Global shifts towards positive species interactions with increasing environmental stress

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INTRODUCTION

The study of species interactions is one of the most fundamental issues in ecology, essential for developing a predictive understanding of community and ecosystem response to accelerating environmental change (Tylianakis et al. 2008; Harmon et al. 2009; Harley 2011). In natural communities, species have been found to affect each other through both negative and positive interactions (Menge & Sutherland 1987; Tilman 1988; Bertness & Callaway 1994; Callaway et al. 2002), and a growing body of literature (Callaway et al. 2002; Bruno et al. 2003; Brooker et al. 2008; Odadi et al. 2011) has shown that positive rather than negative interactions dominate in certain environments. Recognition of the importance of positive species interactions has challenged many basic ecological paradigms and predictions based solely on negative species interactions (Mulder et al. 2001; Bruno et al. 2003). For example, in contrast with negative species interactions that can drive species extinctions (Sax & Gaines 2008) and diversity loss (Hautier et al. 2009), positive interactions can maintain diversity in harsh environments where species often rely on each other to persist (Cavieres & Badano 2009). Positive species interactions can also govern the stability (Butterfield 2009), productivity (Mulder et al. 2001) and energy flux (Ernst & Banks 2002) of ecosystems. Despite increasing recognition of the role played by positive species interactions, their generality and predictability in communities remain unresolved.

Numerous studies on positive species interactions have focused on testing the stress-gradient hypothesis (SGH, Bertness & Callaway 1994). According to the SGH, facilitation in communities increases and competition decreases with increasing abiotic/biotic stress (the ‘stress’ here and hereafter covers disturbances defined in Grime 1979). Despite hundreds of field experiments and intense discussions over recent decades, ecologists still do not agree on the generality of the SGH (Maestre et al. 2005; Brooker 2006; Lortie & Callaway 2006; Callaway 2007). Diverse stresses (e.g. physical, resource, grazing), species characteristics (e.g. origins, life histories, functional traits) and ecosystem types have been suggested to preclude the existence of a widely applicable model of how species interactions shift with increasing stress (Lortie & Callaway 2006; Maestre et al. 2009).

It is generally accepted that facilitation increases with increasing physical stresses like salinity in coastal marshes (e.g. Bertness & Hacker 1994; Bertness & Ewanchuk 2002) and cold in alpine grasslands (e.g. Callaway et al. 2002; Badano et al. 2007). In contrast, mixed evidence for the SGH has been reported in studies on water/rainfall gradients in arid and semi-arid ecosystems (e.g. Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Armas & Pugnaire 2005; Holzapfel et al. 2006). Many have questioned the generality of the SGH, suggesting that the SGH may not be applicable to gradients in resources, such as water and nutrients (Maestre et al. 2005, 2009; Michalet 2007), and that at high levels of resource limitations, resource consumption and competition dominate plant relationships (Maestre et al. 2009). It has also been argued that biotic stress (herbivory) may lead to patterns of species interactions along stress gradients differing from abiotic factors (Smit et al. 2009).

Others have asked whether traits of interacting species can affect species interactions along stress gradients (Lortie & Callaway 2006; Castanho et al. 2012). Many traits including growth form (a trait in...
the broad sense; Cornelissen et al. 2003; but see Violle et al. 2007), life history, stress tolerance, competitive ability and origins (native vs. exotic) are increasingly found to mediate the outcome of plant interactions. For example, herbs often have strong negative effects while shrubs have more facilitative effects (Gómez-Aparicio 2009); juvenile plants are more likely to be beneficiaries, but may turn to be competitors with age (Tewksbury & Lloyd 2001; Shultz et al. 2007); exotic species can be more competitive than natives (Vilà & Weiner 2004). Moreover, stress-tolerant species are more likely to be benefactors, while stress-intolerant species are often beneficiaries (Liancourt et al. 2005; He et al. 2012). If such traits determine the outcome of species interactions, will they affect how species interactions change along stress gradients? A recent review incorporated species’ stress tolerance and competitive ability to refine the SGH (Maestre et al. 2009), and empirical studies are also testing whether plant growth form, life history stage and origins can mediate how species interactions change along stress gradients (Castanho et al. 2012).

It has been also suggested that contradictions in the generality of the SGH among studies may be caused by methodological differences. For example, studies often differ in their measures of fitness, and those reporting survival could draw different conclusions from those on growth or reproduction (Goldberg et al. 1999; Gross et al. 2010). Results from experimental studies may also differ from descriptive studies (Maestre et al. 2005; Michalet 2006), and studies of long-durations and broad stress gradients may produce different findings than those of relatively short-durations and narrow gradients (Holmgren & Scheffer 2010; Lortie 2010; le Roux & McGroech 2010).

