

THE QUARTERLY REVIEW of BIOLOGY



THE DISTRIBUTION OF SPECIES INTERACTIONS

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KEYWORDS

abiotic stress, consumer stress, positive interactions, facilitation, range limits, rules

ABSTRACT

General rules are rare in community ecology, although the relationship between stress and the distribution of species interactions is a notable exception. Negative interactions predominate at low levels of stress and interactions shift toward being more positive at higher levels of stress. Facilitation resulting from habitat amelioration and associational resistance are common where abiotic and consumer stress, respectively, are high. Situations with both high abiotic stress and consumer pressure are uncommon and these two stresses are often negatively correlated. A similar pattern between stress and outcome of interactions also applies for species experiencing nutritional deficiencies. The relationship was initially noticed for plants, but also applies to bacteria and some animals and has received more support for survival rather than growth or reproduction. The pattern holds over many levels of stress, but positive interactions become less strong at very high stress levels, producing a hump-shaped relationship. Range limits are extended by facilitative interactions where stress is strong. The pattern is best supported for interspecific rather than intraspecific interactions. Positive interactions under stress were initially envisioned as arising from greater available resources at lower densities. In addition, phenotypic change (due to plasticity, evolution, or species turnover) can also alter the outcome of interactions.

The Quarterly Review of Biology, volume 98, number 4, December 2023.

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INTRODUCTION

IN AN influential paper, John Lawton concluded that “community ecology is a mess, with so much contingency that useful generalisations are hard to find” (Lawton 1999:178). He viewed community ecology as being “unworkably complicated” (Lawton 1999:180) so that “we have no means of predicting which processes will be important in which types of system” (Lawton 1999:181). He was referring to efforts to understand “the ecology of sets of coexisting species interacting at local scales” (Lawton 1999:180). In other words, he was attempting to explain the organisms and interactions that we can expect to find at a given field site. While regretfully acknowledging that we have no universal laws in any areas of ecology, he viewed population ecology and macroecology as more tractable fields. Lawton argued that those levels of ecological investigation have fewer axes for important contingencies and therefore are better able to yield repeatable patterns. As an example of one such useful general pattern, he cited Robert Whittaker’s figure that categorizes the biomes of the world along two axes, precipitation and temperature (Whittaker 1975:167, Figure 4.10). The figure represents a pattern or correlation between climate and vegetation that Whittaker viewed as causal; he considered the growth forms as convergent adaptations visible at the scale of communities. The figure accurately predicts the distribution of biomes based on these two environmental variables, although both Whittaker and Lawton acknowledged that boundaries among the biomes cannot be located exactly because other variables may also play important roles. It is worth noting that Whittaker’s valuable contribution described a repeatable ecological pattern, although the mechanisms that produce this pattern are less well understood.

In contrast to Whittaker’s tidy categorization of communities along two axes, Lawton cited Schoener’s attempts to catalog species interactions that involved 12 distinct axes (Schoener 1986). Lawton concluded by cautioning that community ecologists interested in species interactions should not expect even simple general rules because of the un-

manageably numerous contingencies that exist at this level of study. Interactions and their outcomes are likely to be more contingent when they are indirect and involve more than two species, and when they are density-dependent or affected by spatial proximity (Bronstein et al. 2006); unfortunately, ecological systems commonly exhibit these conditions (Thompson 2013; Mathis and Bronstein 2020).

We believe that community ecology is in much better shape than Lawton’s bleak characterization. It is certainly true that we have no universal laws, a failing that is shared by other fields in ecology (e.g., population ecology, macroecology) and other largely descriptive sciences (e.g., geology and many fields in biology; Waters 1998). However, community ecologists have been collecting generalizations that have been useful guides for some time, even if these generalizations have exceptions and context dependencies. In fact, the promise of laws in ecology lies in context dependencies.

Species interactions are thought to organize communities. Some of these interactions (e.g., interspecific competition, risk of being eaten) can have strong negative effects on the species involved. Other interactions (e.g., mutualism or facilitation) can be beneficial or even essential for survival. These species interactions occur within the context of local climatic and abiotic conditions and are embedded within broader communities of varying populations and species, many of which change over time (Thompson 2013). These abiotic and living components have the potential to influence the outcomes of species interactions. Are there general rules about the effects of abiotic and biotic drivers on the occurrence or outcomes of species interactions?

Our goal in this paper is to highlight patterns in the distribution of species interactions. We focus on abiotic and biotic stresses and how they predictably shape species interactions. Associations between stress and the distribution of species interactions have been noted for decades (e.g., Menge and Sutherland 1976), with a major advance put forward by Bertness and Callaway (1994). In the current paper, we first review the hypothesis that

they suggested. Next, we consider what we have learned about this pattern since it was described. Where is there support for this generalization, and what are the limits of that support? What are areas that should receive more research attention in the future?

