

Opinion

Integrating Biogeography with Contemporary Niche Theory

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There is no consensus on when biotic interactions impact the range limits of species. Starting from MacArthur's use of invasibility to understand how biotic interactions influence coexistence, here we examine how biotic interactions shape species distributions. Range limits emerge from how birth, death, and movement rates vary with the environment. We clarify some basic issues revolving around niche definitions, illustrated with simple resource–consumer theory. We then highlight two different avenues for linking community theory and range theory; the first based on calculating the effects of biotic interactions on range limits across scales and landscape configurations, and the second based on aggregate measures of diffuse interactions and network strength. We conclude with suggestions for a future research agenda.

Controversy over the Broad-Scale Effects of Biotic Interactions

Biogeographers and community ecologists have long debated the importance of **biotic interactions** (see [Glossary](#)) for species distributions and **range limits** [1–5]. At times, the role of interactions appears clear. For instance, the current distribution of red squirrels in the British Isles has been strongly molded by the introduced grey squirrel, driven by competition and a shared infectious disease [6]. In other cases, interactions appear unimportant, judged by the often-successful use of species distribution models (SDMs) using only information on the abiotic environment [7–12]. Soberón [12] argued that biotic interactions are likely relatively unimportant at the coarse spatial scale considered by biogeographers, and that interactions vanish in a kind of 'Eltonian noise'. This is an intriguing proposition, but we suggest that it is premature to rule out the role of interactions in sculpting range limits. One reason is that the aggregate impact of biotic interactions might be strongly correlated with abiotic variables. As one example, the northern range limits of wintering birds in the USA are predicted well by thermal conditions [13], but humans have facilitated this northward expansion of the ranges of species through winter food supplementation [14]. Including explicit information about food **resources** [15] or putative competitors (e.g., rodents of similar body size [16]) can improve the predictive power of SDMs. We suggest that a fruitful direction of future inquiry will be to more explicitly link coexistence theory from community ecology with biogeographic analyses. Advances in coexistence theory (sketched below) potentially provide tools for examining how local interactions scale up to geographical ranges.

Coexistence theory is concerned with the conditions under which multiple species can occur at the same location over long periods of time. Robert MacArthur crystallized one approach to coexistence that is at the heart of niche theory: identify conditions allowing populations of each species to increase when rare, when other species are at equilibrium at some specified temporal and spatial scale. MacArthur's approach has been used to analyze a diverse set of coexistence mechanisms, ranging from resource partitioning [17], to food webs, the effects of spatial scale, and host–parasite interactions (e.g., Janzen–Connell effects), among others

Trends

We show how analyses of species coexistence can be used to determine when biotic interactions shape range limits.

Coexistence theory predicts that range limits occur when the intrinsic growth rate of a species balances the effect of biotic interactions on population growth.

To study this empirically, the growth rate of a species should be measured when it is rare, with and without biotic interactions.

These insights generalize across spatial scales.

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[18]. This approach has inspired a new generation of empirical methods in community ecology [19–21]. It is our contention that these analyses can inform a general understanding of how biotic interactions shape range limits. Rather than work through this rich smorgasbord of coexistence mechanisms, we reflect on general conceptual issues at the interface of biogeography and niche theory.

One important meaning of ‘niche’ (the **fundamental niche**), as encapsulated by Hutchinson [12], is the range of environments permitting a **focal species** to persist, in the absence of interactions with some other defined set of species [8]. In effect, the fundamental niche picks out those environments where a species has a positive **growth rate** when rare (but see exceptions in [22]). Outside the fundamental niche, a species should decrease in abundance and tend towards local extinction (in the absence of recurrent immigration or strong positive feedbacks). The **realized niche**, according to Hutchinson, denotes environments permitting persistence in the face of biotic interactions (see also [8]). For some authors, the ‘realized niche’ includes all environments where a species occurs, after considering immigration (e.g., sink habitats) and dispersal limitations [23].

The Fundamental Niche and Range Limits

In the absence of biotic interactions and in the presence of just a small amount of dispersal, the range limits of a species should closely match its fundamental niche, given that extinction is expected when a species is exposed to environments outside its niche [23]. Soberón [12] distinguishes between Grinnellian and Eltonian fundamental niches; Grinnellian niches involve scenopoetic abiotic variables (e.g., pH or temperature) that the focal species cannot affect. Eltonian niches involve resources, which are potentially depletable by consumption. The **intrinsic growth rate** of a rare species will often be a joint function of scenopoetic variables and resources, which could therefore be considered distinct attributes of a single fundamental niche.