Recent reviews and modelling studies have tried to resolve the generality of the SGH in light of variation in stress types, plant traits and methodologies (Maestre et al. 2009; Holmgren & Scheffer 2010; Malkinson & Tielbörger 2010). These studies articulate apparent contradictions that cloud the generality of the SGH and identify factors that have generated disagreement. Generally, however, revised hypotheses have not been tested empirically or through quantitative syntheses of existing empirical studies. Individual empirical studies are often limited to examining one or a few species/stress in a specific habitat. Recent meta-analyses have examined the generality of the SGH in arid ecosystems or a small number of well-cited studies (Maestre et al. 2005; Lortie & Callaway 2006; Lortie 2010), but the global generality of the SGH remains to be tested by synthesising the studies that have accumulated over the last several decades.

Here, we present a global synthesis of plant interactions along stress gradients. We focus on interactions among plants because they are the most broadly studied group along stress gradients. Based on extensive literature searches and author data requests, we collected 727 tests of shifts in plant interactions with stress from 206 studies from six continents. Using this global dataset and a number of statistical validations, we test the generality of the SGH. In particular, we test whether facilitation among plants predictably increases and competition decreases with stress and whether this pattern is general across different stresses, plant traits, climates, ecosystems, and methods of investigation. Our results reveal that the SGH is generally applicable to species and ecosystems across the globe, though the strength of the shift towards facilitation with stress can vary depending on the above factors previously identified by ecologists.

**MATERIALS AND METHODS**

**Scope of the meta-analysis**

Our meta-analysis included plant community studies of non-vascular or vascular plants in marine, freshwater or terrestrial habitats. We defined plant interactions as the net outcome of the competitive and facilitative components of interactions that co-occur between plants (Brooker & Callaghan 1998; Bruno et al. 2003), and stress as any biotic, physical, or resource factor that can reduce three measures of fitness: survival, growth and reproduction (Grime 1979; Menge & Sutherland 1987). Resource factors include water, nutrients and light. Physical factors are any abiotic non-resource factor like salinity, cold and wind. For biotic factors that can reduce plant performance, we considered only herbivory due to sample size limitations.

We used the stress gradient identified in each study and contrasted plant interactions at low and high stresses to test if studies conducted around the globe supported the generality of the SGH. We took this approach rather than synthesising a new stress gradient based on absolute values of environmental factors (e.g., aridity, salinity) or primary productivity, because (1) absolute values of environmental factors may not linearly reflect the severity of stress experienced by plants; and (2) we focused on tests of the SGH where there were no changes in the identity of interacting species, whereas species turnover may occur when using primary productivity to synthesise new stress gradients. Using study-specific stress gradients also has the advantage of reducing the effects of methodological variation among studies. Most (~95%) studies had only two or three stress levels, which allowed categorical comparison, but precluded testing nonlinear relationships. We focused on testing the generality of the SGH on the following variables: (1) stress type: physical, resource and biotic, (2) plant traits: growth form (non-vascular, herb, grass, shrub and tree, for target and neighbour plants respectively), life history (annual, juvenile perennial and adult perennial) and origin (native vs. exotic), (3) ecosystem: arctic/alpine, coastal/marine, freshwater wetland, grassland/savanna (including steppe and desert), forest/woodland, old field and common garden and (4) climate: tropical, arid, Mediterranean, temperate and cold. Note that savanna and woodland are both transitional between grassland and forest, but savannas are areas with continuous grass layers and scattered overstory trees (Peterson et al. 2007). We also tested if the applicability of SGH can be affected by the following additional variables: (1) stress gradient length, (2) stress gradient nature: the way the examined stress gradient was created, experimental, temporal or spatial, (3) study approach: descriptive vs. experimental and (4) study duration.

**Building the database**

To compile a comprehensive list of publications on plant interactions across the globe, we searched Web of Science (1980–2011) using the following search item: TS = (competition OR facilitation OR interaction) AND TS = (salinity OR nutrient OR nitrogen OR light OR grazing OR herbivore* OR predation OR water OR moisture OR disturbance OR exposure OR flooding OR burial OR wind OR cold OR thermal OR heat OR trampling OR sedimentation OR temperature OR fertilizer* OR drought OR resource OR precipitation OR salt stress OR rainfall OR acidity OR UV radiation OR...

We examined the resulting studies and retained only those that: (1) were conducted in the field or a common garden, (2) investigated the same plant interactions at different stress levels, (3) determined the survival, growth or reproduction of target plants with and without neighbours, (4) had a stress gradient length > 0.1 and (5) did not have experimental design problems. Detailed descriptions of the above selection criteria and example studies that did not meet the criteria are provided in Text S1 in Supporting Information. Criterion 2 was used, as a number of previous tests of the SGH, especially descriptive studies, had substantial species turnover at different stress levels, i.e. either target species or their neighbours changed. These studies were excluded as the effect of stress on species interactions cannot be separated from that of species turnover. To reduce interdependence, we only included studies with a temporal gradient if they used different plots (when the response variables were determined on a plot basis) or different individuals (when the response variables were determined on a plant individual basis) in different years. Criterion 4 was used because the assignment of stress levels was arbitrary in some studies and did not test if the stress imposed at high stress reduced plant performance. To avoid this (Lortie & Callaway 2006; Callaway 2007), we computed a stress gradient length index: $l_{sg} = (P_L - P_H)/P_L$, where $l_{sg}$ is the stress-gradient length, $P_L$ is the performance of the target plant without neighbours at low stress and $P_H$ at high stress. In our study, $l_{sg}$ varies between 0.1 and 1, and all studies with $l_{sg} < 0.1$ were excluded (e.g. Fig. 3 and 5 data of Bockelmann & Neuhaus 1999; Fig. 2b data of Smit et al. 2007). This means that the performance of target plants at high vs. low stress was reduced by at least 10%, to ensure that all stress gradients used in our study were valid.

