


A case for associational resistance: Apparent support for the stress gradient hypothesis varies with study system

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Abstract

According to the stress gradient hypothesis (SGH), ecological interactions between organisms shift positively as environmental stress increases. In the case of associational resistance, habitat is modified to ameliorate stress, benefitting other organisms. The SGH is contentious due to conflicting evidence and theoretical perspectives, so we adopted a meta-analytic approach to determine if it is widely supported across a variety of contexts, including different kingdoms, ecosystems, habitats, interactions, stressors, and life history stages. We developed an extensive list of Boolean search criteria to search the published ecological literature and successfully detect studies that both directly tested the hypothesis, and those that were relevant but never mentioned it. We found that the SGH is well supported by studies that feature bacteria, plants, terrestrial ecosystems, interspecific negative interactions, adults, survival instead of growth or reproduction, and drought, fire, and nutrient stress. We conclude that the SGH is indeed a broadly relevant ecological hypothesis that is currently held back by cross-disciplinary communication barriers. More SGH research is needed beyond the scope of interspecific plant competition, and more SGH research should feature multifactor stress. There remains a need to account for positive interactions in scientific pursuits, such as associational resistance in tests of the SGH.

KEYWORDS

associational resistance, context-dependency, ecological niche, Hedges' g^* , interspecific, intraspecific, meta-analysis, negative interactions, positive interactions, stress gradient hypothesis

INTRODUCTION

Organismal interactions form the bedrock of ecology, affecting community and evolutionary dynamics including structure, function, coexistence, and productivity (Barracough, 2015; Bertness & Leonard, 1997; Callaway, 1995; Doebeli & Dieckmann, 2000; Molloy & Hertweck, 2017). In the context of environmental stress such as climate change, shifting organismal interactions

have a greater role in population declines and extinctions than physiological climatic tolerances (Cahill et al., 2013; Ockendon et al., 2014). Understanding the nature of how organismal interactions shift is critically important for successful conservation and ecological management, especially because global stress is accelerating at this stage in the Anthropocene (Allen et al., 2015; Büntgen et al., 2020; Hodson & Marvin, 2010; Newman, 2019; Schimel et al., 2013).

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Competitive and predatory antagonism have traditionally garnered more attention than positive organismal interactions (Beaudrot et al., 2020; Elton, 1946; Stachowicz, 2001), leading Bertness and Callaway (1994) to urge community ecologists to follow evolutionary biologists in accounting for positive interactions such as mutualism. Even though greater theoretical incorporation and research investment in positive interactions began after the start of the 21st century (Bronstein, 2001; Brooker et al., 2008; Bruno et al., 2003; Hoeksema & Bruna, 2000; Traveset & Richardson, 2014; Valdez et al., 2020), a great proportion of global stress studies still focus on predation or competition (Harley, 2011; Lancaster et al., 2017; Ockendon et al., 2014; Romero et al., 2018). The stress gradient hypothesis (SGH) is helping to shift this focus. According to the SGH, ecological interactions between organisms become more positive as environmental stress increases (Maestre et al., 2009; Malkinson & Tielbörger, 2010).

Traditionally a reduction in competitive exclusion, which is the principle that species sharing resource requirements cannot coexist (Gause, 1934), has been proposed to explain why ecological interactions become more positive along a gradient of stress. In the seminal paper introducing the SGH, Bertness and Callaway (1994) attributed the phenomenon to an interspecific mechanism, where neighbours take advantage of a 'primary space-holder' better adapted to the stressful conditions. As stress intensifies, the species' degree of adaptation to the stress reduces niche overlap, which reduces the negative interaction of competition. Simultaneously, either mutualism or commensalism is encouraged because neighbours depend on the 'primary space-holder,' a dependence that only increases as conditions become harsher. Fitness costs would result from interacting antagonistically.

The SGH is controversial because conflicting evidence is attributed mainly to context dependence (Holmgren & Scheffer, 2010; Lortie & Callaway, 2006; Maestre et al., 2006; Smit et al., 2009), but the debate also is fuelled by the ambiguous and controversial nature of stress itself (Bijlsma & Loeschcke, 2005; Körner, 2003; Lortie et al., 2004). Systematic reviews such as meta-analyses comprise an ideal outlet for highlighting and navigating inconsistencies in terminology or application (Koricheva & Gurevitch, 2014). Meta-analyses are especially useful in providing a resolution when some primary studies support a particular hypothesis whereas others refute it (Koricheva et al., 2013). Entire books have been written covering the nebulous phenomenon of stress (Steinberg, 2012). We focused this meta-analysis on assessing support for the SGH across the published ecological literature; as such, it was necessary to adopt a broad working definition of the term 'stress' when formulating inclusion criteria for our meta-analysis, following the lead of other meta-analyses published on the topic (Stachowicz, 2001). Any situation that adversely affected an organism's fitness was labelled as 'stress,' regardless if that situation was physical (e.g., resource limitation, disturbance,

weather, climate) or biotic (e.g., trophic, pathogenic). Critical limits of tolerance did not need to be surpassed for us to label an event as 'stress' (Rezende et al., 2014) because too often tolerances, which are invariably species-specific, are unknown.

The SGH has been investigated and debated by plant community ecologists since its conception, but it is not as well known outside of plant community ecology (Barrio et al., 2013; Beaudrot et al., 2020; Daleo & Iribarne, 2009; Dangles et al., 2013). In other ecological fields, studies of the effects of stress may indicate support for or against the SGH without acknowledging the hypothesis' existence, and it is unclear how much the nature of the ecosystem and the stress itself affects conclusions (Lortie & Callaway, 2006; Maestre et al., 2006). There is evidence that the presence of consumers alters the outcome of interactions predicted by the SGH (Smit et al., 2009), contributing to the need to evaluate how well supported the hypothesis is in various contexts, including the nature of the organism or interaction. Studies that explicitly address the SGH tend to feature interspecific competition among adult macroscopic plants and other sessile organisms (Armas et al., 2011; Fugère et al., 2012; Holmgren & Scheffer, 2010; Kawai & Tokeshi, 2007; Maestre et al., 2005). This tendency has been attributed to the perceived importance of interspecific competition in shaping stable communities and to the particularly high prevalence of preemptive competition among sessile organisms (Biswas & Wagner, 2014). The SGH was eventually extended to other interactions, such as intraspecific competition, once explicit evidence accumulated contradicting the assumption derived from Hutchinsonian niche theory (Hutchinson, 1957, 1978) that positive interactions operate minimally among organisms with overlapping niches, especially conspecifics (Fajardo & McIntire, 2011).