Formally, the fundamental niche is the set of environments where a focal species has a positive intrinsic growth rate when rare [24]. This means that the species must be able to tolerate conditions of the abiotic environment and to acquire enough resources to sustain growth. In the absence of immigration (source–sink dynamics), we expect range limits to occur at the locations corresponding to the boundaries of the fundamental niche. Let **E** denote a vector of relevant scenopoetic variables, [8] and **R** a vector of resource availability (e.g., insect prey for an insectivorous bird or chemical nutrients and sunlight for a plant). We can then express the growth rate of a focal species when rare as the difference between per capita birth and death rates at a specific location (Box 1):

$$r(\mathbf{E}, \mathbf{R}) = b(\mathbf{E}, \mathbf{R}) - d(\mathbf{E}, \mathbf{R}) > 0 \quad [1].$$

The fundamental niche is that set of **E** and **R** where births exceed deaths (i.e., where the inequality holds). This formulation assumes continuous, overlapping generations without an internal population structure; however, the basic concept applies broadly. In temporally variable environments, one should consider the long-term average growth rate, and not simply the growth rate under average conditions [25,26], and more generally account for extinction risks due to demographic stochasticity [5].

We are now ready to study the impact of biotic interactions on range limits. This is done by measuring the effect of other species on the intrinsic growth rate of the focal species when the latter is rare. As Hutchinson noted [24], this often involves not the entire biota, but a selected subset (the **focal ensemble**), with the rest of the community in effect assumed to be part of the background environment incorporated into the fundamental niche. For now, we assume that environmental variables vary over broad spatial scales, while species interact at a small spatial

Glossary

- Biotic interactions:** changes in the growth rate of one species that are caused by another species.
- Focal ensemble:** species that might influence the range limit of the species under investigation.
- Focal species:** a species whose range limit is under investigation.
- Fundamental niche:** the set of conditions (i.e., combinations of environmental conditions and resources) where a species of interest has a positive intrinsic growth rate. The regional fundamental niche is the same, but characterized over a broader spatial extent.
- Growth rate:** the difference between the birth and death rate of a population over the time interval of interest. We assume that growth rates are typically measured on a percapita basis.
- Intrinsic growth rate:** the growth rate of a species that is rare in a given abiotic environment. The intrinsic growth rate can consider resources but does not consider other biotic interactions.
- Range limit:** the boundary between locations where a species is present and locations where a species is absent.
- Realized niche:** the environments where a species is present. This includes dispersal and biotic interactions. The regional realized niche is the same at broad spatial scales (where dispersal from external sources can be ignored).
- Resource:** an entity that organisms consume and which increases their growth rate.
- Scale transition theory:** an approach to analyzing differences between local and regional population growth rates, based on the consequences of local interactions, mediated by dispersal among sites, and other processes.

Box 1. Mechanistic Analysis of the Realized Niche

Holt [22] argued that Hutchinson's version of the niche must be grounded in population ecology, such that the difference between births and deaths when a species is rare describes its fundamental niche (inequality 1). Using this perspective, we work through an example of what counts as the fundamental and realized niche of a species based on familiar resource–consumer dynamics [57].

Consider a consumer feeding on a single resource. Either birth rates or death rates could vary with resource levels, and moreover do so in a way that depends on an abiotic environmental variable (\mathbf{E}), say temperature, either directly, or mediated indirectly through resource levels (Equation I):

$$\frac{dR}{dt} = f(\mathbf{R}, \mathbf{E}) - (\text{consumption}) = f(\mathbf{R}, \mathbf{E}) - a(\mathbf{E})RN$$

$$\frac{dN}{dt} = (\text{birth} - \text{death})N = q(\mathbf{E})a(\mathbf{E})RN - d(\mathbf{E})N \quad \text{[I].}$$

In this model, resource (R) renewal is described by $f(R, \mathbf{E})$; the consumer (N) has a linear functional and numerical response to the resource, and death is resource and density independent. The quantity a is an attack rate, q converts consumption to births, and d is mortality rate. All these parameters could in principle vary with scenopoetic environmental variables, \mathbf{E} .

