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Review

Where and When do Species Interactions Set Range Limits?

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A long-standing theory, originating with Darwin, suggests that abiotic forces set species range limits at high latitude, high elevation, and other abiotically 'stressful' areas, while species interactions set range limits in apparently more benign regions. This theory is of considerable importance for both basic and applied ecology, and while it is often assumed to be a ubiquitous pattern, it has not been clearly defined or broadly tested. We review tests of this idea and dissect how the strength of species interactions must vary across stress gradients to generate the predicted pattern. We conclude by suggesting approaches to better test this theory, which will deepen our understanding of the forces that determine species ranges and govern responses to climate change.

Trends

Both climate and species interactions set species range limits, but it is unclear when each is most important.

An old hypothesis, first proposed by Darwin, suggests that abiotic factors should be key drivers of limits in abiotically stressful areas, and species interactions should dominate in abiotically benign areas.

Four distinct mechanisms, ranging from per-capita effects to community-level synergies, could result in differential importance of species interactions across stress gradients.

These mechanisms, operating alone or in tandem, can result in patterns consistent or inconsistent with Darwin's hypothesis, depending on the strength and direction of effects.

The most robust test of this hypothesis, not to date performed in any study, is to analyze how sensitive range limit location is to changes in the strength of one or more species interactions and also to abiotic stressors.

Abiotic and Biotic Determinants of Species Ranges

The ever-mounting evidence of continuing climate change has focused attention on understanding the **geographic ranges** (see Glossary) of species, and in particular how these ranges might shift with changes in climate [1,2]. A major complication to these efforts, often mentioned but rarely formalized, is that all populations occur in a milieu of other species, with multiple, often complex **species interactions** affecting individual performance, population dynamics, and hence geographic ranges. The implicit assumption of most modern work on range shifts is that either directly or indirectly, climate is the predominant determinant of ranges, but interactions among species might also limit species, current and future geographic ranges [3–5]. Determining where and when climate alone creates **range limits**, and where and when it is also critical to consider species interactions, will allow us to identify the most likely forces setting species range limits.

A better understanding of the forces creating range limits is especially important for the accurate prediction of geographic range shifts in the face of both climate change and anthropogenic impacts on species interactions (e.g., introduction of exotic species, shifts in interacting species ranges, and extinction or substantial reductions of native populations [6–9]). For example, predictions of shifts in species distributions might only need to consider direct effects of climate to be accurate, but if species interactions also exert strong effects, we must include both climate and these more complex effects in our predictions. Finally, if species interactions are important in some sections of a species range but not in others, we can be adaptive in the inclusion of these effects when formulating predictions.

We frame our discussion of the drivers of range limits around the long-standing prediction that climate and other abiotic factors are far more important in what appear to be abiotically stressful areas, whereas the effects of species interactions predominate in setting range limits in apparently more benign areas; we call this the '**Species Interactions–Abiotic Stress Hypothesis' (SIASH**; Table 1). To clarify the evidence and possible causal mechanisms underlying SIASH, we first summarize past work on the drivers of range limits. We then propose a more operational statement of the hypothesis and discuss a series of different mechanisms that could explain systematic shifts in the strength of species interactions across abiotic **stress** gradients. We end by discussing ways to better test the factors setting range limits.

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Table 1. Possible Patterns in Abiotic and Biotic Causes of Range Limits

Cause of Cold (Stressful) Edge Range Limit	Cause of Warm (Nonstressful) Edge Range Limit	Pattern Generated
Abiotic stress	Abiotic stress	Only abiotic stressors determine species distribution
Species interactions	Species interactions	Only species interactions determine species distribution
Abiotic stress	Species interactions	SIASH
Species interactions	Abiotic stress	Opposite of SIASH

A Brief History of Range Limit Theory

Most early work on range limits emphasized the role of abiotic stress (e.g., [10,11]; Box 1), but naturalists also speculated that both abiotic stress and species interactions were important determinants of limits (Table 1). For example, Grinnell [12] observed that the California thrasher (*Toxostoma redivivum*) range is loosely constrained to a specific climatic zone, but in the presence of another thrasher species, it is more tightly constrained. Also, not all authors agreed that the importance of species interactions would vary as predicted by SIASH. Griggs [13] found that competition sets northern range limits for some plant species, and Janzen [14] hypothesized that the breadth of abiotic tolerance is narrower in tropical montane species than in temperate montane species, and thus that climate constrains species elevational ranges more tightly in the tropics.

Despite these different ideas, most thinking about the role of species interactions in range limit formation has centered around the predictions of SIASH. As with so many ecological concepts and theories, Darwin, in *On the Origin of Species* [15], provides the first clear articulation of the idea:

> When we travel from south to north, or from a damp region to a dry, we invariably see some species gradually. . .disappearing; and the change of climate being conspicuous, we are tempted to attribute the whole effect to its direct action. But. . .each species. . .is constantly suffering enormous destruction. . .from enemies or from competitors for the same place and food. . .When we travel southward and see a species decreasing in numbers, we may feel

Box 1. Causes of Range Limits

In addition to simple dispersal limitation, three demographic processes can set range limits [73,74]: (i) a reduction of average **deterministic growth rate** such that a population can no longer be established or survive; (ii) increased variability in demographic rates, such that **stochastic growth rates** are too low for establishment or persistence [75]; and (iii) increasingly patchy habitat distributions or lower equilibrium local population sizes, so that extinction–colonization dynamics will no longer support a viable metapopulation. For simplicity, we emphasize declines in mean performance in our presentation, but both of the other processes can also enforce range limits, through similarly interacting effects of species interactions and abiotic variables on demographic rates. Both empirical and modeling work suggest that all of these demographic processes can operate in nature, but this breakdown of demographic causes of range limits is agnostic with respect to underlying abiotic or biotic drivers.

