

REVIEWS AND SYNTHESIS

Global shifts towards positive species interactions with increasing environmental stress

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Abstract

The study of positive species interactions is a rapidly evolving field in ecology. Despite decades of research, controversy has emerged as to whether positive and negative interactions predictably shift with increasing environmental stress as hypothesised by the stress-gradient hypothesis (SGH). Here, we provide a synthesis of 727 tests of the SGH in plant communities across the globe to examine its generality across a variety of ecological factors. Our results show that plant interactions change with stress through an outright shift to facilitation (survival) or a reduction in competition (growth and reproduction). In a limited number of cases, plant interactions do not respond to stress, but they never shift towards competition with stress. These findings are consistent across stress types, plant growth forms, life histories, origins (invasive vs. native), climates, ecosystems and methodologies, though the magnitude of the shifts towards facilitation with stress is dependent on these factors. We suggest that future studies should employ standardised definitions and protocols to test the SGH, take a multi-factorial approach that considers variables such as plant traits in addition to stress, and apply the SGH to better understand how species and communities will respond to environmental change.

Keywords

Biotic interactions, community ecology, ecosystems and climates, environmental stress, facilitation, invasive species, meta-analysis, plant traits, the stress-gradient hypothesis.

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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; Stultz *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 & McGeoch 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 herbivor* 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 fertili* OR drought OR resource OR precipitation OR salt stress OR rainfall OR acidity OR UV radiation OR

hypoxia OR inundation OR waterlogging OR submergence OR browsing OR insect OR environmental gradient OR abiotic stress OR stress gradient) AND TS = (plant OR forb OR shrub OR herb OR grass OR tree OR algae OR phytoplankton OR cactus OR sedge OR seaweed OR seagrass OR kelp). We supplemented this database query by searching more generally for competition, facilitation and interactions in the following general ecological journals and those with a regional focus: *American Naturalist*, *Ecology*, *Ecological Monographs*, *Ecological Applications*, *Ecology Letters*, *Journal of Ecology* and *Oecologia*; *Ecological Research*, *Journal of Integrative Plant Biology*, *Journal of Plant Ecology*, *Acta Botanica Sinica* (Asia); *African Journal of Ecology* (Africa); *Biotropica*, *Austral Ecology*, *Australian Journal of Botany*, *Australian Journal of Ecology*, and *New Zealand Journal of Ecology* (southern hemisphere). Studies from two previous meta-analyses (Maestre *et al.* 2005; Lortie 2010) were also included.

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://ww2.bgbm.org/EuroPlusMed/query.asp>), eFloras (<http://www.efloras.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 2×2 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 (*sensu* 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 χ^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 $l_{sg} = 0.1\text{--}0.3$ (narrow), $0.3\text{--}0.6$ (intermediate) and $0.6\text{--}0.9$ (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

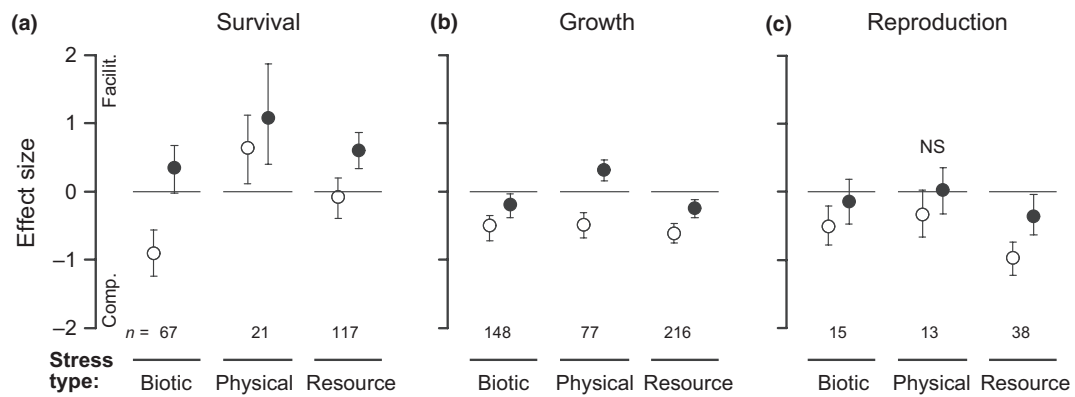


Figure 1 Plant interactions at low (open circles) and high (filled circles) stress sorted by stress type. (a) Survival, (b) growth and (c) reproduction. Shown are medians and 95%-confidence intervals of 999 resampled (with equal probability for different stress-gradient lengths) mixed-model effect size calculations. Plant performance was reduced by ~ 55% at high stress. Differences between low and high stress were estimated using the median between-group heterogeneity of the 999 resampled effect size calculations. All but those noted with NS are significant ($P < 0.05$; see Table S1, S2, S4).