In the absence of the consumer (and its competitors), we assume the resource equilibrates at a standing level $K(\mathbf{E})$. The population of the consumer can increase in density if (Equation II):

$$\underbrace{q(\mathbf{E})a(\mathbf{E})K(\mathbf{E})}_{\text{fundamental Niche}} - \underbrace{d(\mathbf{E})}_{\text{death}} > 0 \quad \text{[II].}$$

Limiting resources of whatever kind (living or not) in our opinion are part of the fundamental niche (this is the convention suggested by close reading of [24,58]). Scenopoetic variables, such as temperature or precipitation, could be used to craft highly predictive ecological niche models, both directly via demography (e.g., d), resource acquisition abilities (a), physiological efficiency at converting resources to newborns (q), or because resource levels are predictable from those same abiotic factors (K).

If exploitative competitors are present, this should depress resource levels to some $R^*(\mathbf{E}) < K(\mathbf{E})$. Realized resource availability will reflect how resident consumers themselves respond directly and indirectly to scenopoetic variables. The intrinsic growth rate of the focal species is now (Equation III):

$$\underbrace{q(\mathbf{E})a(\mathbf{E})K(\mathbf{E})}_{\text{birth}} - \underbrace{d(\mathbf{E})}_{\text{death}} - \underbrace{q(\mathbf{E})a(\mathbf{E})(K(\mathbf{E}) - R^*(\mathbf{E}))}_{\text{growth reduction from competition}} > 0 \quad \text{[III].}$$

Using scenopoetic variables alone to predict a species range should have excellent predictive power if all of these quantities are functions of \mathbf{E} without much noise. A range limit could arise because of direct, basic physiological limitations in certain abiotic conditions, or because those same conditions are excellent predictors of impacts of resident species on ambient resource levels. An open question with the respect of range limits is whether the intensity of these mechanisms varies systematically along broad-scale environmental gradients, thereby influencing range limits.

scale. Later, we relax this assumption so that environmental heterogeneity and species interactions can both matter at the same scale. One can incorporate biotic interactions from the focal ensemble by adding a term to inequality 1 giving us inequality 2, a balance between two components of population growth:

$$r(\mathbf{E}, \mathbf{R}) + l(\mathbf{E}, \mathbf{C}) > 0 \quad \text{[2].}$$

Here, $l(\mathbf{E}, \mathbf{C})$ is the total effect of ecological interactions from the focal ensemble on the per capita growth rate of the focal species [24]. \mathbf{C} is a vector of the abundances of each species in the ensemble. We refer to locations that satisfy inequality 2 as being within the realized niche of a species. We expect the species to be present in these locations, although dispersal limitations and historical contingencies might cause the species to be absent from some locations and dispersal might allow the species to occupy others (as sink populations).