Anywhere a species is extant, we expect that, over the long term, populations are able to grow from small numbers to some stable population density (although not necessarily the same density everywhere), but the demographic reasons that this condition is not met – and hence a range limit is hit – can vary geographically. For example, survival rates could decline at high temperatures, while reproduction fails at low temperatures, such that population growth rates are higher at intermediate temperatures, but fall at both extremes. Similarly, different abiotic stressors might simultaneously vary over a single geographic gradient: at high elevations cold can reduce survival, while at low elevations, drought can do the same (e.g., [76]: for aspen, drought is stressful in southern populations, but cold is stressful in northern populations). In contrast to these examples, the classic assumption behind SIASH, and most tests of SIASH, is that abiotic stress gradients are one dimensional and monotonic in their effects on population growth, either increasing or decreasing along a latitudinal or elevational gradient. SIASH also assumes that each range limit arises either from abiotic or biotic factors, while it is quite likely that many range limits result from strong synergies between abiotic and biotic factors, rather than just one class of factors alone.

Glossary

Deterministic growth rate: population growth rate assuming no temporal variation in growth rate.

Geographic range: the geographic area where a species is extant. In this work, we are primarily concerned with coarse-grained species ranges (e.g., at the continental scale) rather than distributions at a fine-grain scale (e.g., east- versus west-facing slopes of the same mountain).

Low density stochastic growth rate (λ_{LD}): stochastic population growth rate at low densities, such as when a new population is establishing or a current one is on the verge of extinction, both of which will drive range limits. Population growth at higher densities might be strongly affected by negative density dependence and density-dependent species interactions, and thus might provide a biased assessment of the factors driving range limits.

Range limit: the geographic area where a species transitions from being present to being absent. Here we are primarily concerned with coarse-grained species ranges (see 'geographic range').

Sensitivity of population growth rate: how responsive population growth rate is to perturbations from current values of a factor of interest. For example, high sensitivity to pollination indicates that changing pollination rates would substantially change population growth rate; low sensitivity to pollination indicates that changing pollination rates would have minimal effect on population growth rate.

Species Interactions–Abiotic Stress Hypothesis (SIASH): the hypothesis that range limits in stressful areas are more often set by stress tolerance, but range limits in nonstressful areas are more often set by species interactions.

Species interactions: interactions with other organisms that have some effect on individual or population performance, including both positive and negative effects.

Stochastic growth rate: population growth rate including temporal variation in growth rate.

Stress: any number of abiotic conditions that reduce population performance (even if populations are well adapted to 'stressful' conditions), including factors that lead to low average or high variability in

> sure that the cause lies quite as much in other species being favoured, as in this one being hurt. . .When we reach the Arctic regions, or snow-capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements. ([15], Chapter 3, p. 66)

Dobzhansky [16], MacArthur [17], and Brown [18] all emphasized geographic patterns arising from SIASH, suggesting that low-latitude range limits are set by species interactions (most commonly negative interactions such as competition or predation) and higher-latitude limits by abiotic stressors.

population performance or reduced colonization and increased extinction. This definition includes the effects of chronic physical stress, low resource availability, or high disturbance frequency and severity; these are often difficult to disentangle (but see [72]). Different species might find different ends of an abiotic gradient 'stressful.' Note that we do not include biotic stressors under this definition; although many biotic factors can reduce individual and population performance, others, for example, mutualisms, can increase performance. While some biotic interactions are also 'stressful', for our presentation we restrict use of this term to abiotic conditions.

Tests of the Forces Governing Range Limits

A plethora of correlational studies suggest a major role for abiotic stress in setting range limits (see references in [19]), but direct effects of abiotic stress on physiological performance or fitness in the context of range limits have been more difficult to document [20] (we also note that species find many different conditions 'stressful').

There is also abundant evidence that species interactions, both negative and positive (e.g., facilitation or pollination), can and do influence species ranges. In addition to modeling work (e.g., [21]), Sexton *et al.* [20] found that the majority of empirical studies looking for biotic determinants of range limits found support for these effects. Most commonly, studies addressing biotic determinants of range limits show correlations between density of a focal species and that of their competitors or predators (e.g., [22]), or attribute a lack of demonstrable abiotic control over nonstressful or trailing range limits to biotic factors [23,24]. Competition, predator–prey dynamics, or hybridization can all constrain occurrence patterns of species [5,25–27], while mutualisms can extend ranges [28]. However, little work measures effects of biotic factors on demographic or extinction–colonization processes (Box 1; but see [29,30]), and fewer still connect such fine-scale information to geographic range limits (but see [31]).