There have been several excellent quantitative meta-analyses of the hypothesis during the intervening years (e.g., He et al. 2013; Adams et al. 2022). Meta-analyses are useful because they provide a quantitative assessment of patterns that may be obscured by the biases of individual researchers and systems. They also suggest generalities that average over the specific details of individual studies and organisms. For example, a meta-analysis revealed that the hypothesis that stress can predictably alter species interactions was well supported for plants and bacteria, although studies involving bacteria were not explicitly designed to test this hypothesis (Adams et al. 2022). The hypothesis was not supported generally by studies involving animals, fungi, and chromists as focal species. Nonetheless, this averaging can also make some patterns harder to detect if relevant details and mechanisms are not explicitly included in the analysis. The conclusions of meta-analyses are also dependent on the particular response variables that are considered (Aschwenden 2015). Although we report some of the generalities that have emerged from these meta-analyses, our approach is different. We summarize the conceptual ideas about the distribution of species interactions and evaluate where we expect those ideas to be well-supported by empirical studies. We have attempted to understand the messy biological details producing the patterns and we consider the possible mechanisms that could be driving them. Although decidedly less quantitative, and subject to the examples we choose, our goal is to provoke advances that embrace the ecological contingencies that are not yet sufficiently replicated for meta-analyses.

THE STRESS-GRADIENT HYPOTHESIS

In contrast with Lawton's appraisal, the stress-gradient hypothesis has been successful at predicting the net outcomes of inter-

actions between pairs of species (Bertness and Callaway 1994; Maestre et al. 2009). Low levels of abiotic stress lead to biotic interactions that are more negative, often because competitors clamor for resources and consumers feed unfettered. As conditions become more stressful, positive interactions (facilitation and mutualism) between species become more frequent and stronger compared to less stressful conditions. Inter-specific facilitation occurs when the presence of one species improves the performance or numbers of another species; mutualism occurs when both species facilitate each other.

Conditions favoring greater facilitation include both high levels of abiotic stress and high consumer pressure. As such, this hypothesis presents a simple two-dimensional representation of species interactions, not unlike the one developed by Whittaker for biomes (Figure 1). At high levels of abiotic stress, neighbors often ameliorate that stress by improving conditions (e.g., by providing shade, moisture, thermal insulation). For example, the presence of *Juncus* neighbors changed levels of soil salinity and oxygen in a coastal marsh allowing other plants to succeed in those habitats (Bertness and Hacker 1994). At high levels of consumer pressure, neighbors often reduce risk by physically protecting more vulnerable individuals or by making them harder for consumers to detect, a phenomenon that is termed associational

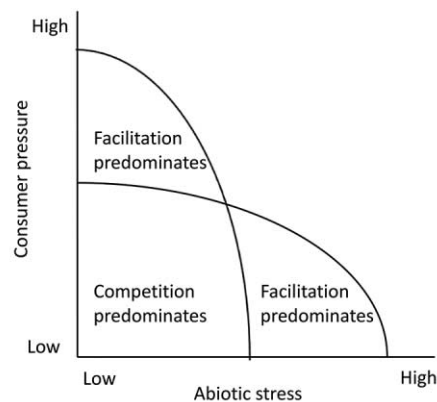


FIGURE 1. THE DISTRIBUTION OF SPECIES INTERACTIONS PREDICTED BY THE RELATIVE STRENGTH OF ABIOTIC STRESS AND CONSUMER PRESSURE

resistance (Atsatt and O'Dowd 1976; Callaway 2007).

Whittaker's figure included precise values for his axes (mean annual precipitation and temperature) while Figure 1 leaves the scale of the axes ambiguous. At the very least, we can try to define stress precisely; Grime (1977) defined stress for plants as a factor that limited an organism's ability to convert energy to biomass. This definition includes both abiotic and consumer stress and seems applicable to animals as well as plants. Abiotic stress can be evaluated by calculating community-level productivity—organisms facing more stress will be less productive. Consumer pressure can be quantified as the percentage of biomass (e.g., leaf area) that is removed over some period of time. We can expand Grime's definition of stress to include factors that reduce an organism's expected fitness, although fitness loss is harder to quantify than biomass. It is important to recognize that this definition is inherently species-specific. Plant species adapted to high light environments will experience different levels of stress than those adapted to forest understories. This makes it less meaningful (and potentially misleading) to characterize habitats as more or less stressful for all organisms. Despite the lack of quantitative predictions in Figure 1, it is still possible for empiricists to test the relative changes in the frequency and strength of the positive and negative interactions along gradients of relative levels of abiotic and consumer stress.