Positive intraspecific interactions are common phenomena, and major examples include adults that nurse younger organisms (Dvorský et al., 2013; Nuñez et al., 2009; Thierry & Anderson, 1986) and adults that maintain communal assemblages (Grant, 2018; Wheeler, 2015). It is therefore of broad interest to evaluate how positive intraspecific interactions shift when stress is applied and to compare juveniles to adults. Selective pressures are known to differ depending on the life history stage; for example, juveniles are particularly challenged by matters of nutrient acquisition and less so by matters of reproduction relative to adults (Schluter et al., 1991). Stress may be more likely to shift ecological interactions negatively among juveniles, in direct opposition to the SGH, as when overcrowding leads to cannibalism (Schutt, 2018). Assistive behaviour directed toward other organisms is more likely to occur if there is a reproductive benefit involved, such as in primates when a low-ranking individual grooms a high-ranking individual to eventually receive either protection or mating opportunities from the high-ranking individual (Schino & Aureli, 2010). There is greater pressure on adults to

acquire reproductive benefits relative to juveniles, so assistive interactions toward other organisms and support for the SGH should be more common among adults.

Although the SGH may hold up particularly well in cases of interspecific competition because of Hutchinsonian niche dynamics, which shaped the original framework for the hypothesis, Eltonian and Grinnellian processes (Elton, 1946, 2001; Grinnell, 1917; Soberón, 2007) may cause it to be well supported in other contexts. For example, we expected the SGH to be well supported in the contexts of parasitism and mutualism. From an Eltonian perspective, SGH expectations should be fulfilled in cases where participants respond to stress by modifying their habitats in ameliorative ways, thus benefitting all participants in the interaction. This phenomenon has been named ‘associational resistance’ (Smit et al., 2009), and many mutualisms that influence community structuring meet this criterion (Stachowicz, 2001). The term ‘associational resistance’ has been used interchangeably with the term ‘associational defence’ in plant ecology literature, but here we prefer ‘resistance’ because it extends beyond the context of a plant species benefitting from the chemical defence of a different plant species (Smit et al., 2009). As an example, it accounts for intraspecificity well, for organisms that modify their habitat to improve conditions for themselves should attract other organisms of the same type. From a Grinnellian perspective, SGH expectations should be fulfilled in interactions such as mutualism and parasitism because the fitness and subsequent adaptations of each interaction participant depend on those of the other participants. For example, a parasite may reduce its antagonism of its host as stress increases because its fitness is contingent upon the host surviving the stress (May & Anderson, 1990). It may even begin to behave in ways that benefit its host because of this contingency, transitioning the Grinnellian mechanism of SGH support into an Eltonian one (Fellous & Salvaudon, 2009). We therefore expected support for the SGH to rely on the degree to which coevolution governs the interaction. Specifically, the shift of interaction toward positivity should be strongest among interactions where participants are intimate and their fitness is codependent, as in mutualism and parasitism.

We adopted a meta-analytic approach to broadly address whether ecological interactions between organisms shift in a positive direction as environmental stress increases as claimed by the SGH. Specifically, we asked (1) Does the SGH extend across kingdoms, beyond Plantae? (2) Is the shift proposed by the SGH more common for certain interaction types, such as interspecific or intraspecific, and certain types of positive or negative interactions? (3) Is the shift proposed by the SGH more common for certain ecosystems, habitats, response variables, life history stages, and types of stress? Other systematic reviews on this topic have been restricted to plants or plant-like organisms (Dohn et al., 2013; He et al., 2013; Holmgren &

Scheffer, 2010; Maestre et al., 2005, 2006). Ours is the first systematic review and specifically the first meta-analysis that attempts to answer these questions.

MATERIALS AND METHODS

Search inclusion

We searched for peer-reviewed primary publications to examine if, and in which direction, stress shifted ecological interactions. We provide a full bibliographic detail of these primary publications in the ‘References’ section of this paper. Data were included regardless of the age of the study, and studies fell in the time range of 1900–2019. We tracked experimental and observational studies, as this is a good common practice for meta-analyses (Côté & Jennions, 2013). We examined if the type of study influenced the outcome and if there was a deficit of either type of study for this topic.

An ecological study may provide support for or against the SGH yet never acknowledge the hypothesis because it is not widely known beyond the field of plant community ecology. Although this ignorance reduces possible confirmation bias, we nonetheless developed an extensive list of Boolean search terms to successfully gather data for as many stressors and interactions as possible (Table S1). Combinations varied, but key predictor phrases included: stress gradient hypothesis, stress gradient, environmental gradient, environmental stress, biotic stress, global change, climate change, temperature, drought, rainfall, flood, and disturbance. Likewise, key response phrases included *compet**, *mutuali**, *parasit**, *predat**, *pollinat**, *decomp**, *facilitat**, *altrui**, *cooperat**, *negative interac**, *positive interac**, *alloparent**, *amensal**, *commensal**, *neutral**, *nutrient*, *climate*, *plant**, *microb**, *animal**, *interspec**, and *intraspec**.

Ecological interactions we considered included (1) intraspecific interactions, which were generally nontrophic except for cases of cannibalism, (2) interspecific interactions, which encompassed either different taxa occupying the same trophic level, or different taxa occupying different trophic levels, (3) direct interactions, where individuals directly engaged with each other, (4) indirect interactions, where a third party modulated the relationship between individuals (5) positive interactions, defined as those where participants in the interaction do not harm each other and at least one participant benefits, such as mutualism, pollination, commensalism, and decomposition, and (6) negative interactions, defined as those harming one or more participant in the interaction, such as parasitism, amensalism, competition, and predation. We classified organism interactions according to the stress-free condition of the interaction. For example, if an interaction started as parasitism but shifted to mutualism, in our data collection we referred to that interaction by its starting condition of

parasitism. The purpose of this classification was to assess if it is more common for certain starting conditions to shift than others. We differentiated pollination from other mutualisms because the interaction itself is short-lived and coevolution between participants is particularly high (Bronstein et al., 2006; Kiester et al., 1984; Lunau, 2004). Decomposition was differentiated because benefits tend to be indirect and coevolution between participants is relatively low (Kreuzer et al., 2004; Lohmann et al., 2009; Mack & D'Antonio, 2003).

In addition to ecological interactions, we examined a range of abiotic and biotic stressors (Table S1). We defined biotic stress as any incidence of adversity directly imposed by another organism on another (competition, predation, parasitism). All other stress was classified as abiotic. Certain biotic variables could be either a predictor or a response variable in this meta-analysis; it

depended on the study. For example, the predatory, competitive, or parasitic interaction in a study could respond to a stressor such as heat. In other cases, predators, competitors, or parasites did not experience stress, but acted as a source of stress for the participants in a different interaction such as mutualism.