It is even more difficult to quantify the fraction of range limits set by abiotic versus biotic factors, or when and where abiotic versus biotic factors will dominate, much less why such patterns might arise. Doing so is primarily limited by a lack of studies that address both abiotic and biotic determinants of species ranges in the same system. Nonetheless, studies in several ecological systems allow provisional tests of SIASH, although often with a lack of connection between work on local processes and large-scale patterns. At the fine scale, Kunstler *et al.* [32] show that tree growth is more reduced by competitors in areas with greater water availability and temperature. Conversely, for an annual plant along a moisture gradient, Moeller *et al.* [33] show that plant reproduction is more limited by pollinator service in stressful than in benign locations. There are also many large-scale studies suggestive of SIASH: in conifers, abiotic stress more often limits growth at high elevations, while other factors, presumably species interactions, are more important at low-elevation limits [23] (but see [34], which finds no variation in the strength of competition across elevations), and similar work shows correlations suggestive of SIASH in crabs [35] and birds [36]. Stott and Loehle's work [37] on boreal trees also supports SIASH. In a meta-analysis of over-the-range-limit transplant experiments, Hargreaves *et al.* [38] demonstrated that fitness is often reduced beyond high latitude or high elevation limits (consistent with limits set by abiotic stress), whereas fitness remains high beyond most low latitude or low elevation limits (consistent with at least partial control by species interactions). Studies of invasive species, which are often known or suspected of having reduced enemies or competitors in their introduced range, show mixed results. In the tropics, many invasive birds and mammals have very broad geographic ranges, suggesting that their native ranges were tightly controlled by species interactions, consistent with SIASH. However, outside the tropics, most high-latitude invasive species have larger range sizes than extratropical lower-latitude invasive species, inconsistent with SIASH [39]. Importantly, a minority of these studies use experimental manipulations [33,38].

The rocky intertidal offers the best work on the mechanisms settings range limits at both large and small scales. These systems offer clear local stress gradients and harbor many experimentally tractable species, with low adult mobility and clear-cut range limits; all of the studies cited below use experimental manipulations. At the fine-scale, Connell [40,41] found support for SIASH: predation and competition more strongly affect population density in the lower intertidal, which is less abiotically stressful than the upper intertidal. Subsequent work found similar patterns for these and other interactions, including predation [42] (but see [43], one of multiple studies showing large effects of predation by birds in the upper intertidal), competition [44,45], and herbivory [46], (but see [47], where herbivores prevent establishment of algae in the upper intertidal). At the macroecological scale, Sanford *et al.* [48] found support for SIASH, with increased frequency of predation on the mussel *Mytilus californianus* in low latitudes (see also [49,50]). Wethey [45,51] has shown that for intertidal barnacles, high-latitude limits are set by competition and low-latitude limits by temperature intolerance, a pattern conforming to the prediction of SIASH regarding abiotic stress, but not the common latitudinal pattern in range limits that assumes stress is lowest in the tropics.

A Clear Definition of SIASH

Although there is an extensive literature on the causes of range limits, and ecologists often assume that SIASH is a strong generality (e.g., [23,38,40]), a clear operational definition of the hypothesis is lacking. Many of the studies discussed above show evidence that one or more performance measures are differentially affected by biotic or abiotic forces, but not evidence concerning their influence on range limits or expansion or population growth at range margins. An added complication is that 'stress' is extremely difficult to define or manipulate (e.g., [52,53]), since multiple conditions can be stressful, many species are known to find both ends of an abiotic gradient stressful (e.g., thermal neutral zones of endotherms and physiological activity ranges of ecotherms), and many abiotic stressors are negatively correlated (e.g., drought stress and freezing stress along an elevational gradient). Before delving further into how the patterns predicted by SIASH could arise, we therefore suggest this definition: 'amelioration of biotic limits to growth would expand the range much more at the nonstressful than the stressful end of some gradient in abiotic conditions, and conversely for amelioration of abiotic stress'. This definition also has a corollary about the forces governing local population growth at range limits: **low density stochastic growth rate** (λ_{LD}) of local populations is predicted to be more strongly influenced by species interactions at the nonstressful end of an abiotic gradient, and by abiotic forces near to the stressful end; because population presence or extinction are functions of population growth at low densities, controls on performance under these conditions are the critical metric of effects on range limits. This definition emphasizes the dual pattern that SIASH predicts, has a clear graphical interpretation (Figure 1, Key Figure), and also can be analyzed using standard demographic methods (Box 2). We also know of no studies that quantify response of range-limit growth rate to different drivers while accounting for density to arrive at estimates of low-density growth rate.

Possible Mechanisms Determining Species Interaction Strength across Stress Gradients

It is evident (and perhaps even tautological) that abiotic stress will be limiting in places that are abiotically stressful. The less obvious aspect of SIASH is why species interactions should be weak in stressful areas and strong in abiotically benign areas. Understanding if these patterns hold is therefore a key part of testing the generality of SIASH. There are a number of aspects or levels of species interactions, not all of which necessarily lead to SIASH, but few statements of the theory are specific about what component of species interactions are alleged to change across stress gradients. For example, SIASH predicts that parasitism should exert stronger effects on range limits in less stressful areas. However, one might predict that where stress is high, there should be larger effects of a given parasite load on host performance because of

Key Figure

A Functional Definition of Species Interactions–Abiotic Stress Hypothesis (SIASH) Patterns and Predictions