BROADENING THE STRESS-GRADIENT HYPOTHESIS

It is useful to consider where the hypothesis has been well supported and where it has not predicted the outcome of interactions or not received much testing. The hypothesis was developed with plants and sessile marine invertebrates in mind and the early evidence to support it came from these taxa (Bertness and Callaway 1994). An early global meta-analysis that included 727 studies of interactions between plant species revealed that interactions affecting survival became more positive as physical, consumer, or resource stress increased and interactions involving

growth and reproduction became less negative over this same gradient (He et al. 2013). A more recent meta-analysis that was more taxonomically inclusive found strong support for the hypothesis among bacteria and plants but failed to find support among animals and other taxa, although these latter groups have been less commonly examined (Beaudrot et al. 2020; Adams et al. 2022). The pattern received more support when survival and abundance were the response variables and less support when growth, reproduction, or biomass were considered (Adams et al. 2022).

Studies that explicitly manipulated stress found better support for the hypothesis, although this criterion excluded many observational studies (Adams et al. 2022). Observational studies along elevational gradients have often been used to evaluate the hypothesis. Elevational gradients are useful since abiotic conditions (such as temperature and length of the growing season) become more stressful for many species at higher elevations. Comparisons of plant communities along elevational gradients offered some of the strongest support for the hypothesis. Interactions between neighboring plant species were found to be more competitive at lower elevation sites and more facilitative at higher elevation sites (Duarte et al. 2021). For example, in a replicated study at 11 montane sites around the world, removing neighbors had more positive effects on focal plants at lower elevations (less abiotic stress, stronger competition) and less positive effects at higher elevations (more abiotic stress, weaker competition; Callaway et al. 2002). In these cases, changes in species composition (and hence traits) were associated with altered abiotic tolerances and species interactions. In other words, under high stress conditions both the identities of the species that were present and the sign and strength of interspecific interactions changed.

At very high levels of stress, the positive effects of facilitating species may be unable to ameliorate conditions sufficiently to outweigh negative effects (Holmgren et al. 1997; Holmgren and Scheffer 2010). This limitation has been noted for amelioration of extreme abiotic stresses (e.g., Michalet

et al. 2006) and for extreme levels of consumer pressure (e.g., Brooker et al. 2006; Levenbach 2009). At very high levels of stress, densities of the affected species may be sufficiently reduced so that resource limitation becomes negligible, and the benefits of facilitation also become negligible. When facilitation is based on procuring a limiting resource (e.g., water), the relationship may become competitive at extreme levels of stress because the “facilitator” is no longer able to increase resource acquisition (Maestre et al. 2009). As a result, the relationship between net benefits of interactions and stress becomes hump-shaped (Figure 2). This hump-shaped relationship is reminiscent of the intermediate disturbance hypothesis (Grime 1973; Connell 1978). According to this hypothesis, competition dominates at low levels of stress (Grime’s model) or disturbance (Connell’s model). At very high levels of stress or disturbance, only those few species that were specifically adapted to stressful situations could prosper but at intermediate levels, and competitive interactions were diminished or became less important than dispersal. It should be noted that this hump-shaped intermediate dispersal hypothesis has not been well supported by empirical studies (Mackey and Currie 2001; Fox 2013). In summary, responses to a gradient of stress may be better represented by nonlinear or threshold models than by linear models; when this is the case, responses to moderate levels of stress that are observed under many condi-

tions and times cannot predict the effects of extreme stressors (Reyer et al. 2013). These observations beg the questions: How often in nature do species find themselves dealing with stresses that are sufficiently severe as to cause the net outcome of interactions to become negative? Will extreme stresses become more common in the future as the result of anthropogenic influences?

Patterns associated with stress and species interactions have been described to play out over relatively restricted spatial scales. Nevertheless, species interactions and abiotic factors that occur locally can potentially scale up to determine species’ ranges. Many naturalists have observed that range limits in stressful conditions are set primarily by abiotic conditions while those in less stressful conditions are set by species interactions (Figure 3). Darwin (1859) noted this phenomenon as he described traveling north toward the Arctic or approaching dry deserts. More recently, many studies from a variety of systems have found support for this interpretation (see Gaston 2003; Sexton et al. 2009; and Louthan et al. 2015 for reviews). One of the earliest and most convincing tests of this idea was Connell’s study involving microenvironmental distributions of barnacles off the coast of Scotland (Connell 1961). In the less stressful lower intertidal zone, the limit to the distribution of a focal species was set by competition for space, while in the more stressful upper zone the limit to the distribution was set by the ability to tolerate heat and desiccation. Subsequent studies indicated that predation could also limit the distribution of intertidal species in zones with less abiotic stress (Paine 1974). It is worth noting that these studies considered zonation, range limits over very small spatial scales.