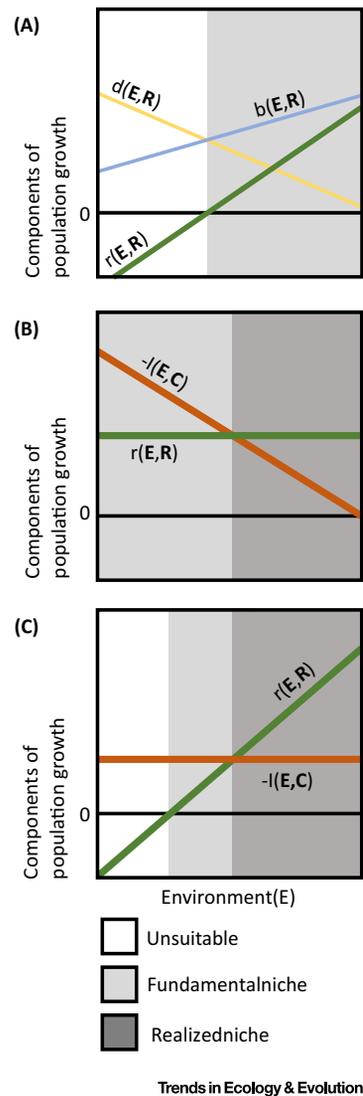


Figure 1. Graphical Model of How Range Limits Change the Distribution of a Species. As we move along an environmental gradient (E) the ecology of a species changes. (A) The ecology of a species in the absence of biotic interactions. Here, birth rates [$b(E,R)$; blue line] and death rates [$d(E,R)$; yellow line] change as we move along an environmental gradient. The boundary of the fundamental niche is the point where births equal deaths. We can further simplify this picture by looking at the difference between births and deaths [$r(E,R)$; green line]. The fundamental niche represents environments where $r(E,R)$ is above 0. (B) A species influenced by biotic interactions. Here, the harm inflicted by competitors declines as we move across the environmental gradient. The boundary of the realized niche represents the point where the ability of the species to grow in the absence of biotic interactions [$r(E,R)$] is exactly counterbalanced by the harm inflicted by a community of competitors [$-I(E,C)$ brown line]; that is, the point where the green line crosses the brown line. The focal species can be present when the harm is less than the growth rate. Focal species 1 is absent when the harm inflicted by other species exceeds its growth rate in this picture; these are environments inside the fundamental niche but outside of the realized niche (light gray). Even if the impact of biotic interactions is constant across the environmental gradient, biotic interactions can still shape range limits. For example, in (C), $r(E,R)$ increases as we move to the right along the gradient, while $I(E,C)$ remains unchanged. These changes in $r(E,R)$ result in a boundary in both the fundamental and realized niche.

Biotic interactions can shape range limits when the $I(E,C)$ changes the sign of the growth rate of the species when rare (Figure 1). The quantity $I(E,C)$ is positive when biotic interactions increase the growth rate (e.g., due to mutualism) [8,23], but negative when biotic interactions decrease the growth rate of the focal species (e.g., due to competition). Inequality 2 suggests that ecologists

should focus on the magnitude of $r(\mathbf{E}, \mathbf{R})$ relative to $I(\mathbf{E}, \mathbf{C})$, and how both these vary across space. Even when the total effect of biotic interactions is constant along a gradient, variation in the intrinsic growth rate can interact with biotic interactions to determine range limits (Figure 1C).

Of course, $I(\mathbf{E}, \mathbf{C})$ is often a function of the environment [5,27,28]. Formally, the total impact of a given resident species j on the focal species can be expressed as the product of the population size $[N_j(\mathbf{E})]$ of that member of the focal ensemble when the focal species is rare, and the per capita effect of species j $[\alpha_{ij}(\mathbf{E})]$ on the intrinsic growth rate of focal species i . Both the population size and per capita strength of biotic interactions could change along gradients and alter $I(\mathbf{E}, \mathbf{C})$, and the net effect of biotic interactions on a focal species would be a summation across the resident species. Ecologists currently have a weak empirical understanding of how the total effect of biotic interactions changes over broad-scale gradients [28,29], and how this tends to compare with changes in $r(\mathbf{E}, \mathbf{R})$. There are noticeable trends in the relationship between top-down control and temperature [30], but ecologists have a limited understanding of parallel variation in per capita interaction strengths [31].

The two components of population growth describing the realized niche (Figure 1) can be evaluated with modified transplant experiments (Box 2). This permits powerful tests of when effects of biotic interactions on local population dynamics are strong enough to shape range limits [32]. This requires studying the growth rates of a species along an environmental gradient when alone and in presence of biotic interactions, with the focal species at low density and the focal ensemble at equilibrium. Promising experimental investigations of biotic interactions at range limits are on the way, although much work remains to be done. Alexander *et al.* [33], for instance, performed reciprocal transplant experiments along altitudinal gradients to show that competitive interactions could significantly alter the performance of invading populations at otherwise favorable locations, thus suggesting that the $I(\mathbf{E}, \mathbf{C})$ term significantly influences establishment success. Conducting such studies is challenging for large numbers of species, but niche theory suggests a series of simplifications, some of which we highlight below [34].

Species-Rich Communities and Diffuse Interactions

In multispecies communities, the focal species can establish when its intrinsic growth rate is high enough to counteract negative impacts of all other species. Assuming traditional Lotka–Volterra equations of multispecies interactions, the total effect of interactions on species i will be (Equation 3):

$$I_i(\mathbf{E}, \mathbf{C}) = \sum_{j \neq i}^S \alpha_{ij}(\mathbf{E}) N_j^*(\mathbf{E}) \quad [3],$$

Box 2. Experimental Tests of Biotic Interactions at Range Limits

A careful analysis of when a species can establish [5] might help to clarify when biotic interactions shape range limits. Here, we show how existing experiments in community ecology meet this objective and how they can be modified to determine whether biotic interactions modify range limits.