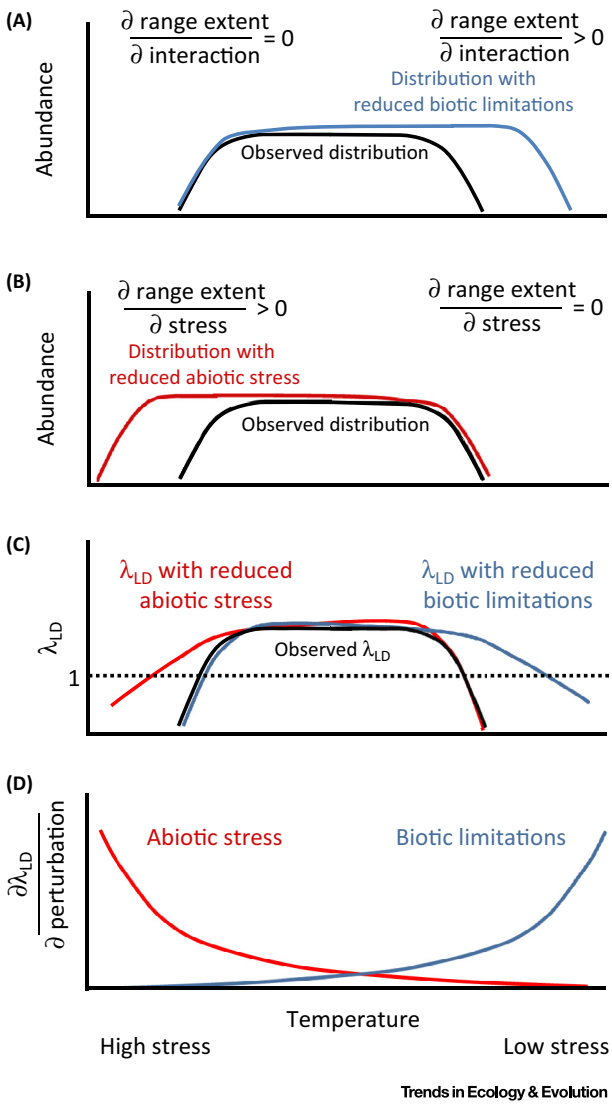

Figure 1. (A) SIASH predicts that the sensitivity of range extent to species interactions (∂range extent/∂interaction) is high at the nonstressful end of a species range. At the nonstressful end, species interactions drive local abundances to zero (i.e., set the range limit), so that release from these limitations (blue line) would lead to significant, stable expansion from the observed distribution (black line). (B) Conversely, SIASH predicts that sensitivity of range extent to stress (∂range extent/∂stress) is high at the stressful end of a species range, such that release from these limitations (red line) will result in stable range expansion from the observed distribution (black line). (C) While conducting experiments to measure actual range expansion is generally difficult (Connell's experimental work on barnacles [40] is perhaps the best example of such a study), under realistic assumptions, sensitivities of low-density population growth rate (λ_{LD}) mirror sensitivities of range extent, such that alleviation of biotic limitations or stress results in range expansion (species is extant where λ_{LD}\ge 1; colors as in A and B). (D) SIASH can be tested by assessing the sensitivity of λ_{LD} to perturbations in both species interactions and abiotic stress (∂λ_{LD}/∂perturbation; red is sensitivity to abiotic stress and blue to biotic limitations).

decreased ability to recover from infection. Where stress is low, conversely, there might be weaker effects of that same parasite load due to increased reproductive rates that compensate for negative effects of parasites. In this scenario, we would actually expect that parasitism will have larger effects in stressful places, contrary to the predictions of SIASH. To further complicate matters, variation in parasite load, parasite infection rate, and parasite species diversity will also influence the net effect of the interaction.

There are at least four nonexclusive mechanisms underlying any species interaction that together control whether and how the effect of the interaction will vary across stress gradients

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Box 2. Formulating Demographic Tests of SIASH

SIASH is sometimes phrased in a way that denies contradiction: a range limit at the stressful end of an abiotic gradient is determined by stress, and the range limit at the other, nonstressful end of the gradient is determined by something else (species interactions), because there is no abiotic stress there. Stress gradients are also often assumed to follow what humans might see as stressful versus nonstressful conditions. However, both ends of even a simple abiotic gradient can pose difficulties for a species, and many stress gradients are nonlinear or polytonic. Finally, range limits can be determined by multiple, interacting factors, with biotic and abiotic factors exerting some control over population performance across a species range.

Given these difficulties, the most robust test of SIASH is analyzing how sensitive range limit location is to changes in the strength of one or more species interactions (in the currency of any of the four mechanisms we outline) versus abiotic stressors. SIASH predicts that the sensitivity of range limit expansion to the alleviation of a biotic limitation (reduction of a negative interaction or increase in a positive one) will be much greater at the low-stress end of a geographic range than the other, with a converse sensitivity to abiotic stress alleviation (Figure 1) over the long term.

SIASH could be tested using across-range-limit transplants combined with manipulations of abiotic and abiotic factors. However, such experiments can be difficult, must be conducted over fairly long time periods, and are sometimes inadvisable ethically. An alternative is to evaluate whether λ_{LD} values of populations at low-stress range limits have greater sensitivity to experimental reduction of biotic limitations than do λ_{LD} values at high-stress limits (and, whether sensitivity to abiotic stress shows the converse pattern). Low-density growth rates, which determine probability of population establishment or extinction, will best correlate with population presence and persistence even if range limit populations are at high density [77]. In established populations, short-term focal individual manipulations (e.g., local density reductions) can be used to estimate λ_{LD}. Assuming that this sensitivity is a continuous function of abiotic conditions and such conditions change continuously across range limits, sensitivity of λ_{LD} to abiotic or biotic factors should mirror the sensitivity of range limitation (Figure 1). Discontinuities in either abiotic stressors or species interactions across range limits will obviously complicate the interpretation of this measure of range limitation sensitivity.