Results from several experimental studies of plant distributions over larger scales have also been consistent with this pattern. For example, the lower range limits of several plants on Mount Rainier were more strongly affected by competition while the upper limits were more strongly affected by abiotic conditions and perhaps mutualisms (HilleRisLambers et al. 2013). At the range edge with strong abiotic stress, the availability of pollinator mutualists became more limiting to populations

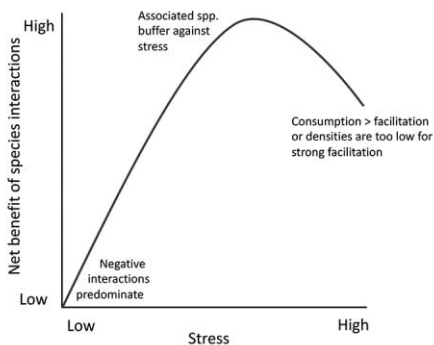


FIGURE 2. A HUMP-SHAPED RELATIONSHIP BETWEEN LEVELS OF STRESS AND THE FREQUENCY OR STRENGTH OF SPECIES INTERACTIONS

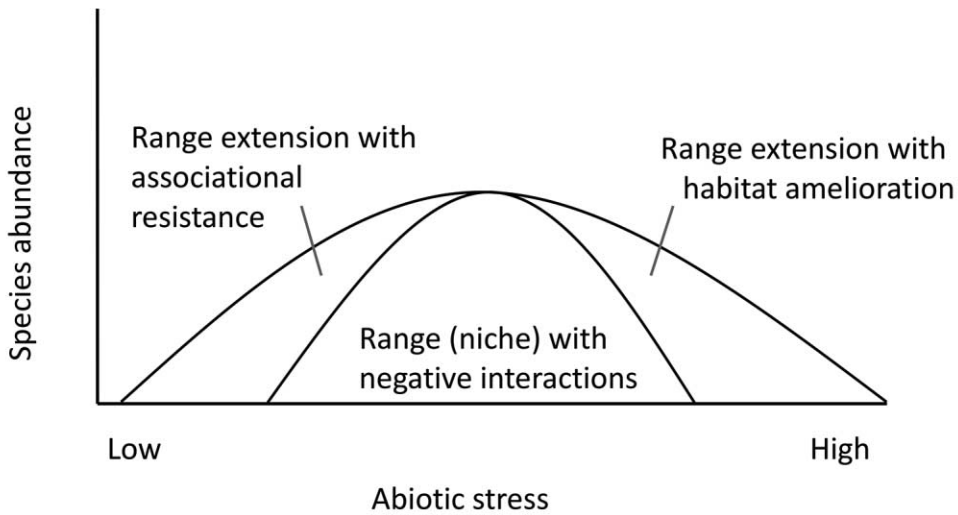


FIGURE 3. RANGE LIMITS FOR SPECIES AS A FUNCTION OF THE RELATIVE LEVELS OF ABIOTIC STRESS

At high levels of abiotic stress, amelioration of stress due to facilitation allows expansion of range limits. At low levels of abiotic stress, consumer pressure is often higher and associational resistance to consumers facilitated by interactions allows expansion of range limits.

of *Clarkia xantiana* than in the climatically favorable center of the range (Moeller et al. 2012). In this system, facilitative soil microbes were also necessary to provide tolerance to abiotic stress in order to expand the range (Benning and Moeller 2021). Similarly, *Bromus laevipes* was able to expand its range into drier habitats when it co-occurred with a fungal endophyte (Afkhami et al. 2014). Thus, persistence under stressful conditions, especially at range edges and beyond, often requires positive interactions, although most of this support comes from studies at small spatial scales (Bruno et al. 2003). In summary, most studies of the effects of stress on species interactions have measured a limited number of demographic parameters (e.g., growth, survival) over small spatial scales and it is unclear whether these results will scale up to shape larger scale properties (e.g., population sizes, range limits).

The validity of the stress-gradient hypothesis across different spatial scales has received more consideration than its relevance at different temporal scales, a bias that has been repeated for many processes in ecology. Most experiments and observations that support the hypothesis are of relatively short duration and we have less information about outcomes

over longer time periods. Individuals that exhibited net competitive effects during times when conditions were less stressful had more positive effects during more stressful times (Veblen 2008; Biswas and Wagner 2014). This scenario is consistent with observations of stronger facilitative effects early in succession when soil nutrients such as N are relatively scarce and stronger competitive effects later when nutrients are more available (Vitousek et al. 2013; Koffel et al. 2018).

One component of timing that affects the outcome of species interactions is the increase in body size over an individual's development. As such, effects of stress may be stage-dependent. Many naturalists have observed that small individuals are more vulnerable to both abiotic and consumer stress than larger, older individuals of the same species (e.g., Darwin 1859:Chapter III; Zalucki et al. 2002; Barton and Koricheva 2010; Quintero et al. 2013). Small individuals are at more risk of desiccation and are less buffered against heat and cold. Larger individuals gain a size refuge against many potential predators and defenses other than size are better expressed in older, larger individuals. Many examples of facilitation involve a relatively large benefactor and a relatively smaller beneficiary.

Large individuals are able to provide resources such as shade and protection from consumers to smaller individuals with little cost to themselves.