For each study that met the above criteria, we extracted the performance data with and without neighbours at low and high stress by collecting them from tables or digitising from figures. To incorporate as comprehensive a dataset as possible and collect as many unpublished data as possible, for studies published after 1995 we contacted authors for data if sample sizes, standard errors, or standard deviations were not shown, or if the authors mentioned that they determined a response variable suitable for this study but did not present it, or if the data were presented as means (standard errors) pooled across treatments. The type of data collected from each study, and their source (table, figure, text or author) are provided in Dataset S1. We also recorded the following variables that may affect the generality of the SGH as described above: stress type, stress factor (e.g. salinity, nutrient, water), stress nature; name, growth form, life history and origin of interacting species; ecosystem and climate; and study approach and duration (estimated on the basis of year, growing season or month). The assignment of the above variables generally followed those assigned by the author(s). For species traits, if target species or their neighbours were mixtures of species with different traits, we used the traits of the dominant species (as the authors described), or defined them as “mixed” if dominant species were not explicitly described. If not described in a study, the growth form, life history and origin of interacting species were determined by searching the Plants Database (http://plants.usda.gov), The Euro + Med PlantBase (http://www2.bgbm.org/EuroPlusMed/query.asp), eFloras (http://www.efforas.org), or searching for other scholarly records on Google. If a plant trait could not be determined, it was excluded from the analysis on that trait. Climate was assigned using the climatic zones of the Köppen–Geiger system (Kottek et al. 2006). We combined snow and polar climates as “cold” climate, and separated Mediterranean from temperate climates.

Meta-analysis

We summarised survival data in $2 \times 2$ contingency tables and calculated odds ratios as the log of the ratio of the odds of survival with and without neighbours (Borenstein et al. 2009). For growth and reproduction data, we calculated Hedges’ $g^*$, which measures the unbiased, standardised mean difference (Borenstein et al. 2009) in performance between treatments with and without neighbours. For both log odds ratio and Hedges’ $g^*$ effect sizes, negative values indicate competition while positive values indicate facilitation. These effect sizes quantify the intensity, not the importance, of species interactions (Jonsén Kikvidze et al. 2011). Although interaction importance and intensity can change differentially along stress gradients (Brooker et al. 2008; Kikvidze et al. 2011), interaction importance cannot be quantified for most studies.

Using mixed-effect models (Borenstein et al. 2009), we estimated mean effect sizes at each of the low and high stress levels for the entire dataset and its subsets. Subsets were obtained by dividing the dataset by the following mediating variables: stress type, target traits, neighbour traits, climate, and ecosystem (only by stress type for reproduction due to low sample size). Testing potential interactions among the above mediating variables were impossible due to the required sample size. Mean effect sizes are considered significantly different from zero when their 95%-confidence intervals do not overlap zero. We used the between-group heterogeneity of the mixed-effect models (a weighted sum of squares following a $\chi^2$ distribution describing variation in effect size between groups) to test if effect size differed between low and high stress. Following Gibson et al. (2011), we repeated this procedure using 999 bootstrap samples and estimated their median effect sizes and between-group heterogeneity. To minimise the influence of differences in stress-gradient length among subsets (Lortie & Callaway 2006; Callaway 2007), the 999 bootstrap samples were generated by resampling with equal probability for every 0.05 change of $l_{sg}$ (if missing, the probability of the gradient length closest to the missing and the intermediate stress-gradient length 0.50–0.60 were multiplied). Except in a few cases where the stress-gradient length was highly biased due to low sample size, the 999 bootstrap samples had a median stress-gradient length of ~0.55 that was approxi-
mately the mean of the raw gradient length data (see Table S1, S2, S4).