(Figure 2). For clarity, we illustrate these different mechanisms using herbivore effects on plants (see Box 3 for a review of empirical plant–herbivore interactions in the context of SIASH), but the same breakdown applies to other interactions, as follows.

Mechanism 1: Effect per Encounter

The demographic effect of each interspecific encounter (e.g., one bite from one herbivore) changes across stress gradients, such that focal individuals respond differentially to an encounter as a function of abiotic stress level. For example, the ability of an individual plant to maintain $\lambda = 1$ following one feeding bout by one herbivore appears likely to decrease as stress increases (Figure 2), opposing SIASH.

Mechanism 2: Effect per Interactor

The effect of an individual interactor on a focal individual (e.g., the effect of one herbivore on one plant over their lifetimes) varies across stress gradients. For example, colder conditions are likely to mean greater energetic needs for endothermic herbivores and hence higher feeding rates (Figure 2); this would contradict SIASH. Alternatively, a generalist herbivore might feed on a variety of plant species in stressful, low-primary-productivity environments, but specialize on a focal plant species in nonstressful, high-productivity environments; this could support SIASH.

Mechanism 3: Effects of Density

The ratio of the population densities of two species changes across stress gradients, such that population-level effects of the interaction vary. For example, herbivore-to-plant ratios might increase with increasing temperature or rainfall, supporting SIASH (Figure 2), or show the opposite pattern, contradicting SIASH.

Mechanism 4: Community Assemblage

Finally, the richness or diversity of species within a guild changes across stress gradients, with resulting changes in the limitations imposed on species the guild interacts with. For example, a plant suffering more types of damage from a richer herbivore community might be more strongly

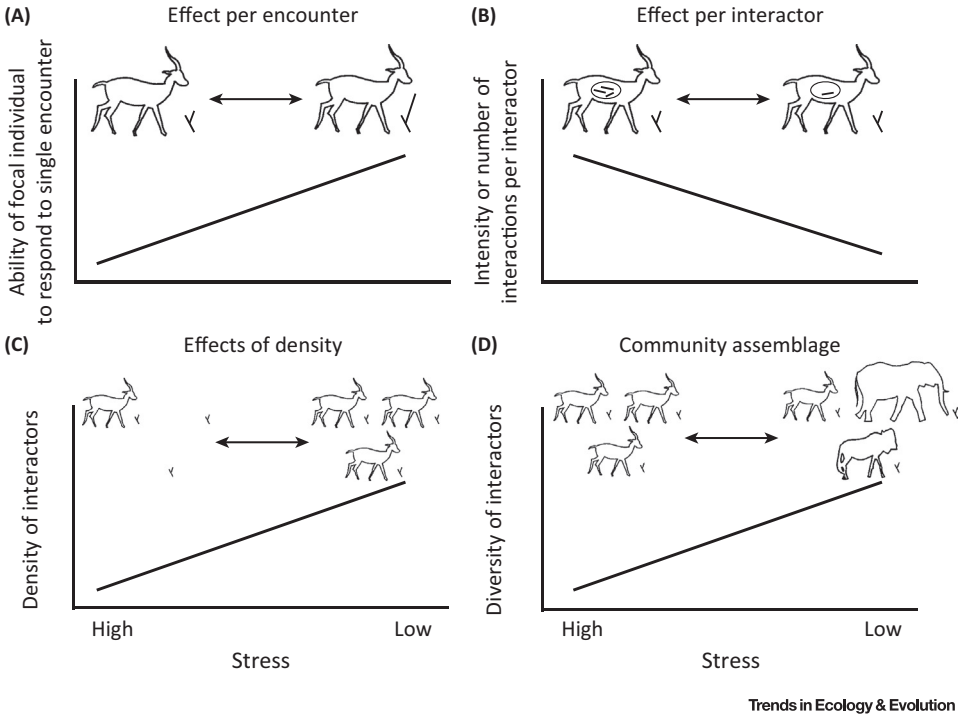

Figure 2. Four Mechanisms Dictating the Strength of Species Interactions. At least four mechanisms combine to influence how the strength of species interactions will vary across stress gradients, as shown here for plausible patterns in plant–herbivore interactions. Each level of the interaction is expected to respond to a gradient of decreasing stress, as might occur with increasing temperature, rainfall, or nutrient availability. Inset pictographs illustrate these mechanisms for interactions between a focal food plant and its gazelle herbivore. (A) Effect per encounter. The impact of a single feeding bout on the fitness of an individual plant, with increased plant regrowth following herbivory in low-stress areas. (B) Effect per interactor. Cumulative effects of a lifetime of interactions between one gazelle and one plant, with higher consumption, and hence impact, in high-stress areas. (C) Effects of density. The effect of a population of gazelle on the population of a focal plant, with higher gazelle-to-plant ratio in low-stress areas. (D) Community assemblage. Effects of a guild of interactors on a plant population, with greater diversity of herbivore species in low-stress areas. The direction of each mechanism across a stress gradient might be positive or negative, and will not necessarily conform to the pattern shown in these panels (see text for more details).

impacted than one living with a less diverse set of consumers (Figure 2). If herbivore communities are richer in low-stress areas than in high-stress areas, this would support SIASH.