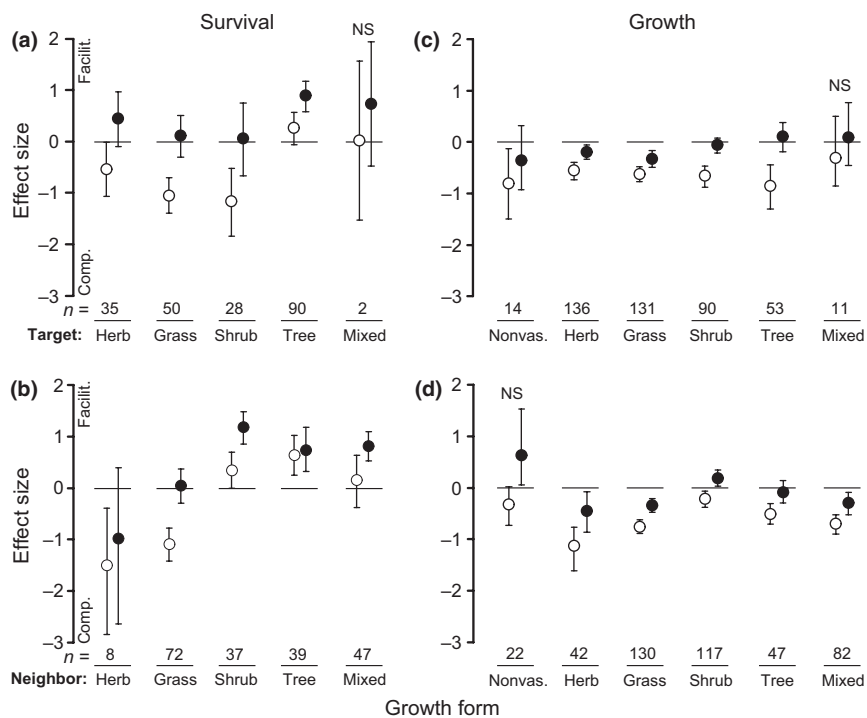


Figure 2 Plant interactions at low and high stress sorted by target (a, c) and neighbour (b, d) growth form. For traits, herb includes all herbaceous species other than grasses; nonvas. indicates non-vascular plants. Other details follow Fig. 1.

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 spe-

cies 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).

