

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.

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.

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.

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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

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