 4 | CONCLUSIONS

Improving our knowledge of the context dependency of complementarity processes in general, and plant-plant interactions in particular, is needed to better understand the effect of biodiversity on ecosystem functions and the possible discrepancy between BEF experiments and natural environmental gradients. Following the predictions of the original SGH (Bertness & Callaway, 1994), we predict that the overall complementarity effect should be the greatest in the most abiotically stressful environments. Alternatively, both the 'collapse of facilitation' and the 'shift back to competition' scenarios would predict the highest overall complementary effect for productivity to occur at an intermediate position along environmental gradients, where species richness is highest and where facilitation should peak. More precise measurements of productivity of herbaceous and shrubland communities are needed to test these alternative hypotheses. A better characterization of the context dependency of complementarity processes should help focusing conservation efforts where ecosystem functioning is most likely to be negatively affected by the current diversity loss associated to global change.

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## AUTHORS' CONTRIBUTIONS

R.M. conceived the idea and wrote the first draft of the manuscript; F.D., P.L. and F.I.P. contributed critically to the writing.

## DATA AVAILABILITY STATEMENT

There are no data to be archived.

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