To examine the robustness of our results, we supplemented the above analysis in three ways. First, we estimated mean effect sizes at each of the low and high stress levels for the dataset and its subsets by the mediating variables using mixed-effect models on the raw data with no resampling. Second, to address potential autocorrelation, we calculated mixed-model effect sizes for the dataset and its subsets using 999 bootstrap samples generated with replacement and estimated their median effect sizes and between-group heterogeneity. In consideration of potential autocorrelation from publications that included multiple tests of the SGH, we calculated mixed-model effect sizes for the dataset by resampling one test per publication, again using 999 bootstrap samples (Gibson et al. 2011). Third, to address the dependence of the two effect sizes (low and high stress) from the same study, we calculated a difference score between low and high stress and used a random-effect model to estimate mean difference scores for the dataset and its subsets by each of the mediating variables. Difference score was calculated as (effect size at high stress) – (effect size at low stress), and variance of the difference score as (variance at high stress) + (variance at low stress) (Borenstein et al. 2009). Significant positive mean difference scores indicate increasing positive interactions with stress, and vice versa.

To address the influence of stress-gradient length on the SGH (Lortie & Callaway 2006; Callaway 2007), we categorised the dataset into three subsets by stress gradient length \( l_{sg} = 0.1–0.3 \) (narrow), 0.3–0.6 (intermediate) and 0.6–0.9 (broad), respectively, and used mixed-effect models to estimate mean effect sizes at low and high stresses for each subset. Difference scores were similarly estimated using random-effect models. To examine influences of methodological differences, we estimated mean effect sizes at low and high stresses for the dataset’s subsets by stress-gradient nature, study approach and study duration.

**Tests of publication bias**

We used two approaches to assess publication bias. First, we visually examined funnel plots of effect size standard errors against effect size residuals based on mixed-model effect size calculations (Figure S1). The funnel plots suggest that for survival, there is no publication bias. For growth and reproduction, however, the funnel plots are asymmetrical due to some data with large, negative residual values and high variances. We removed these data (see Dataset S1) to adjust the publication bias for our analysis described above. Effect size calculations after removing these studies had little influence on our results (Table S2, S4). Second, we repeated random-model difference score calculations for the dataset and its subsets by each of the mediating variables before and after adjusting the publication bias quantitatively using the trim and fill method, a non-parametric data augmentation technique that estimates the number of studies missing due to the suppression of the most extreme results on one side of the funnel plot (Borenstein et al. 2009). Adjusting publication bias using this method did not compromise our results (Table S3), so we concluded that the influence of publication bias on our results was negligible. We conducted mixed/random-model effect size calculations and publication bias tests using metafor package (Viechtbauer 2010), and other analyses in R v2.13 (R Development Core Team 2011).

**RESULTS**

Of the 727 tests of plant interactions along stress gradients, 205, 452 and 70 examined the responses of survival, growth and reproduction respectively. Across the entire dataset, plant interactions measured as survival shifted from highly competitive to highly facilitative with increased stress, while plant interactions measured as growth and reproduction also shifted towards facilitation, but remained competitive (Table S1–S4). The results were robust to publication bias, data autocorrelation and interdependence (Table S1–S4). All results were based on the 999 resampled (with equal probability for different stress-gradient lengths) mixed-model effect size calculations, except where noted.

**Stress type**

We found decreasing competition and increasing facilitation with increasing biotic, physical and resource stresses (Fig. 1). For survival, increases in biotic stress shifted interactions from highly competitive to highly facilitative, and increases in resource stress that included water, nutrients and light shifted interactions from neutral to highly facilitative. For physical stresses that included salinity, cold and wind exposure, interactions were highly facilitative even at low stress, but grew increasingly positive with increased stress. For growth and reproduction, increases in biotic, physical and resource stresses often shifted plant interactions from highly competitive to less competitive or neutral, except for growth with physical stresses where interactions shifted from highly competitive to highly facilitative with increasing stress and for reproduction with physical stresses where we found no change with stress. Generally, we found the same results when additional analyses were done using: (1) raw data without resampling, (2) resampled data with replacement, (3) difference scores that accounted for data interdependence and (4) difference scores with bias adjusted, except for reproduction with physical stress (Table S1–S4). For reproduction with physical stress, all additional analyses showed significant shifts in interactions from highly competitive to neutral with increased stress (\( P < 0.05 \)).

**Plant traits**

Examining survival across all traits (growth forms, life histories and origins of neighbours and targets), we found significant increases in facilitation and decreases in competition with stress for all 21 plant traits, except for juvenile perennial neighbours whose competitive effect did not change with stress (\( P > 0.05 \); Fig. 2 and 3). For growth, we found reduced competition with stress for 21 traits, shifts from competition to facilitation for one trait (neighbouring shrubs), and no significant change for four traits (Figs. 2 and 3). Stress did not increase competition for any plant trait or fitness measure.