Extraction

Figure 1 shows our extraction process from start to finish, in the format of a PRISMA diagram (Stovold et al., 2014). We excluded both theoretical data from modelling papers and molecular studies, the latter because ecological interactions between organisms usually were not incorporated. We call these papers 'irrelevant' in our PRISMA diagram, while exclusion based on 'unsuitable

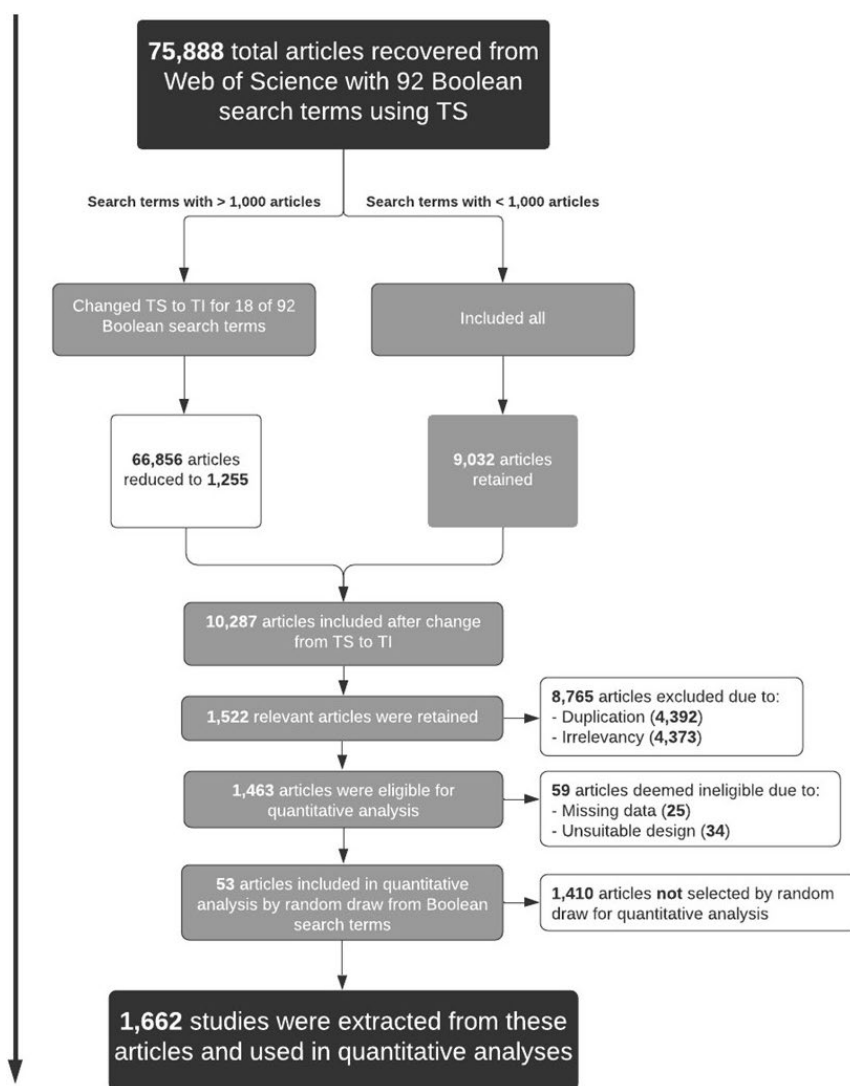


FIGURE 1 PRISMA diagram of the literature extraction process from Web of Science 1900–2019 searches. When a search term yielded more than 1000 articles, the search was repeated based on title (TI) instead of topic (TS). 'Irrelevancy' included genetic/molecular and modelling papers. 'Unsuitable design' included studies without stressors, measured responses to stress, or at least two organisms interacting. 'Missing data' included studies that either did not report means, standard deviations, and sample sizes, or reported suspect values (e.g. standard deviation of 0)

study design' encompassed studies that lacked stressor(s), quantified responses to stress, or interactions between two or more organisms. We extracted sample sizes, standard deviations, and means for controls and treatments (Appendix S1). For observational studies, we considered the absence of stress the 'controls' and the presence of stress the 'treatments' (He et al., 2013). Studies were excluded if any of these values were not reported or could not be determined. We quality-checked data three times to ensure accurate summary statistics were recorded for the included studies. We excluded a study if accuracy was suspect; for example, studies that reported standard deviations equal to zero were excluded. Collectively, these exclusion criteria led us to narrow down the 10000+ studies we originally found to 1662 total studies that could be used in the final analysis.

Because our main objective was to assess an ecological hypothesis, the data came from text, appendices, tables and figures presented in peer-reviewed published primary literature that we searched using the advanced search tool in Web of Science. This database was chosen because it has the widest coverage of journals that contain published primary literature and a wide range of publication years. We stored the PDF files of relevant literature in Open Science Framework (OSF).

Because our Boolean search criteria covered such a wide range of predictors and interactions (Table S1), a search would sometimes yield 1000 or more papers. This happened for 18 of 94 combinations of search terms. When this happened, we searched based on title (TI) instead of topic (TS) to reduce the sample size to more manageable quantities. For example, 2480 papers were retrieved using the search criterion $TS = ((\text{'global change' OR 'climate change' AND cooperat*}))$. After substituting TI for TS before the phrase, 178 papers were returned.

We found eleven types of performance responses for the 1662 relevant studies we gathered, including biodiversity, abundance, biomass, defence, growth, immunity, metabolism, water potential, nutrition, reproduction, and survival (Figure S1a). We included biodiversity along with the other ten response variables because we found cases where lower biodiversity suggested a lower level of coexistence, thus opposing the SGH, while higher biodiversity suggested a higher level of coexistence, thus supporting the SGH. These responses came from organisms in five kingdoms: Animalia, Bacteria, Chromista, Fungi, and Plantae (Figure S1b). We also found 14 stressors, including drought, elevation, fire, flood, heat, light, nutrients, chemicals, shading, wind, human disturbance, competition, parasitism, predation (Figure S1c). Observational studies did not greatly outnumber experimental studies (Figure S1d). The number of studies we found for each of the following variables are summarised in Figure S1e) aquatic vs terrestrial habitat, (f) interspecific vs intraspecific interactions, (g) adult vs juvenile organisms, (h) commensalism, competition,

decomposition, mutualism, pollination, parasitism, predation, and (i) grassland, agricultural, coastal, desert, forest, freshwater, laboratory, marine, montane, and wetland ecosystems.