The most fundamental difference among the above mechanisms is between effects generated by the interactions between pairs of individuals (mechanisms 1 and 2) versus effects generated by the populations and communities of interacting species (mechanisms 3 and 4). The original proponents of SIASH [15–18] emphasized that gradients in interactor density or richness, mechanisms 3 and 4, are common along gradients in abiotic stress. Similarly, Menge and Sutherland's formulation of this hypothesis [54] relies on increased food web complexity in nonstressful areas. A recent review by Schemske *et al.* [55] suggests that, concomitant with the well-known decreases in species richness with latitude, the frequency of many types of species interactions also decrease with latitude for a wide variety of species. We might predict that increases in interactor density and species richness with decreasing stress (and by extension, increased number and diversity of interactions) might make SIASH very common in nature. However, variation in interaction strength (mechanisms 1 or 2) could strongly influence this conclusion. For example, if a prey's risk of capture increases with stress (mechanism 1), but, simultaneously, predator density decreases with stress (mechanism 3), the net effect of predation might not vary. Similarly, if predators require more food in stressful areas to maintain

Box 3. The Breakdown of Species Interactions Effects for Herbivory

Studies of herbivory, a particularly well-studied set of species interactions, help illustrate how the direction and strength of the four mechanisms can differ along a stress gradient. The Compensatory Continuum Hypothesis (CCH) predicts that stressed plants are less able to compensate for herbivore damage (mechanism 1 [78]; although [79] predicts the opposite, also see [80]). Relevant to mechanism 2, herbivore metabolic rate, and thus food intake, is also often higher in thermally stressful areas [81,82], but the opposite is true for precipitation [83,84]. Supporting our illustration of mechanisms 3 and 4, herbivore densities, herbivore/plant ratios, and herbivore species richness are generally higher in dense plant stands and nonstressful areas [85–91].

Some studies of herbivory also quantify the relative strength of multiple mechanisms. Pennings *et al.* [92] found very high herbivory rates on low latitude salt marsh plants, consistent with SIASH, resulting from a combination of higher herbivore feeding rates (mechanism 2) and much higher herbivore densities (mechanism 3) in low latitudes than in high latitudes (but high herbivore densities have also been shown to drastically impact salt marsh plants in the high arctic [93]). However, differences in the strength and direction of these very same mechanisms can lead to net effects inconsistent with SIASH: in *Piper* plants, herbivore densities are highest at the equator, but lower herbivore feeding rates in these same areas (possibility due to higher plant defenses) mean that herbivory rates do not differ with latitude [91].

Different mechanisms can also exert strong feedback on one another, further complicating efforts to predict when we expect to see SIASH-like patterns. Miller *et al.* [94] showed that cactus (*Opuntia imbricata*) herbivores were most abundant at low elevations (mechanism 3); in turn, this high herbivore pressure acted to reduce cactus densities, thus increasing per-capita effect of herbivores (mechanism 2) due to lack of food. These examples serve to illustrate that mechanisms can exacerbate or nullify one another and, that in some cases, the pattern generated by multiple mechanisms is extremely difficult to predict using only limited data on single mechanisms.

body condition (mechanism 2), but predator density decreases with stress (mechanism 3), the net effect of predation might vary in either direction. Different combinations of these mechanisms can generate an overall pattern consistent or inconsistent with SIASH (Box 4, Figure 3).

Box 4. A Simple Model

We use a simple heuristic model of plant response to herbivory to show how the four mechanisms composing a species interaction could contribute to the generation of range limits. We simplify herbivory, the only species interaction in this example, to a simple consumptive effect that results in an immediate reduction in plant size and growth. We use this model to explore how different mechanisms contribute to the sum effect of herbivory on plant populations across a temperature gradient.

We base our model on the modified Nicholson–Bailey predator–prey dynamics [95,96] that incorporate spatial clumping of the herbivore [97], as well as density dependence of both the plant (after [98,99]) and the herbivore. We model N_t, the density of a focal plant species, and H_t, the density of a generalist herbivore, across a gradient of increasing temperature:

$$N_{t+1} = N_t e^{\left(r_N - r_N \frac{N_t}{K_N}\right)} \left[\left(1 + (a_2 - a_1)\frac{H_t}{k}\right)^{-k}\right] \quad [I]$$

$$H_{t+1} = H_t \left[\left[(N_t + M)\left(1 - \left(\left(1 + a_2 \frac{H_t}{k}\right)^{-k}\right)\right)\frac{e^{r_H}}{H_t}\right]^{\left(1 - \frac{H_t}{K_H}\right)}\right] \quad [II]$$

Here, a_2 is the average reduction in plant size following an encounter with one herbivore, and a_1 governs the extent of compensatory regrowth following that encounter. r_N represents the intrinsic rate of increase of the plant, K_N the carrying capacity, and k the spatial clumping of herbivores. Analogously, r_H represents the conversion rate of plants to herbivores and K_H herbivore carrying capacity; M is the density of other food sources of herbivores. We model mechanism 1 (effect per encounter) by increasing a_1 with temperature, mechanism 2 (effect per herbivore) by increasing a_2 with temperature, and mechanisms 3 and 4 via increasing r_H with temperature.