Our results showed that plant traits can predictably dictate the strength and nature of species interactions, especially when performance was measured by survival. For growth forms, grasses and herbs often exhibited highly competitive responses and effects at low stress (Fig. 2a, b). In contrast, trees often exhibited strong facilitative responses and effects (Fig. 2a, b). Shrubs exhibited competitive responses but facilitative effects at low stress (Fig. 2a, b). For life histories, annuals often had strong competitive responses and effects at low stress, juvenile perennials often had neutral responses.
and effects, and adult perennials had competitive responses but neutral effects (Fig. 3a, c). For origins, exotic species often had strong competitive responses and effects at low stress, while natives had both neutral responses and effects (Fig. 3a, c). When plant performance was measured by growth, however, species of most growth forms, life histories and origins exhibited strong competitive responses and effects at low stress, though the intensity of competition varied (Figs. 2 and 3). Interestingly, growth forms, life histories and origins, regardless of the magnitude of their competitive effects/responses, always showed decreasing competition and increasing facilitation with stress. Typically, highly competitive species had decreased competitive or neutral effects at high stress, whereas less competitive species had strong facilitative effects at high stress (Figs. 2 and 3).

When autocorrelation, interdependence and publication biases within in the dataset were taken into account with additional analyses, the results consistently showed that for the majority of plant traits examined, plant interactions shifted towards facilitation or decreased competition with increasing stress; for a few plant traits, plant interactions did not change; and we never found shifts in plant interactions towards competition for any fitness measure or plant traits (Table 1, Table S1–S3).
We found consistent shifts towards facilitation or decreased competition with increasing stress across climates and ecosystems (Fig. 4). When measured as survival, changes in interactions with increasing stress were not detected in arid climates, but they were significant when measured as growth \((P < 0.05)\). In Mediterranean and cold climates, interactions measured as survival were neutral at low stress and facilitative at high stress. Interactions measured as growth, on the other hand, were competitive at low stress, but tended to be neutral at high stress. In contrast, in temperate climates, interactions measured as survival shifted from competitive at low stress to facilitative at high stress, though competitive effects on growth were reduced but remained strong even at high stress (Fig. 4a, b). With additional analyses, we found that these results were generally robust (Table S1-S3), except that: (1) for arid climates, tests using difference scores that accounted for data interdependence showed significant shifts in plant interactions towards facilitation with increased stress; and (2) when publication biases were adjusted, we found significant shifts towards facilitation with increased stress for

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**Ecosystems and climates**

We found consistent shifts towards facilitation or decreased competition with increasing stress across climates and ecosystems (Fig. 4). When measured as survival, changes in interactions with increasing stress were not detected in arid climates, but they were significant when measured as growth \((P < 0.05)\). In Mediterranean and cold climates, interactions measured as survival were neutral at low stress and facilitative at high stress. Interactions measured as growth, on the other hand, were competitive at low stress, but tended to be neutral at high stress. In contrast, in temperate climates, interactions measured as survival shifted from competitive at low stress to facilitative at high stress, though competitive effects on growth were reduced but remained strong even at high stress (Fig. 4a, b). With additional analyses, we found that these results were generally robust (Table S1-S3), except that: (1) for arid climates, tests using difference scores that accounted for data interdependence showed significant shifts in plant interactions towards facilitation with increased stress; and (2) when publication biases were adjusted, we found significant shifts towards facilitation with increased stress for...
tropical climates and no change for Mediterranean climates (Table S3).

Across ecosystems (Fig. 4c, d), we found most pronounced changes in interactions with stress for survival in coastal/marine, wetland and grassland/savanna ecosystems, and significant change for growth in all ecosystems. For survival, species interactions were highly competitive at low stress in coastal/marine, freshwater wetland and grassland/savanna ecosystems, but tended to shift to facilitative with increased stress; species interactions in forest/woodland ecosystems were highly facilitative at low stress, and grew increasingly positive with increased stress; in other ecosystems, plant interactions were neutral at both low and high stress, and no change was detected. For growth, however, competitive interactions were reduced but remained strong even at high stress in all kinds of ecosystems except that: (1) in arctic/alpine ecosystems interactions were neutral at low stress, but significantly facilitative at high stress and (2) in forest/woodland ecosystems, interactions were highly competitive at low stress, but neutral or facilitative at high stress. The above results held when different analytical methods were used and when autocorrelation, interdependence and publication biases were considered, except that for growth we found no shifts in plant interactions with increased stress for common garden ecosystems when examined using different scores (Table S1–S3).

**Influence of stress gradient length**

For all fitness measures, we found significant shifts in plant interactions towards facilitation or decreased competition with increased stress for all narrow ($l_{sg} = 0.1–0.3$), intermediate ($l_{sg} = 0.3–0.6$) and broad ($l_{sg} = 0.6–0.9$) stress gradients (Fig. 5). Tests using difference scores yielded similar results (Table S3). Based on random-effect models, mean difference scores for narrow, intermediate and broad stress gradients were 0.65, 0.68 and 1.03 for survival, 0.21, 0.37 and 0.61 for growth, and 0.36, 0.47 and 0.65 for reproduction, respectively, suggesting larger shifts towards facilitation with larger shifts in stress.

**Methodological differences**

We found that shifts towards facilitation or decreased competition with increasing stress were generally evident in both experimental and descriptive studies, in studies of different durations, and in studies using temporal, spatial or experimentally created stress gradients (Fig. 6). The few exceptions were: for survival, we found no shifts with increasing stress in studies with > 3-year durations and in those examining spatial stress gradients; and for growth, we found no shifts in studies examining temporal gradients (Fig. 6).