Our main objectives were to compare qualitative contexts (categories of organisms, habitats, ecosystems, interactions, stressful phenomena, and response) rather than quantitative contexts. By quantitative contexts, we mean any quantification of the severity of the stress. Stressfulness could potentially be scored relative to the organisms' physiological critical limits of tolerance, indicating if the stress was mild, moderate, or severe in magnitude. As another example, the duration of the interaction under stress relative to the organisms' average lifespan could reveal if the stress was short-term or long-term, and the extent to which this was the case. These factors can further be combined in 'tolerance landscape' models, which express survival probability (Rezende et al., 2014). Standardising quantitative contexts to compare SGH support across organisms and their interactions is a monumental task, fraught with challenges and worthy of expansion in either its own meta-analysis or theoretical modelling paper. The latter may be more appropriate given the current empirical evidence limitations of critical limits in non-model organisms, non-laboratory settings, and for non-thermal stressors (Cooper et al., 2008; Hoffmann et al., 1997, 2003; Rezende & Santos, 2012; Rezende et al., 2011). Quantitative context is undoubtedly important in evaluating the SGH, especially as moderately stressful conditions may have a different outcome relative to harsher conditions (Holmgren & Scheffer, 2010). We attempted to account for it but ultimately judged it too tenuous to include.

Analysis

We calculated Hedges' g^* effect sizes by dividing the difference between control and treatment means by the pooled standard deviation (He et al., 2013). The Hedges' g^* effect size statistic is interpreted similarly to Cohen's d , but its incorporation of the pooled standard deviation reduces bias and makes it a better estimate, especially for small sample sizes. It is also negligibly biased for larger sample sizes. This makes it the ideal effect size statistic to report in a meta-analysis, provided enough of the included studies report the sample sizes and summary statistics necessary to calculate it (Hedges & Olkin, 2014). Sample sizes and the control and treatment standard deviations allowed us to calculate the pooled standard deviation: $S_p = \sqrt{[(n_1-1) s_1^2 + (n_2-1) s_2^2]/((n_1-1) + (n_2-1))}$.

Hedges' g^* was estimated per study (i.e., per row of data) with a Bayesian model developed in JAGS and run via package 'rjags' in R (Plummer, 2016). Individual estimates and their associated uncertainties were fed hierarchically into another JAGS model that estimated

Hedges' g^* for each subset of data, such as kingdom Plantae or terrestrial habitat. At each step, posterior distributions of estimates were generated via 10,000 Monte Carlo iterations of three Markov chains. Standard trace plots revealed an excellent mixture in parameter space, so we had no need to thin or otherwise subsample the posteriors.

We analysed our data for possible publication bias to see if support for the SGH differed between studies that were directly inspired by it, those that did not directly test it but mentioned it posthoc, and those that made no mention of it at all. For each of the eleven response variables, we estimated mean effect size with the hierarchical Bayesian model outlined above. Resultant estimates (Figure 2) were summarised with basic box plots (SigmaPlot 14.0) to show median (line), 25th and 75th percentiles (box), 10th and 90th percentiles (whiskers), and 5th and 95th percentiles (dots).

Because studies published between 1900 and 2019 were included in the literature search, we accounted for possible temporal changes in effect sizes with a Bayesian analogue to a time-series regression (Figure S2). There is no evidence that effect size varied with publication date (slope = -0.015 , 95% credible interval = $-0.062, 0.031$).

We ran a series of Bayesian analogues to a factorial ANOVA to estimate how effect size varied with various combinations of predictors. We ranked resultant models with the deviance information criteria (DIC), chiefly to see which predictor or combinations thereof best accounted for variance in effect size (Table S2). Representative interaction plots were built with ggplot2 (Figure S3).

RESULTS

Predictor combinations

Predictors that best accounted for variance in effect size were ecosystem (agricultural, coastal, desert, forest, freshwater, grassland, lab bench, marine, mountain, wetland), fitness proxy (abundance, biodiversity, biomass, defence, growth, immunity, metabolism, nutrition, reproduction, survival, water potential), the condition of intraspecificity or interspecificity, and kingdom (Bacteria, Chromista, Fungi, Plantae, Animalia). Easily (deviance information criterion, DIC, a metric of model fit with lower values better, is >20 units lower) the two best combined models were ecosystem \times response (DIC = 9641.0; Figure S4) and ecosystem \times response \times intra/interspecificity (DIC = 9643.4). Intraspecific interactions were not represented in the cases of agricultural, coastal, grassland, and wetland ecosystems. When intraspecific interactions were represented, their effect sizes were always more negative than the effect sizes of interspecific interactions, and this difference was typically small, yet a statistical interaction is evident (Figure S3). Notable exceptions were in desert and freshwater ecosystems, which showed a sizeable difference between intraspecificity and interspecificity. Intraspecific interactions shifted decisively in a negative direction (-3.5 for desert and -1.0 for freshwater ecosystems) while interspecific interactions shifted positively (2.8 for deserts and 0.5 for freshwater ecosystems). Combinations of ecosystem \times kingdom \times intra/interspecificity (DIC = 9666.9) and ecosystem \times intra/interspecificity (DIC = 9670.7; Figure S3) provide the only other broadly competitive