We first consider each mechanism in isolation, assuming what seem to us plausible directions for these effects with increasing temperature, and then explore combinations of mechanisms. While effects of each mechanism in isolation are relatively easy to predict (Figure 3A–C), when considering multiple mechanisms, support for SIASH is highly contingent on the strength of individual effects (Figure 3D–F), illustrating that the conditions under which SIASH is supported or refuted will depend on the strength and exact pattern of each of the four mechanisms and how they vary with stress. These results suggest that the net pattern generated by multiple mechanisms is impossible to predict in the absence of quantitative data on the relative strength of different mechanisms. No empirical study to our knowledge measures the strength of all of these mechanisms for any one species or type of interaction.

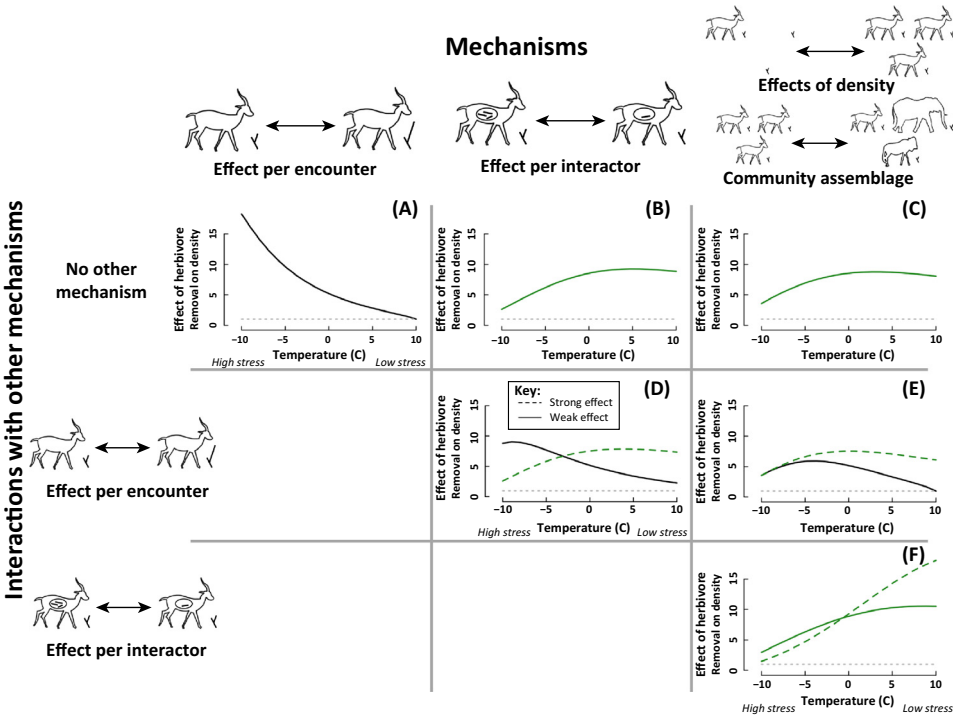

Figure 3. *A Priori* Support for SIASH Is Mixed when considering the Mechanisms Underlying Species Interactions, with Some Mechanisms Leading to the Predicted SIASH Pattern and Others Opposing it. Lines in each subplot show the effect of herbivores on relative plant density (density in the absence of herbivores/density in the presence of herbivores) across a temperature gradient that ranges from highly stressful at low temperatures to nonstressful at warmer temperatures; predictions come from a Nicholson–Bailey predator–prey model modified to reflect plant–herbivore interactions (Box 3). High effect values indicate strong suppression of plant abundance by herbivores, while a value of 1 indicates no effect of herbivory (gray dashed line). Lines in green indicate mechanisms and scenarios conforming to the SIASH pattern, whereas those in black show results that oppose SIASH predictions. We show the effects of each mechanism in isolation (A–C), as well as in combination (D–F), for both weak (solid line; shallow gradient in the numerical difference between mechanism strengths) and strong (dashed line; steep gradient) effects. We group mechanisms 3 and 4 together because they will show the same pattern of effects if different herbivore species have additive or synergistic effects. Importantly, not all mechanisms operating alone result in patterns consistent with the SIASH. Further, when multiple mechanisms operate simultaneously, a pattern consistent with the SIASH is sometimes generated (e.g., F), but sometimes not (e.g., E, black line), and in some cases, whether or not the SIASH pattern occurs depends on the strength of the mechanisms operating (e.g., D). While we illustrate these patterns with effects on equilibrium densities, the same approach can be used to look for effects on λ_{LD} (and most results for the parameter combinations used here are qualitatively similar). In all cases, $k = 0.25$, $M = 10\,000$, $K_H = 1000$, and with increasing rainfall, r_N increases linearly from 0.1 to 0.5 and K_N increases from 5×10^4, plateauing at 10×10^4. In (A), a_1 increases linearly from 0 to 0.01, $a_2 = 0.01$, and $e^{r_H} = 0.01$. In (B), $a_1 = 0.$, a_2 increases linearly from 0.004 to 0.016, and $e^{r_H} = 0.01$. In (C), $a_1 = 0$, $a_2 = 0.01$, and e^{r_H} increases linearly from 0.005 to 0.015. In (D), a_1 increases linearly from 0 to 0.01 (weak) or 0 to 0.003 (strong), a_2 increases linearly from 0.008 to 0.012 (weak) or 0.004 to 0.016 (strong), and $e^{r_H} = 0.01$. In (E), a_1 increases linearly from 0 to 0.01 (weak) or 0 to 0.003 (strong), $a_2 = 0.01$, and e^{r_H} increases from 0.005 to 0.015. In (F), $a_1 = 0$, a_2 increases from 0.008 to 0.012 (weak) or 0.0045 to 0.016 (strong), and e^{r_H} increases linearly from 0.0055 to 0.015. SIASH, Species Interactions–Abiotic Stress Hypothesis.