**DISCUSSION**

Our synthesis of > 700 tests conducted in six continents presents a unique global perspective of how plant interactions change along stress gradients. Our results reveal that plant interactions generally change with increased environmental stress, and always in the direction of a shift to facilitation (typical for survival responses) or a reduction in competition (typical for growth and reproduction responses). In a limited number of cases, like plant reproductive response with physical stress and effects of non-vascular and juvenile...
nile perennial neighbours, plant interactions do not change with stress, but they never shift towards competition with stress. These findings are generally consistent across stress types, plant growth forms, life histories, origins, climates, ecosystems, and methodologies, though the outcome of plant interactions and the magnitude of their shifts towards facilitation with stress vary depending on these factors.

Our results suggest that variation in fitness measure has a large impact on the outcome of plant interactions (Goldberg et al. 1999; Howard & Goldberg 2001; Gómez-Aparicio 2009). When measured as survival, plant interactions are often facilitative, particularly at high stress; in contrast, when measured as growth and reproduction, plant interactions are often competitive. Nevertheless, our results show that fitness measure does not influence the overall pattern of shifts towards facilitation with increasing stress. The key difference is that for survival, plant interactions shift to facilitation at high stress, while for growth and reproduction, shifts are a reduction of competition.

**Stress type**

Our results reveal that shifts in plant interactions towards facilitation with increasing stress are generally evident across different stress types, though the magnitude and nature of the shifts vary with stress type. For example, physical stresses often shift plant interactions measured as growth from highly competitive to facilitative, while biotic and resource stresses simply decrease the intensity of competition. These differences between stress types may contribute to the disparity between studies. Moreover, the departure of several field studies on water/drought gradients (e.g. Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Armas & Pugnaire 2005; Holzapfel et al. 2006) from the trend that emerged in our global dataset, where we observe shifts to facilitation or reductions in competitive interactions for resource gradients that included water/drought, may have arisen for several other reasons described below:

First, some studies did not work on a functional stress gradient that reduced the performance of target plants at high stress (see also Lortie & Callaway 2006; Lortie 2010). For example, Maestre & Cortina (2004) worked along a rainfall gradient in an arid ecosystem. They found no evidence for the SGH, as the effect of the tussock grass *Stipa tenacissima* on the shrub *Pistacia lentiscus* was competitive at both ends of the rainfall gradient (their assumed stress gradients). Re-analysis of their data, however, revealed that the rainfall gradient did not limit the performance of *S. tenacissima* in bare patches, so did not have any stress effects (Figure S2). In fact, a simple regression of interaction intensity and the performance of the target plant in no neighbour treatments (a measure of stress, see Kawai & Tokeshi 2007 and additional discussions in Figure S2) revealed significant increases in facilitation with stress. Whether other studies that found no shifts towards facilitation with increasing stress (e.g. Bowker et al. 2010; Granda et al. 2012) have resulted from a similar effect remains unclear, but the functionality of stress gradients was assessed in neither study. Also, both studies used
co-occurrence indices as estimates of species interactions, and such methods have known limitations (Hastings 1987). Second, studies may not find shifts towards facilitation with increasing stress if they were confounded by temporal effects. For example, tests of the SGH may compare the performance of the same individuals (or permanent plots) of a species with and without neighbours in years of different stress severity. But, the outcome of plant interactions has been shown to depend on ontogeny (Armas & Pugnaire 2005; Miriti 2006; Reisman-Berman 2007; Shultz et al. 2007). Third, studies may substantially change either target species or neighbours across stress levels. For example, plant zonation studies often transplant the same target species to zones that differ in both levels of stress and neighbouring vegetation, thereby examining their interactions with different neighbours (e.g. Pennings & Callaway 1992). In these studies, the effect of stress on species interactions cannot be separated from that of species turnover, so they should not be considered as tests of how the same plant interactions change along stress gradients, but a previous meta-analysis on this (Maestre et al. 2005) nevertheless included such studies. Additional example studies with different neighbours/targets at different stress levels are provided in Text S1.