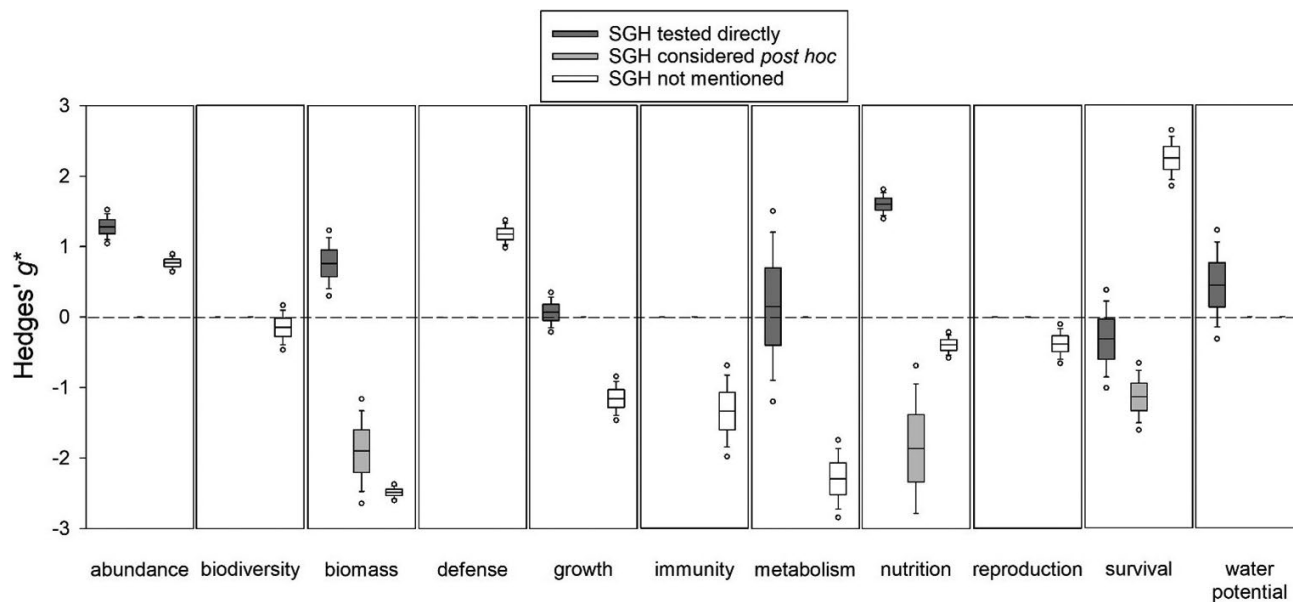


FIGURE 2 Mean effect size (Hedges' g^*) relative to response variable measured and whether the stress gradient hypothesis (SGH) was tested or not. Note the tendency toward positive effect size when SGH was tested directly vs. whether it was mentioned in a discussion or not mentioned at all

models ($\Delta\text{DIC} < 30$ from ‘best’). We assessed other predictor combinations as well but found no other notable patterns except that biomass was a more common and temperamental metric in desert ecosystems relative to other ecosystems and response types.

Kingdoms

Overall, stress decreased positive ecological interactions and increased negative ecological interactions, opposing the SGH, as shown by a pooled effect size of -0.2 and a narrow distribution (Figure 3). This was more apparent among observational studies, while experimental work more often captured reduced negativity in ecological interactions. Distributions were narrow and non-overlapping for observational and experimental studies. There were clear differences among kingdoms; two even exhibited a pattern opposite to the overall trend.

Plantae and Bacteria both had positive effect sizes, indicating a shift towards more positive and less negative ecological interactions under stress; this was more pronounced for Bacteria (Figure 3). The tail end of the

distribution for Plantae overlapped zero whereas the distribution for Bacteria was entirely positive. Effect sizes were negative for three of the five biological kingdoms represented in the data: Chromista, Fungi, and Animalia, indicating opposition to the SGH due to a shift towards more negative and less positive ecological interactions under stress. There was greater uncertainty of estimate among Chromista, Fungi, and Bacteria relative to Animalia and Plantae.

Interaction type

Certain ecological interactions became more positive or less negative under stress, such as interspecific interactions, while others showed the opposite pattern, such as intraspecific interactions (Figure 4). The effect size was small and positive for interspecific interactions (0.3), while the effect size for intraspecific interactions was large and negative (-1.2). Direct interactions had a relatively narrow distribution and a negative effect size (-0.2), while indirect interactions varied more and were half as negative (-0.1) relative to direct interactions.

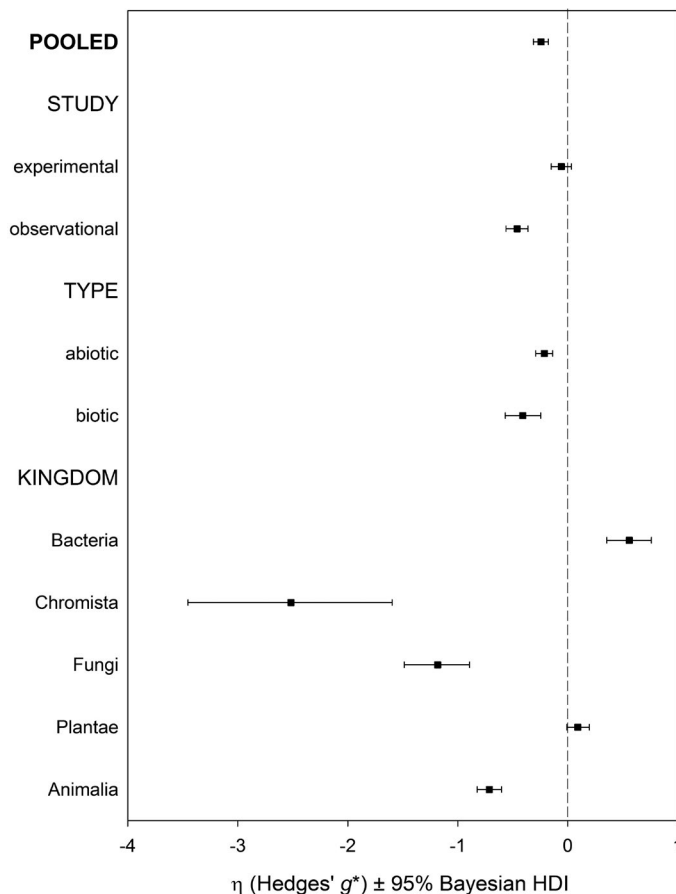


FIGURE 3 Hedges' g^* effect sizes ($\pm 95\%$ Bayesian highest density intervals) of biological response to stress across different kingdoms (Bacteria, Chromista, Fungi, Plantae, Animalia), stress types (abiotic and biotic), study types (experimental and observational), and all species and systems (pooled). Positive effect sizes reflect increases in positive ecological interactions and decreases in negative ecological interactions as expected from the stress gradient hypothesis (SGH), while negative values reflect the opposite of that