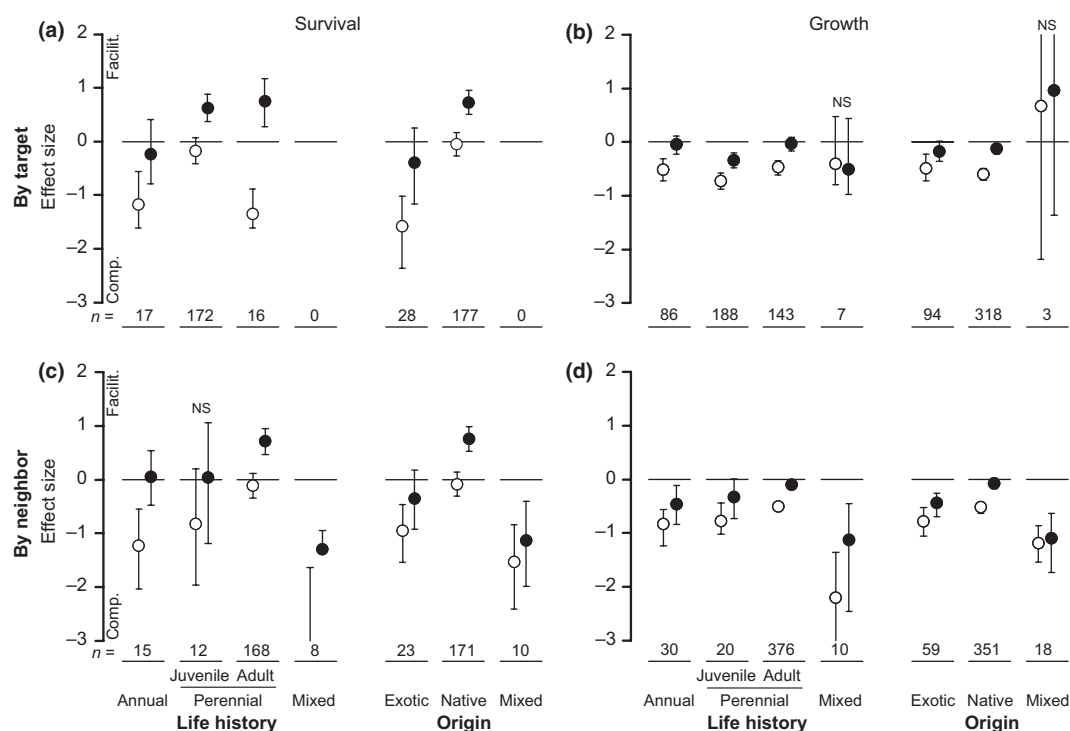


Figure 3 Plant interactions at low and high stress sorted by life history and origin of target (a, b) and neighbour (c, d) species. For life histories, annual includes seasonal, annual and biennial; juvenile perennial includes seedlings and saplings; and adult perennial includes vegetative reproduces and established vegetation prior to introduction of target plants. Other details follow Fig. 1.

Table 1 Summary of the generality of the SGH across plant traits. Five different tests were used to examine the robustness of the statistical results, using: (i) raw data, (ii) resampled data with replacement, (iii) resampled data with equal stress gradient length (ESGL), (iv) difference score and (v) biased-adjusted difference score respectively. Number of traits for each type of shift was at the significance level of $P < 0.05$. The traits for 'to facilitation' include those to decreased competition. In a few cases, the statistical requirements of each method were not met by the data structure (e.g. low sample size), so the total number of traits changed slightly with test method

Response variable	Tests	Total number of traits	Number of traits for		
			To facilitation	No change	To competition
Survival	Raw data	22	16	6	0
	Resampled data with replacement	21	18	3	0
	Resampled data with ESGL	21	20	1	0
	Difference score	22	19	3	0
	Biased-adjusted difference score	20	14	6	0
Growth	Raw data	26	22	4	0
	Resampled data with replacement	26	21	5	0
	Resampled data with ESGL	26	22	4	0
	Difference score	26	20	6	0
	Biased-adjusted difference score	26	20	6	0