**Plant traits**

Our finding that plant traits strongly influence the outcome of plant interactions agrees with previous studies (Gaudet & Keddy 1988; Tilman 1988). Neighbour traits have been thought or found to be more important than target traits in determining interaction outcomes (Callaway 2007; Gómez-Aparicio 2009). Our global synthesis, however, reveals that both target and neighbour traits are important. For growth forms, grass targets and neighbours are strong competitors, likely due to fibrous roots and large root:shoot ratios allowing grasses to compete for soil resources (Caldwell & Richards 1986; Gómez-Aparicio 2009). In contrast, tree targets are beneficiaries of facilitation, because they are late successional and often intolerant of stress (Gómez-Aparicio 2009), making them more dependent on amelioration of environmental stress by neighbours, while tree neighbours are often benefactors due to large above-ground size that shades, retains water/nutrients and protects beneficiaries from herbivory (Callaway & Walker 1997; Callaway 2007). For life histories, our results are consistent with current hypotheses that juveniles are more likely than adults to be beneficiaries of facilitation as they are more susceptible to environmental stress (Callaway & Walker 1997; Miriti 2006). When measured as survival at low stress, annual targets and neighbours were stronger competitors than perennials, consistent with Gómez-Aparicio (2009). For origins, our finding that competition typically characterised interactions involving exotic neighbours and targets while native neighbours and targets exhibited neutral interactions is consistent with invasion ecology hypotheses (Levine et al. 2003; Vilà & Weiner 2004). It should be noted, however, that grasses have been identified as facilitators (Bertness & Ewanchuk 2002; Van Uytvanck et al. 2008), shrubs/trees as competitors (Dullinger et al. 2005), and exotics as facilitators (Yang et al. 2009) under certain conditions. So while our study identified general patterns across many studies, the outcome of plant interactions is the product of the traits of both target and neighbour species and the stress conditions of their specific habitats.

Likely due to the influences of traits on plant interactions, some previous studies have suggested refinements of models of how species interactions shift with stress (Maestre et al. 2009). However, our results show that species with both strong and weak competitive traits generally support decreasing competition and increasing facilitation with stress. The key difference is that highly competitive species have decreased competitive or neutral effects at high stress, whereas less competitive species have strong facilitative effects at high stress. We did find that interactions of some species with particular traits (e.g. non-vascular neighbours on growth, juvenile perennial neighbours on survival, and targets of mixed life histories on growth) did not shift with increasing stress. However, in these cases, often very small sample sizes were available (n < 13), except for the effects of non-vascular neighbours on growth. These results based on small sample sizes should be viewed with caution, and are areas that deserve further study, as the estimate of the between-studies variance will have poor precision when sample sizes are small (Borenstein et al. 2009). Why the effects of non-vascular neighbours on growth did not change with increasing stress remains unclear, but non-vascular plants may have different growth strategies than vascular plants (Marion et al. 1982; Bret-Harte et al. 2004).

**Climates and ecosystems**

Our study shows that plant interactions vary with climates and ecosystems. Previous studies on facilitation have often focused on cold or arid climates/ecosystems. Our results reveal that when measured as survival, plant interactions are more positive in cold than in temperate climates (see also Gómez-Aparicio 2009), but strong effects of facilitation are not necessarily restricted to climates/ecosystems that are traditionally considered stressful. Early establishment of plants is sensitive to variation in environmental stress that can occur in various ecosystems. There are also empirical studies that found facilitation to be essential for seedlings in moister or warmer ecosystems, such as temperate or tropical forests (Ganade & Brown 2002; Pages & Michalet 2003). Holmgren & Scheffer (2010) suggest that moister or warmer ecosystems may be just apparently benign and that species present there can still be stressed. A recent meta-analysis on the role of facilitation in restoration has also revealed strong effects of facilitation on plant survival in tropical ecosystems (Gómez-Aparicio 2009). In contrast, when measured as growth, plant interactions strongly depend on climate and ecosystem, being less competitive and more facilitative in cold and arid climates than in temperate and Mediterranean climates. This provides global evidence for the idea that plant competition is less common in arid and semi-arid than in humid regions (see Fowler 1986); and competition may also be weaker in arid and semi-arid regions. The effects of plant interactions on growth have also been shown to be more negative in temperate and wetland systems than in semi-arid systems in a previous meta-analysis (Gómez-Aparicio 2009).

Despite variation in the outcome of plant interactions with climate and ecosystem, our study shows no support for the argument that the generality of the SGH is constrained to specific ecosystems. Species present in a given ecosystem are adapted to the local conditions (Holmgren & Scheffer 2010), and increased environmental stress will generally lead to deviations from their evolved optima where facilitative interactions with neighbours are expected to increase (Choler et al. 2001; Wang et al. 2008). Where two previous widely cited studies found no increase in positive interactions with stress in arid ecosystems (Maestre & Cortina 2004; Maestre et al. 2005), stricter re-analyses of their data showed increasing facilitation.
and decreasing competition with stress (Lortie & Callaway 2006; Callaway 2007; Figure S2). We found very few studies for tropical dry forests/coasts and no studies for tropical rainforests, so the tropical patterns with stress should be viewed with caution and as an opportunity for future empirical work.