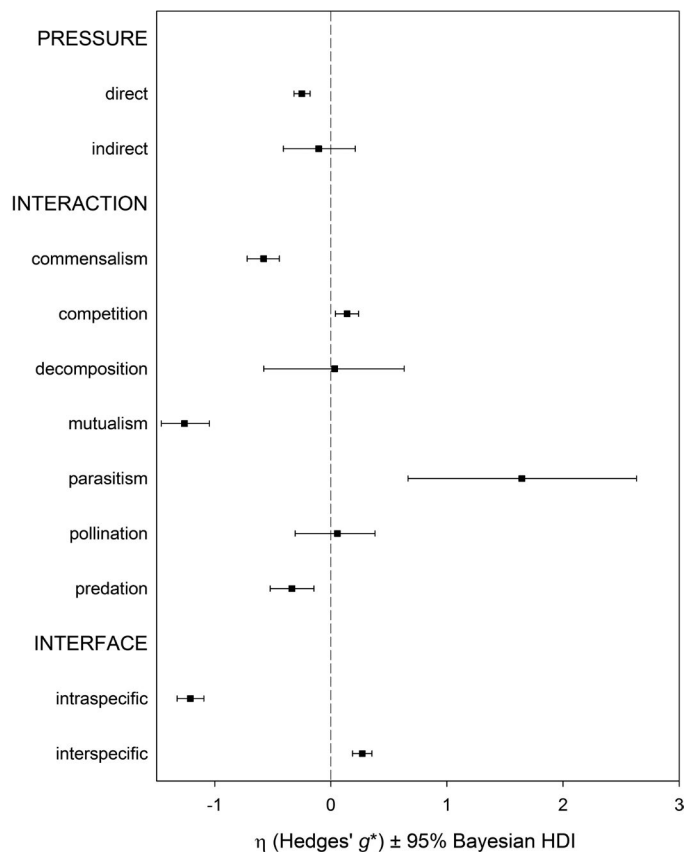


FIGURE 4 Hedges' g^* effect sizes ($\pm 95\%$ Bayesian highest density intervals) of biological response to stress across different types of ecological interactions (intraspecific, interspecific, commensalism, competition, decomposition, mutualism, parasitism, pollination, predation, direct, and indirect). Positive effect sizes reflect increases in positive ecological interactions and decreases in negative ecological interactions as expected from the stress gradient hypothesis (SGH), while negative values reflect the opposite of that

Stress reduced negative ecological interactions, except in the case of predation. Parasitism had the highest positive effect size (1.75) of any interaction type, and even though the distribution was broad it did not overlap zero. The competition had the second highest positive effect size (0.1) with a narrow distribution that did not overlap zero. In contrast, stress intensified predatory interactions, indicated by a negative effect size (-0.2).

Positive ecological interactions such as mutualisms shifted to become negative ecological interactions in response to stress, except in the case of pollination. Overall, mutualisms had the most negative effect size (-1.2) out of all interaction types, followed by commensalisms (-0.6). Pollination deviated greatly from other mutualisms, as it had the third most positive effect size (0.5) that did not differ greatly from the effect size of decomposition (0.3). Although the effect sizes of pollination and decomposition were positive, indicating support for the SGH, broad distributions that extend below zero indicate cases of opposition to the SGH.

Ecosystems and habitat

There were pronounced differences in ecological stress responses based on the type of habitat and ecosystem

(Figure 5). Effect sizes for aquatic and terrestrial habitats differed by an order of magnitude, with aquatic systems exhibiting greater negativity and variation. Marine, coastal, and freshwater ecosystems were decisively negative, ranging from -1.7 to -0.5 effect sizes, while terrestrial ecosystems ranged from -1.4 to 1.8 effect sizes. In aquatic ecosystems, negative ecological interactions intensify and positive interactions shift to become negative. Freshwater ecosystems showed less negativity relative to the saline ecosystems. In contrast, the phenomenon of positive ecological interactions intensifying and negative ecological interactions shifting to become positive was captured for terrestrial ecosystems, but this depended on the type of terrestrial ecosystem. Grasslands and deserts did not show SGH support, for example.

Among terrestrial ecosystems, grasslands had the most negative effect size (-1.4), followed by deserts (-0.8), while the remainder were positive. Evidence was strongest for increased positive and decreased negative ecological interactions among wetland and agricultural ecosystems. Effect sizes did not differ greatly between forest (0.75) and laboratory (0.7) ecosystems, but forest and laboratory effect sizes were approximately three times greater than montane ecosystems (0.25).

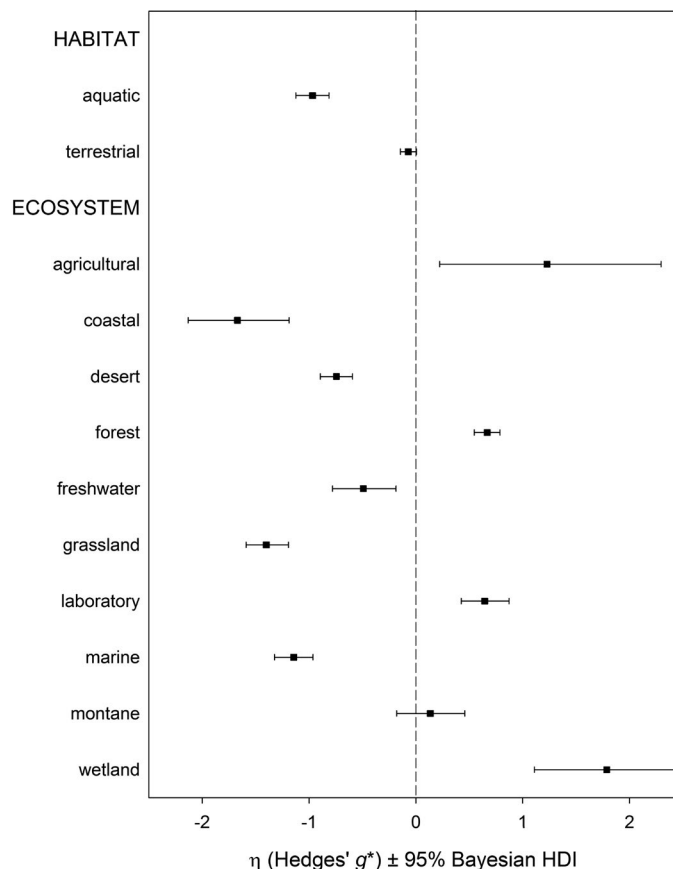


FIGURE 5 Hedges' g^* effect sizes ($\pm 95\%$ Bayesian highest density intervals) of biological response to stress across different ecosystems (agricultural, coastal, desert, forest, freshwater, grassland, laboratory, marine, montane, wetland) and habitats (aquatic and terrestrial). Positive effect sizes reflect increases in positive ecological interactions and decreases in negative ecological interactions as expected from the stress gradient hypothesis (SGH), while negative values reflect the opposite of that

Response type

Stress responses varied depending on the age of the organism and the particular type of biological response to stress (Figure 6). Juvenile organisms had a more negative effect size relative to adult organisms, in opposition to the SGH. Although the adult effect size was negative, also in opposition to the SGH, the distribution extended slightly above zero, indicating cases of SGH support. Biodiversity and water potential among organisms varied widely in both directions, but effect sizes for other response types were clearly positive or negative. Positive effect sizes, listed in order of highest to lowest magnitude, included defence, abundance, survival, and nutrition. These measurements generally supported the SGH. Negative effect sizes, listed in order of highest to lowest magnitude, included biomass, metabolism, immunity, growth, and reproduction. These measurements generally opposed the SGH.