ABIOTIC AND CONSUMER STRESS ARE NEGATIVELY ASSOCIATED

The stress-gradient hypothesis considered two sources of stress—difficult abiotic conditions and high consumer pressure. Ecologists have noted a trend for organisms to be able to cope with environments that challenge them with high levels of either physical or consumer stress, but typically not both (Menge and Sutherland 1976). In other words, species are well represented on the upper left or lower right of Figure 1, but not in the upper right. The two types of stresses are often negatively correlated. For example, predation in rocky intertidal habitats was found to be weak where abiotic stress was strong, and strong where abiotic stress was reduced (Menge 2003). Similarly, an examination of morphological defenses of diverse marine organisms suggested that predation pressure decreased as physiological stress increased over longer time frames (Vermeij 1978). Conversely, marine systems characterized by productive upwelling experience very high levels of consumer pressure (Thompson et al. 2012). Most researchers who documented a negative correlation between abiotic stress and consumer pressure have assumed that abiotic stress is the driver of this relationship. In stressful habitats, if consumers are more sensitive to abiotic stress than their prey, this could lead to a spatial refuge from predators, which could be reinforced by selection for stress tolerance at the cost of defense against predators.

A dearth of species in the upper right of Figure 1 has also been reported for terrestrial systems. For example, where herbivore pressure was strong and abiotic stress was high on Mount St. Helens, few plants were able to recolonize (Fagan and Bishop 2000). Comparisons along elevational gradients have also been consistent with negative associations between abiotic stress and consumer pressure. Recent work suggests that consumer pressure is greater at lower elevation sites that

provide weaker abiotic stress (corresponding to the upper left in Figure 1). Consumers exhibited higher population sizes and species richness at lower elevations and these conditions were associated with higher levels of herbivore pressure (Moreira et al. 2018). Similarly, a large meta-analysis indicated that herbivory was greater at lower elevations for woody plants (Figure 1, upper left), but not for nonwoody species (Galmán et al. 2018). These authors speculated that smaller herbaceous plants experienced relatively low levels of herbivory by being ephemeral and less apparent to potential herbivores (*sensu* Feeny 1976).

In a study of 20 Amazonian trees species, Fine et al. (2004) reported that protection from herbivores for species on resource rich soils resulted in increased plant growth, while the same treatment for phylogenetically paired species on poor soils did not. Thus, the negative impact of herbivory was weaker in communities that experienced more abiotic stress. In general, plants growing in situations with less abiotic stress are better able to regrow and tolerate tissue loss to consumers compared to plants in more stressful conditions with access to fewer resources (Endara and Coley 2011). In addition, high levels of defense in stress-adapted plants may contribute to lower impacts of herbivores under stressful conditions. Thus, differential impacts of stress on interacting species, as well as their evolved traits, may promote the negative association observed between stresses. As discussed below, when comparing more or less stressful communities, measuring densities and traits of the species involved is likely to provide insight into why or why not results follow expected patterns.

The generality of the negative association between abiotic stress and consumer pressure has been questioned in a meta-analysis that found that abiotic stress and consumer pressure could interact antagonistically, synergistically, or independently (Silliman and He 2018). Nonetheless, many of the studies that failed to find this negative association were short-term pulse experiments manipulating one of the stressors. Short-term experiments that are sufficient to affect individual

performance may or may not scale up to affect persistent differences in species interactions. In particular, we argue that there is a fundamental difference between communities that are somewhat equilibrated to differential stresses (e.g., along elevational gradients, in distinct habitat types, or at distinct times in a successional trajectory) compared to those that receive one-time acute stresses (e.g., in response to severe climatic events or the outbreak of an invasive pest). The former comparisons of longer-term, more consistent stresses test predictions about the community outcomes we are interested in here, where densities and traits of species have been exposed to directional selection. The latter (short-term effects) are important for understanding issues related to acute stresses, but may be less predictive of patterns in community ecology.

NUTRITIONAL STRESS

The stress-gradient hypothesis originally considered abiotic stress and high consumer pressure; a third type of stress that organisms commonly encounter is insufficient or incomplete nutrition. For many autotrophs, abiotic conditions will determine the nutrients that are available and nutritional stress may be considered as a subset of abiotic stress. This is less often the case for heterotrophs. Stress caused by insufficient nutrients has received less attention than abiotic and consumer stresses, although it is widespread and could be considered as a third axis in Figure 1. Associations with other species can potentially alleviate nutritional deficiencies, but these associations are not necessarily beneficial and range from negative to positive. For example, plants have sophisticated defenses that recognize and defend against most fungi. However, these plants may allow the colonization and exchange of nutrients with mycorrhizal fungi that extract carbohydrates from plants, but provide their hosts with water and minerals. In these cases, the plants and fungi monitor the costs and benefits of their respective contributions, adjusting them to increase the net benefits they receive (Kiers et al. 2011). Similarly, in legume-rhizobia interactions, mutual benefits to the

partners and investment in the mutualism are the strongest when soil nutrients are limiting (Elias and Agrawal 2021). Indeed, when nutritional stress has been included in tests of the stress-gradient hypothesis, it has provided some of the strongest support for shifts to facilitation with increasing levels of stress (Adams et al. 2022).