**Influence of stress gradient length**

Except in a few cases with small sample sizes, plant performance at high stress without neighbours in our study was reduced by on average ~ 55% relative to low stress (ranging between 10% and 100%). It has been suggested that along stress gradients of different lengths, different forms of shifts in species interactions will be observed (Kawai & Tokeshi 2007; le Roux & McGeoch 2010). Our study reveals that along narrow, intermediate and broad stress gradients, plant interactions consistently shift towards facilitation; and with wider stress gradients, the shifts are larger. Some empirical studies have shown that the relative strength of facilitation reaches an asymptote (le Roux & McGeoch 2010), or reaches a peak and then decreases to neutrality (Levenbach 2009) at extremely stressful conditions. Our results based on low vs. high stress comparisons, however, are limited from substantiating nonlinear forms of the relationship between net species interactions and stress. Our results do show that along wide stress gradients where plant performance can be reduced by 60–90% at high vs. low stress, plant interactions remain significantly more positive at high than at low stress. Studies along stress gradients as wide as the entire range of examined species have also found support for increasing facilitation with stress (Armas et al. 2011; Dohn et al. 2013; re-analysis of Maestre & Cortina 2004 in Figure S2).

Conditions that fall outside the realised niches of target species have also been put forth as tests of the SGH (see He et al. 2011). Although these conditions can occur naturally, such as during climatic extremes (Koyama & Tsuyuzaki 2013), along intertidal stress gradients (Bertness et al. 1999) and in extremely grazed habitats (Levenbach 2009; Le Bagousse-Pinguet et al. 2011), they represent cases where stress amelioration by neighbours, though present, will be insufficient to positively affect target species (He et al. 2011). We suggest that while stress amelioration can have the paradoxical effect of making the realised niche larger than the fundamental niche of species (Bruno et al. 2003), the SGH should be applied only within the realised niche of a plant (including the part that exist due to facilitation).

**Methodological differences**

Our study shows no support for the idea that methodological differences among studies can strongly influence how species interactions shift with stress (Maestre et al. 2005; Michalet 2006), although subtle distinctions do exist. Plant interactions reported in descriptive studies are often facilitative or neutral, while those reported in manipulative studies are often competitive, at least at low stress. This may be because plant interactions in descriptive studies have often been examined by comparing the performance of target plants with neighbours possessing conspicuous, potentially facilitative, aboveground structure and those without neighbours in open areas. Moreover, experiments can put plants into unstable competitive interactions and configurations that would not persist nor be observed under natural conditions. We found no evidence for stronger competition with longer study durations, possibly because different functional groups are typically selected for studies of different durations (see also Gómez-Aparicio 2009). Studies of short durations often examined herbs and grasses, while those of longer durations often examined trees and shrubs (Table S5).

Despite little evidence for the influence of methodological variation within our dataset, while building the dataset we found that some purported tests of the SGH (described above) can be compromised by methodological issues (see also Lortie & Callaway 2006). We suggest that future tests of the SGH should utilise identical definitions of stress, critically evaluate the functionality of their gradients and follow standardised protocols to avoid problems that may compromise valid tests of the SGH. Lortie (2010) provided detailed recommendations for that. For example, effect sizes and variances at examined stress levels should be reported (see Caviezas & Sierra-Almeida 2012). We concur and our study selection criteria follow his recommendations, but with the following caveats: (1) stress should be defined at the plant’s perspective, not compromised by unidentified co-varying factors (Michalet 2006) and stress gradients should be verified against environmental gradients (Shipley 2010); and (2) species identity and ontogenetic stage should be held constant across the levels of stress.

**Limitations**

Our study has several limitations. First, our results should be interpreted as general patterns that may differ from results reported in some specific systems/species. Second, our synthesis is limited to comparing species interactions at two points (low vs. high) of stress by data availability. Recent studies of species interactions across multiple stress levels (Callaway et al. 2002; Kawai & Tokeshi 2007; Levenbach 2009; le Roux & McGeoch 2010) have documented nonlinear relationships between species interactions and stress, which should be further explored. Nevertheless, all narrow, intermediate and broad stress gradients support increases in positive interactions with stress, and we never found shifts towards competition with increasing stress in any case, indicating that our results should be generally applicable to stress gradients of various lengths. The general trends in our study are also consistent with several previous meta-analyses (Lortie & Callaway 2006; Lortie 2010; Dohn et al. 2013).

**Concluding remarks**

The study of positive species interactions has been heavily influenced by the SGH. However, as increasingly recognised and supported by our synthesis, positive species interactions are a function of not only the severity of stress but can also be fundamentally determined by other factors including plant traits. Although future tests of the SGH, especially along multiple stress gradients, and in less explored taxa (e.g. animals) and systems (e.g. tropical forests), should be encouraged, we suggest that research should move forward by taking a multi-factorial approach that considers variables such as plant traits in addition to stress to understand facilitation in communities. Furthermore, we hope that in addition to basic ecological research that has dominated the literature to date, future research will apply the SGH to understand how species and communities will respond to environmental change. Given the general relevance of the SGH as revealed in our study, we expect that the study of positive species interactions will continue to be a fruitful line of research where the biggest discoveries may be over the horizon.

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AUTHORSHIP

QH, MDB and AHA designed the research, wrote and revised earlier drafts of the manuscript. QH built the database and performed the analysis.

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