Stress type

Drought and nutrient stress, especially when combined, shifted ecological interactions positively

(Figure S5). Even though the distribution was broad for drought and nutrient stress, it never overlapped zero and the positive effect size (5.5) was higher than any other evaluated in the meta-analysis, providing the strongest support for the SGH. In comparison, other stressors that shifted ecological interactions positively, such as chemicals, fire, and wind, had smaller effect sizes closer to one and zero.

When biological agents were a source of stress in a system, ecological interactions shifted negatively, opposing the SGH. The sole exception to this was when drought was involved. The effect size of drought alone did not differ from the effect size of drought combined with predation. Fire shifted ecological interactions positively, but this was neutralised if predators were also a source of stress.

There were more stressors that were either neutral or shifted ecological interactions negatively, not supporting the SGH. Neutral stressors included flooding, elevation, and human disturbance. Heat and shading had the most negative effect sizes, followed by the biotic stressors of competition, parasitism, and predation. Light stress also shifted ecological interactions negatively and did not greatly differ from parasitism and predation.

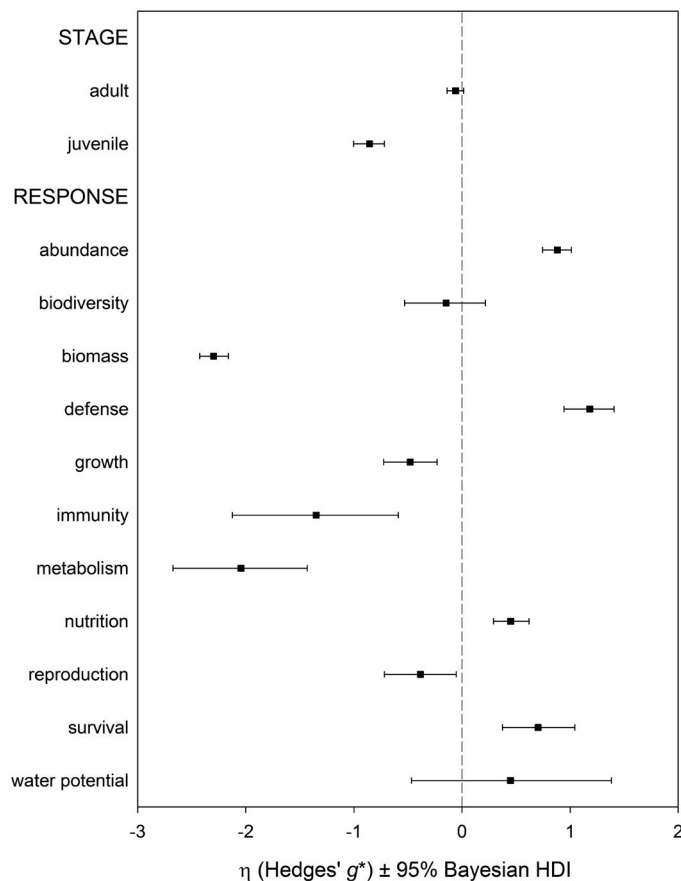


FIGURE 6 Hedges' g^* effect sizes (+95% Bayesian highest density intervals) of biological response to stress for different response types (abundance, biodiversity, biomass, growth, immunity, metabolism, nutrition, reproduction, survival, water potential) and life history stages (adult vs. juvenile). Positive effect sizes reflect increases in positive ecological interactions and decreases in negative ecological interactions as expected from the stress gradient hypothesis (SGH), while negative values reflect the opposite of that

DISCUSSION

The stress gradient hypothesis, in which ecological interactions shift in a positive direction with increasing environmental stress, is controversial among ecologists, in part because of contradictory support (He et al., 2013; Maestre et al., 2009; Malkinson & Tielbörger, 2010). Although context-dependency has been acknowledged for the SGH, stressors, responses, ecosystems, habitat, and interactions have not been assessed as specifically as they were in this meta-analysis. Ours is the first to examine the SGH in the context of organisms from different kingdoms and life history stages and to compare intraspecificity and interspecificity.

Kingdoms

Although the SGH is explicitly tested most often in studies of plant community ecology, we found that greater support for it existed among bacteria than for any other kingdom. This finding was especially striking because the quantity of SGH relevant studies

featuring bacteria was not far off from the quantity of SGH relevant studies featuring plants. As we extracted from the ecological microbiology literature, we noticed that the SGH was usually not mentioned or described even when results supported it. Although plant community ecologists proposed the hypothesis and have diligently tested and debated it over the years, this finding demonstrates that the SGH is relevant to bacteriologists.

Based on our findings, the SGH is a broadly relevant ecological hypothesis currently held back by cross-disciplinary communication barriers. It was generally not supported in studies featuring kingdoms other than Plantae and Bacteria, but there were fewer SGH relevant studies featuring other kingdoms to begin with so we encourage support of SGH studies targeting these kingdoms. Because life history strategies differ dramatically even within kingdoms, future work comparing finer taxonomic distinctions than the kingdom level would be useful. We urge ecologists who test the SGH to consider communicating their findings in journals, conferences, and other platforms that will reach a wide audience of ecologists.

Interaction type

We compared intraspecific and interspecific interactions and found that SGH support is more likely for interspecific interactions, which aligns with theory differentiating intraspecific and interspecific interaction types. For example, according to the principle of competitive exclusion, long-term coexistence is not possible if niches overlap (Hardin, 1960). Intraspecific competition is stronger than interspecific competition (Adler et al., 2018). In addition, according to principles in sociobiology, positive intraspecific interactions are more likely in stressful conditions if organisms are kin related due to indirect fitness benefits. If stress produces more costs than benefits in terms of direct fitness for individuals, and if there is little to no indirect fitness advantage for individuals, intraspecific interactions will shift negatively (Wilson & Wilson, 2007). According to our findings, this happens often. We did not evaluate how the duration of an interaction may affect the patterns we detected, so we suggest it as a future research direction, especially since we found positive interactions were more likely to shift in a negative direction except for the shorter-term positive interaction of pollination.

Ecosystems and habitat

Even though famous examples of SGH support feature marine invertebrates (Bertness & Leonard, 1997; Bertness et al., 1999), overall we found that the SGH was not supported in aquatic contexts any more than in terrestrial. The mechanism behind the difference in aquatic and terrestrial SGH support is likely tied either to trophic cascades or to the rarity of evolutionary transitions between aquatic and terrestrial systems (Vermeij & Dudley, 2000). We believe the former to be more directly involved, considering the sizeable differences that exist between aquatic and terrestrial food web function and structure (Chase, 2000; Wiegert & Owen, 1971).