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

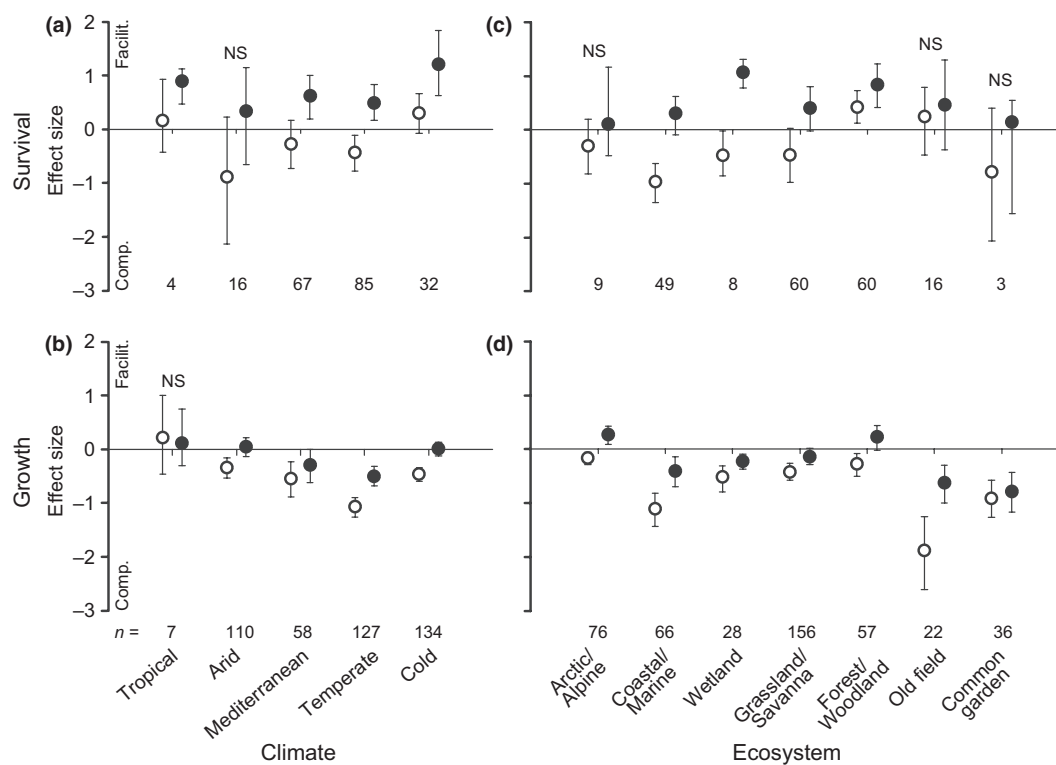


Figure 4 Plant interactions at low and high stress sorted by climate and ecosystem. (a) Survival by climate, (b) growth by climate, (c) survival by ecosystem and (d) growth by ecosystem. Grassland/Savanna includes shrubland, steppe and desert and Wetland indicates freshwater other than coastal and estuarine ones. Other details follow Fig. 1.

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 ($I_{sg} = 0.1–0.3$), intermediate ($I_{sg} = 0.3–0.6$) and

broad ($I_{sg} = 0.6–0.9$) 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 juve-

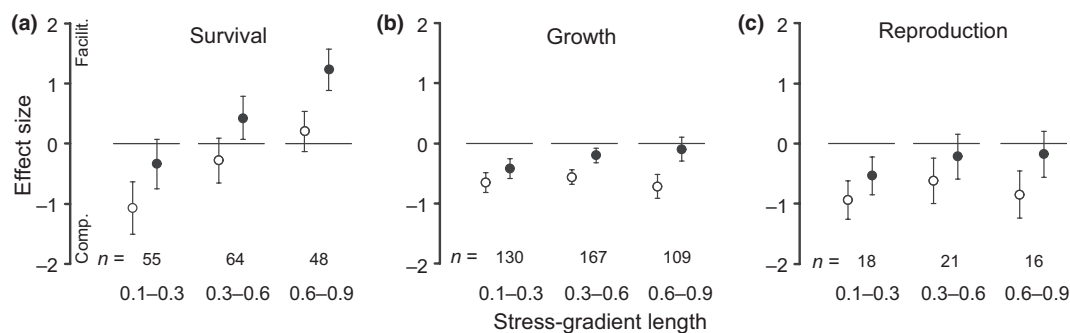


Figure 5 Influence of stress-gradient length on change of plant interactions with stress. (a) Survival, (b) growth and (c) reproduction. Shown are means and 95%-confidence intervals of mixed-model effect size calculations. Other details follow Fig. 1.

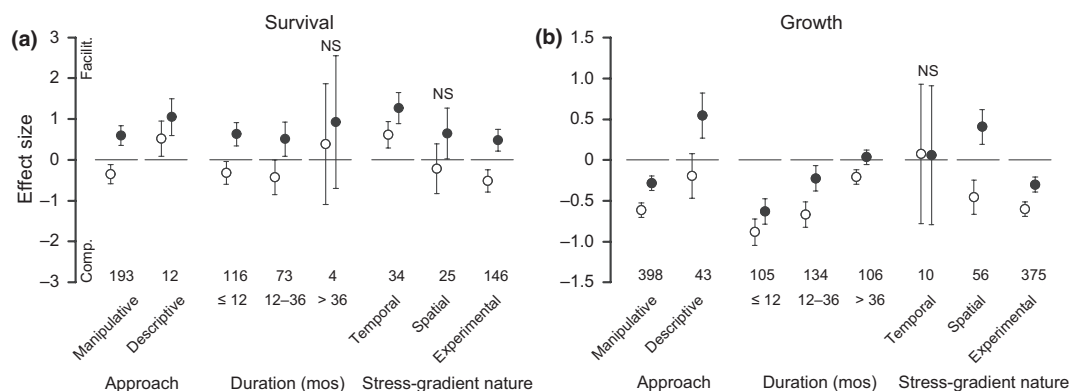


Figure 6 Influence of study approach, study duration and stress-gradient nature on change of plant interactions with stress. (a) Survival and (b) growth. Shown are means and 95%-confidence intervals of mixed-model effect size calculations. Other details follow Fig. 1.

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 facilita-

tive, 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; Stultz *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 spe-

cies 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 Cavieres & 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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