EFFECTS OF INTERACTIONS AT DIFFERENT ECOLOGICAL LEVELS OF ORGANIZATION

The stress-gradient hypothesis was developed for interactions between species, and this is the most common level of study for much of community ecology (and the level that Lawton was most discouraged about). Among pairs of species, positive interactions are more often noted among distantly related species and less likely among more closely related species (Valiente-Banuet and Verdú 2013; Verdú et al. 2021). This relationship likely arises because phylogeny reflects phenotypic similarity and similar species are likely to respond similarly to stresses and to use similar niches. This may be particularly important for establishment of immature individuals (e.g., Valiente-Banuet and Verdú 2007). Many of the examples of facilitation that reduce the impacts of stress can be considered by-products of the normal activities of the facilitator species (*sensu* Connor 1995). This is especially important for distantly related pairs of species where a by-product for one species can be a limiting factor for another. This situation is often true for amelioration of stressful abiotic conditions (e.g., shade provided by a neighbor), tolerance of partial consumption (e.g., tissue loss to herbivory; Agrawal 2000), and nutrients provided to species growing in resource-poor environments (e.g., plant-mycorrhizal contributions; Kiers and van der Heiden 2006). When the resources or services provided by facilitators in stressful situations are by-products of their normal activities, they are less costly to provide; reduced cost makes these net positive interactions more likely to be stable (Agrawal 2000).

The stress-gradient hypothesis could potentially apply to interactions among individuals of the same species or to those among

clades of related species. Individuals that are more similar are more likely to compete for resources, mates, and so on, as noted above. This has given rise to the general pattern that intraspecific competition is usually stronger than interspecific competition (Darwin 1859; Hardin 1960). Negative competitive effects between conspecifics have been best documented for survival, but interactions with conspecifics can also be positive in terms of opportunities for mating and cooperating. For example, Allee effects, which are positively density-dependent at least at low population sizes, can be critical for population growth (Angulo et al. 2018). Nonetheless, in a meta-analysis, interspecific interactions were often positive while intraspecific interactions were more strongly negative (Adams et al. 2022). In summary, although intraspecific interactions can be positive under some conditions, this outcome occurs less frequently compared to interspecific interactions.

The stress-gradient hypothesis also predicts patterns at higher taxonomic levels. Positive interactions between ancestral species may have allowed those species to be successful and radiate. As a result, we now see entire clades of species that engage in similar facilitative interactions. Many clades of animals that subsist solely on food regimes that lack a full complement of nutrients engage in obligate mutualistic relationships with digestive microbes that make their dietary regimes possible. For example, many species of termites that feed on cellulose (Brune 2009), heteropterans that feed on xylem fluid (Ankrah et al. 2018), and tsetse flies that feed on blood (Hirose et al. 2012) all form obligate mutualistic relationships with bacteria that supplement their diets. Similarly, lichens, which consist of associations between diverse species of fungi that live with algae or cyanobacteria, are successful under more conditions than these species would be without their symbiotic partners. When living in extreme environments (or on extreme diets), positive interdependencies (“metaorganisms”) appear as common strategies (Bang et al. 2018).

Clades of organisms also engage in mutualistic relationships that provide protection from potential consumers. Many terrestrial

invertebrates associate with ant species that actively defend them (Bronstein 1998). For example, caterpillars that face high consumer pressure produce nectar rewards that attract ant bodyguards (Agrawal and Fordyce 2000). Adult periodical cicadas of several species emerge synchronously in extraordinarily high numbers; individuals that emerge alone or in smaller groups are less likely to satiate predators and leave fewer offspring as a result (Karban 1982). Cicada species that have evolved with less risk of predation have not adopted this strategy (Lloyd and Dybas 1966a,b).

At an ecosystem scale, facilitation under stress may form the basis of persistent communities. For example, biological soil crusts are mutualistic associations of cyanobacteria, algae, fungi, and plants that are found in the most stressful hot deserts and tundra (West 1990; Pointing and Belnap 2012). Biocrusts facilitate soil formation, prevent erosion, and regulate water and nutrient cycles; establishment of vascular plants is enhanced by their presence in these extreme habitats. Similarly, in freshwater systems, facilitators that modify habitats often produce positive effects on other species under stressful conditions (Albertson et al. 2021). For example, beavers act as ecosystem engineers that reconfigure ecosystems and facilitate many other species that would otherwise find conditions too stressful to survive during drought years (Hood and Larson 2014).