Ecosystems that typically lack severe nutrient-deficiency were far more likely to show interactions that shifted positively. Severe nutrient deficiency does not typically characterise wetlands, agroecosystems, and laboratories; hence, we posit that the mechanism driving the SGH is tied to nutrient availability or acquisition in these systems. Nutrient stress alone or in combination with other stressors shifted interactions positively. This finding is consistent with other SGH systematic reviews that have featured plants only, which suggested that moderate nutrient limitations best promote the SGH while nutrient limitations in the harshest of conditions will shift organism interactions negatively (Holmgren & Scheffer, 2010). We compared categories of stressors and ecosystems, but follow-up work that singles out given stressors and establishes a standardised continuous format for comparing the magnitude of the stress across

studies may provide clearer insight into the mechanisms driving the patterns we detected.

Response type

Our meta-analysis is the first to demonstrate that study design matters when it comes to the SGH. We found that the metric of performance affects conclusions about support for the SGH (Figure 2). Metrics related to survival are more likely to support the SGH but metrics related to growth and reproduction are more likely to oppose the SGH. At present, support for the SGH is particularly weak in the context of desert-based intraspecific interactions, but it may be better supported in this context than currently documented because growth was the primary metric in desert studies (Figures 3 and 5). Because of this key finding, we suggest that experimental work assessing the SGH should be as comprehensive as possible in how participants are evaluated in an ecological interaction. This finding reinforces the importance of accounting for trade-offs in survival, growth, and reproduction when evaluating the SGH, as selection pressures on these factors, especially at different life history stages, may oppose each other (Brouwer et al., 2019; Cox et al., 2010; Schluter et al., 1991; Schluter & Smith, 1986).

Time scales and the empirical status of the study design should also be carefully accounted for when choosing metrics for tests of the SGH. The contrast between survival and growth highlighted in our analyses may be driven by temporality, as studies at the intraspecific level in particular have generally revealed growth to be a shorter term response and survival a longer term response (Loison & Langvatn, 1998). Temporal gradients shape stress tolerance landscapes alongside physical gradients such as space (Rezende et al., 2014), but we know of only one study that has implemented a test of the SGH explicitly from a temporal perspective (Biswas & Wagner, 2014). This dearth happened to be a case where the researchers intentionally tested the SGH in an intraspecific context, and the main findings were that (1) there was stronger support for the SGH as more time passed, so it is possible that the SGH may be more widely supported in intraspecific contexts than the literature currently suggests, and (2) when experimental and observational approaches to SGH testing were compared side by side, effects were weaker in the observational design relative to the experimental design, consistent with our own comparison of observational and experimental designs across a wide sampling of studies (Figure 3). While observational designs have been criticised because confounding factors in natural settings may call into question the reliability of their results (Shaffer & Johnson, 2008), here observational designs contributed less than experimental designs did to the degree of researchers' confirmation bias in studies explicitly testing the SGH (Figures 2 and 3). This highlights that there are

disadvantages in both experimental and observational approaches to SGH testing. Researchers should take care in their design choices and may be well served to implement both approaches whenever possible since it is not apparent that one approach is superior to the other.

Furthermore, if physiological responses are selected to be measured instead of survival and growth, the response may be non-linear (Maestre et al., 2009; Malkinson & Tielbörger, 2010). Temporality may once again play a role here, as it factors into acclimation. As organisms acclimate to stress, the fitness gains from interacting with each other in a positive manner may diminish, and non-linear patterns of response that do not necessarily clearly support or contradict the SGH may result (Callaway & Walker, 1997; Stachowicz, 2001).

Stress type

Finally, we emphasise the need for more multifactor stress studies, as the only multifactor stress studies in our meta-analysis were cases of bifactor stress. We accounted for as many stressors as possible in our search phrases, so we attribute this scarcity to a lack of published data. More work is needed to show how three or more stressors may interact to shift ecological interactions. Only 30% of published climate change studies incorporate multifactor stress, which can be interactive rather than additive (Collins, 2009; Matesanz & Ramírez-Valiente, 2019) as we found when drought and nutrient stress and fire and predator stress were combined. There are not enough multifactor stress experiments out there to effectively evaluate support for or against the SGH, and this is urgently needed in the context of climate change to accurately predict organism resilience and extinction for improving ecosystem and conservation management.

Additional testing is urgently needed to resolve the theoretical controversies surrounding the SGH. Multiple frameworks have emerged regarding mechanisms of SGH support in situations of combined stress, and mechanistic understanding cannot be achieved without the accumulation of empirical evidence. One such framework expands upon the original Hutchinsonian principles upon which the SGH was originally based by emphasising context evaluation in terms of whether resources are limited or not (Maestre et al., 2009). If any stress factors are combined with the factor of resource stress, negative interactions should increase. In the absence of resource limitations, the SGH should be supported. Contrary to this framework, we found that support for the SGH is higher in cases of coupled resource limitations such as drought and nutrient stress, leading us to conclude that mechanics of the Hutchinsonian niche mechanics—which is intrinsic to species—are not the principal driving force behind the fulfilment of SGH expectations. We subscribe to an alternative framework presented by Smit et al. (2009), which incorporates elements of the

Grinnellian or Eltonian niches—which are extrinsic to species and instead of a function of the environment, whether as main effects or interactions, respectively—by predicting that associational resistance tracks in a hump-shaped curve across resource gradients. This modification explains why contrary to our expectations SGH studies did not detect the phenomenon of mutualisms other than pollination increasing in positivity. Nevertheless, the idea of combining resource limitations with three or more other stress types simultaneously has rarely been tested (Graff & Aguiar, 2017), so the relative importance of Hutchinsonian resource factors relative to biotic variables such as adaptations and behaviours remains unresolved. The need persists for community ecologists to follow the lead of evolutionary biologists in accounting for positive interactions in scientific pursuits, such as associational resistance in tests of the SGH.

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AUTHORSHIP

A.E.A. conceived the ideas, drafted methodology, and led the writing of the manuscript. A.E.A., E.M.B., and G.S. collected, processed, and managed the data and searched related literature. E.M.B., G.S., and M.A.P. offered feedback to improve methodology. E.M.B. and A.E.A. conceived the workflow figures and tables. M.A.P. conceived the statistical analyses and results figures and copyedited the main text. All authors contributed critically to the drafts and gave final approval for publication.

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DATA AND CODE AVAILABILITY

Datasets and code associated with the manuscript have been deposited in the Open Science Framework (OSF) repository: <https://doi.org/10.17605/OSF.IO/YDFG6>.

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