The different mechanisms by which stress affects species interactions, and how these effects could in turn generate or suppress the SIASH pattern, emphasize that studies of interaction frequencies (say, leaf damage rates) or of single components of fitness (say, individual reproductive success) are not in and of themselves sufficient to determine what factor is primarily determining any given range limit, and thus to fully test the generality of SIASH. Some of the most convincing studies of latitudinal gradients in species interactions address mechanisms 1 or 2 above, showing that attack rates of a herbivore or predator are higher per unit time with decreasing latitudes (e.g., higher annual herbivory on tropical versus temperate broad-leaved

forest trees [56], and 18 times higher predation pressure on tropical versus temperate insects [57]). But these results by themselves do not show that these interactions control occurrence patterns of victims more strongly in the tropics. Ideally, studies of the generation of range limits should quantify all four mechanisms, although we recognize that this is a tall order. A well-designed study of SIASH for aridity and herbivory might assess sensitivity of λ_{LD} to rainfall and herbivore density at range limits and conduct over-the-range-limit transplants with and without supplemental watering treatments and herbivore exclosures (Box 2). Support for or against SIASH might arise due to any of the four mechanisms detailed above.

Concluding Remarks and Future Directions

Understanding why range limits are where they are, and predicting how climate change, species losses, and other global changes will alter them are key questions in applied and basic ecology. While SIASH is a long-standing hypothesis, there are still few thorough tests of its predictions. Whether or not SIASH provides a strong generality depends on the relative strength of different mechanisms that will combine to create or negate patterns in the importance of abiotic versus biotic limitations to population persistence (Figure 3). However, we currently lack empirical tests of the underlying processes or exact predictions of the hypothesis that would be needed to judge support for SIASH (see Outstanding Questions).

We see three avenues to increase our understanding of when and where SIASH is a useful generality. First, field studies that quantify the strength of each of the four interaction mechanisms affecting population growth rate could be used to parameterize simple models (e.g., Box 4) to assess support for SIASH. Such work could use relatively simple experiments replicated across broad-scale geographic gradients to fill in information in already well-studied systems [58].

A second need is for studies of how demographic processes vary with stress, or multiple stressors, across a species range, and thus the effect of stress in limiting low-density population growth rates. For example, if seedling germination is already limited by abiotic determinants of safe site abundance, reduction of plant fecundity by herbivores might have muted effects on plant abundance; conversely, if recruitment is not safe site-limited, reduction of fecundity by herbivores will have large population-level effects [58]. Few studies address variation in vital rates and **sensitivity of population growth rate** to those vital rates across broad geographic ranges (but see [59–62]), and even fewer quantify the factors driving variation in these rates (e.g., [31,60,63]) or consider density effects.

Finally, even if the predictions of SIASH are supported, there are very few studies that directly address whether simple reductions in local population performance are usually the key factor limiting ranges (Box 1), [59–61]. In particular, we have little empirical evidence showing how metapopulation dynamics affect range limits [64]. In addition, it is unclear if small-scale determinants of species range limits at the local scale are governed by mechanisms similar to determinants that operate at geographic scales. Thus, studies trying to address determinants of range limits should clearly articulate the scale of their work relative to the range of the study species (e.g., [65]).

Predicting where and when the inclusion of species interactions will meaningfully improve range limit predictions is critical to predicting the ecological consequences of climate change [66,67], but we have evidence that there is wide variation in how important these species interactions are [68]. Focusing on the relative importance of different factors in driving ranges and their dynamics are particularly important because species might shift their ranges idiosyncratically with climate, resulting in novel communities, and because many climate change-caused extinction events have been suggested to arise via altered species interactions, rather than climate shifts *per se* [69–71]. While the predictions of SIASH might or might not prove robust to empirical tests, the

Outstanding Questions

Do abiotic stress or species interactions have a strong influence on species range limits? Whereas there is ample evidence from the literature that both abiotic stress and species interactions can set limits, some species limits may be caused by dispersal limitation, or ranges may not be at equilibrium. Thus, we encourage ecologists to devote substantial time to observing causes of reduced performance at range limits, and assessing whether abiotic and biotic factors are likely drivers, before quantifying their influence on population growth.

What is the effect of both abiotic and biotic forces on fitness or population growth? Many existing studies quantify responses of only one fitness component to abiotic or biotic forces, but not overall population growth, especially at low densities, and hence range limits.

What is the total effect of a given species interaction across abiotic gradients, considering potentially different trends at multiple levels of the interaction, including individual responses, as well as density and community assemblage effects? The four mechanisms we outline here are a starting point to consider effects at multiple levels; measuring the strength of poorly studied mechanisms in well-studied systems that have already measured some mechanisms could be especially productive.

How do different demographic processes vary with abiotic stress? We have a poor understanding of how abiotic stress affects vital rates for many species, and thus a limited ability to predict how species interactions will influence population growth.

Are reductions in local population performance or metapopulation persistence the key driver of range limits? Conducting more studies comparing these two forces would both increase our ability to predict whether SIASH is a strong generality, as well as further our understanding of all species range limits and geographic shifts in those limits with climate change.

four mechanisms underlying SIASH provide a framework for testing the most likely forces setting species range limits in a variety of systems and thus could help us more accurately predict shifts in geographic ranges.

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