The stress-gradient hypothesis can also inform our understanding of patterns of diversity. Many studies have found that positive interactions that ameliorate stress ultimately increase species richness (e.g., Hacker and Gaines 1997; Michalet et al. 2006; Angelini et al. 2011; Cavieres et al. 2014; Duarte et al. 2021), although other outcomes have also been noted (e.g., Bulleri et al. 2016; Albertson et al. 2021). When positive effects on species richness were observed, the facilitators were often foundational species that caused large habitat modifications and increases in heterogeneity, allowing less competitive species to coexist. Positive effects that increase diversity are often critical for recruitment and establishment of younger individuals. For example, nurse plants were associated with

increased richness under stressful conditions (Valiente-Banuet and Verdú 2007; Soliveres et al. 2012).

DIFFERENT RESPONSES TO INCREASING STRESS

As stress increases in a system, we can imagine several different ecological processes (mechanisms) occurring (Table 1). First, when comparing habitats with large and persistent variation in levels of stress, the species found in different locations (stress levels) will likely turn over, and many aspects of their ecologies will differ. The strong pattern of greater facilitation in places with more stressful habitats may reflect both differences in densities and traits of the species present (Callaway et al. 2002). This tendency was rec-

ognized by early ecologists who studied primary plant succession. Species interactions that permitted the establishment of vegetation on dunes or following glacial retreat often involved facilitation (Cowles 1899; Crocker and Major 1955). In addition to species turnover, less stressful habitats tend to support a greater diversity of species. For example, the community of herbivores has often been noted to be more diverse in less stressful situations and this more diverse community is predicted to include one or more species that can exert a strong negative impact on their host plants (Menge and Sutherland 1987), although this hypothesis has met with mixed support in comparisons between tropical and temperate habitats (e.g., Novotny et al. 2006; Salazar and Marquis 2012).

TABLE 1
Mechanisms underlying the stress-gradient hypothesis that species interactions are less negative as environmental stress increases

Mechanism	Example	Key comparison groups
<i>1. Density is reduced by stress</i>		
1A. Density is strongly reduced causing species turnover	Species identity (and thus traits of interacting species) differs in communities with high and low stress impacting the outcome (e.g., Fine et al. 2004)	Assess the traits of species in communities with different, but phylogenetically related, species and relate these traits to the outcomes of interactions
1B. Mean density is reduced—competition is relaxed	Stress limits population density making more resources available (e.g., Callaway 2007)	Remove neighbors in more and less stressful communities and assess abundance of the focal species
1C. Density of species in trophic interactions differentially affected	Predator abundance is more strongly disrupted by stress than prey, thereby reducing impacts of predators (e.g., Menge and Olson 1990)	Assess effects of stress on each trophic group's abundance, as well as the net outcome of the interaction
<i>2. Traits are affected by stress</i>		
2A. Increased tolerance of stress resulting from phenotypic plasticity	Phenotypic response to stress in either (or both) interaction partner impacts the outcome (e.g., Agrawal and Fordyce 2000)	Assess effects of stress on phenotypes of interacting species and relate this to the outcome of the interaction
2B. Local adaptation that changes interactions	Evolutionary response of either (or both) interaction partner impacts the outcome (e.g., Formenti et al. 2021)	Assess genetically differentiated phenotypes from populations with different levels of stress (e.g., in a common garden) and relate these adaptations to outcomes of interactions

In each case, more and less stressful communities are examined, typically by the removal of a focal community member to assess the strength of the interactions between that focal species and others in the community.

Reductions in density have been thought to be the primary drivers of positive interactions for comparisons of communities with similar species present but with increasing levels of stress. Fewer individuals will compete less strongly for existing resources. Regardless of the type of stress that limits densities, more food and more protected refuges may be available to those individuals that can tolerate the stress. Additionally, as discussed above, differential sensitivity to stress may alter densities of some groups more than others (i.e., predators more than prey), predictably altering the frequency of interactions. These two density-mediated effects (second and third rows of Table 1) represent changes associated with stress that alter interactions within a community of the same species.

In addition to effects of stress on the densities of interacting species, stress-induced altered phenotypes within species may also change the outcome of ecological interactions. Whether phenotypic change is associated with phenotypic plasticity as discussed above or with local adaptation (a more permanent change), both can impact the outcome of species interactions. For example, cold temperatures often force consumers to capture and ingest more food, presumably intensifying the effects of consumptive interactions (Dell et al. 2011). Prior experience may dampen the effects of stress on organisms. For example, adaptive responses (plastic or evolutionary) to prior stress may reduce the positive effects of facilitation under stress (Espeland and Rice 2007). Ultimately, both the densities and traits of organisms that respond to stress will determine the strength and outcome of species interactions.

When designing and interpreting studies that impose stress or remove neighboring species, it is important to be aware of the time frame involved. When possible, long-term experiments are the ideal. Experiments that are of short duration may not allow sufficient time for species to experience and respond to the negative consequences of abiotic and consumer stress. This temporal limitation may also be addressed by also including longer-term natural comparisons with low replication and less confidence about causation

(e.g., comparing areas with and without vertebrate predators). Advances in statistical methods that consider joint species distributions and include other variables such as levels of stress can also be informative (Warton et al. 2015; Van Ee et al. 2022). As discussed above, when comparing sites in which adaptation or species turnover have changed the effects of stress on species interactions, understanding the traits involved will aid in developing a predictive framework. Multiple mechanisms that affect the traits and interaction strengths of species in a community along a stress gradient are possible; the predictability of each mechanism, its relative importance, and longer-term implications are not well known and are worthy of attention.

CONCLUSIONS

Stress has been widely studied as a mediator of ecological interactions and the stress-gradient hypothesis has shown considerable power in explaining the distribution of ecological interactions. The original stress-gradient hypothesis provides a useful generalization that applies to many taxa, in many situations, and at many scales (summarized in Table 2). Net effects of species interactions tend to be more positive under abiotic stress, high consumer pressure, and nutritional limitations. Most fundamentally, stress often results in poor performance of some individuals, induces phenotypically plastic responses, imposes natural selection, and causes species turnover in communities. Stress may free up resources, especially when some species perform poorly, and there may be reduced levels of competition or predation. Alternately, when phenotypes change (due to plasticity, evolution, or species turnover), these new phenotypes may shuffle the relative importance of ecological interactions. Some of these changes indicate that positive interactions are necessary for survival and reproduction under stressful conditions. Other changes result in muted negative species interactions under stress. Thus, stress has the potential to provide an explanation for both short- and long-term ecological changes and

TABLE 2

Summary of the original stress-gradient hypothesis (Bertness and Callaway 1994) that explained the distribution of species interactions and an assessment of current evidence evaluating the hypothesis

Original hypothesis	Support	Limitations	Explanation
<i>Taxa:</i> plants and sessile marine invertebrates	Strong support for plants and bacteria	Weak support for animals, chromists, and fungi	Animals have a diversity of strategies including movement
<i>Types of stress:</i> abiotic and consumer stress	Strong support for abiotic stress and for nutritional, resource stress	Weaker support for consumer stress	Effects associated with consumers can be negative if neighbors are attractive to consumers
<i>Response assessed:</i> frequency of interactions	Strength of interactions (effect sizes)	Frequency and other response metrics are less commonly measured	
<i>Demographic response:</i> survival	Strong support for effects on survival	Weaker support for growth and reproduction	Growth is shorter term than survival; reproduction occurs later in development; aftereffects are no longer visible
<i>Scale of the pattern:</i> full range of stress gradient	Strong support at intermediate stress levels (Holmgren et al. 1997; Brooker et al. 2006)	Effect diminished at very high levels of stress (Holmgren et al. 1997; Brooker et al. 2006)	Intermediate levels of stress reduce competition or allow facilitation without completely suppressing the focal species
<i>Scale:</i> comparison among species	Strong support in interspecific comparisons	Weak support in intraspecific comparisons	Intraspecific phenotypes may be too close to allow for facilitation without competition
<i>Scale:</i> individual species	Species diversity is also increased by facilitation (e.g., Hacker and Gaines 1997; Duarte et al. 2021)	This pattern is likely saturating and highly conditional	Changes in diversity will be dependent on the species pool and priority effects
<i>Spatial scale:</i> small scale zonation	Prediction: facilitation can also increase species' ranges (Figure 3; see also Afkhami et al. 2014)	Range edges typically have multiple altered environmental factors	The net effect of facilitation may depend (as always) on the relative balance of benefits versus other challenges faced at the edges
<i>Temporal scale:</i> largely unexplored	Prediction: more support early in ontogeny of individuals and early in succession	Unclear	Costs of stress and benefits to organisms may be dynamic over time

Data from He et al. 2013 and Adams et al. 2022, unless otherwise noted.

outcomes, although the mechanisms vary. Exceptions certainly exist, but exploring these exceptions will strengthen our understanding. Even with these exceptions, the relationship between stress and the frequency and strength of species interactions represents a useful and widespread pattern in community ecology.

Other widespread patterns have also been reported. For example, we can predict the number of trophic levels in a system based on levels of primary productivity (Oksanen et al. 1981). It has also been observed that predators and parasites often have cascading

effects that reverberate through ecological webs, influencing the abundances and traits of species at lower trophic levels (e.g., Strong 1992). These generalizations cannot be considered rules in the strict sense, but they do indicate that community ecology is less of an idiosyncratic mess than Lawton feared.

ACKNOWLEDGMENTS

We thank Amy Hastings, Sharon Lawler, Eric LoPresti, Bruce Menge, Adam Pepi, Danielle Rutkowski, Jay Stachowicz, and Rachel Vannette for suggestions and discussions that shaped our thinking about these issues.

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