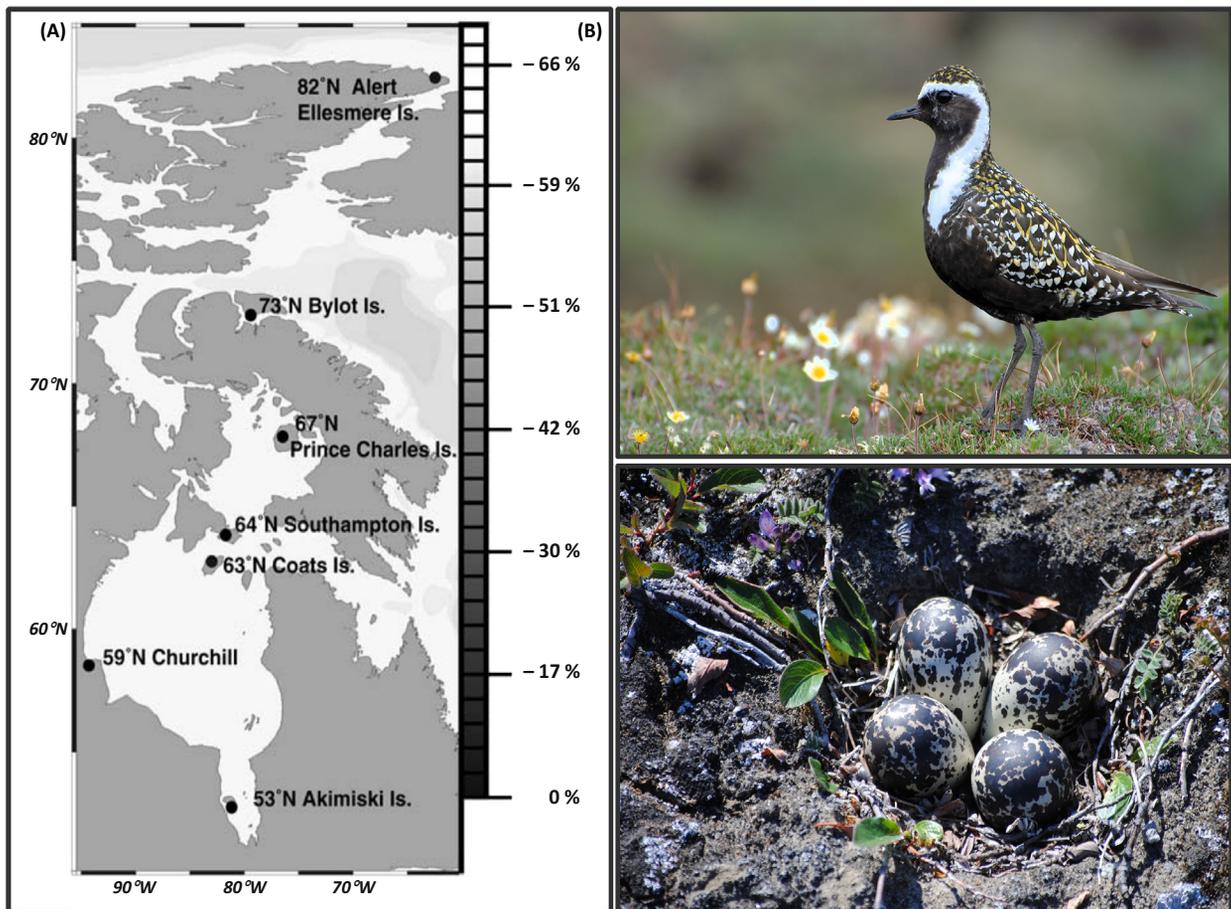
The experimental protocol for determining whether an environment is in the fundamental niche is well known (although often challenging to implement). It involves measuring reproductive output along a given environmental gradient, in the absence of ecological interactions after removing the relevant interacting species [54,59]. When predation or herbivory is important, enclosure experiments can permit assessment of the fundamental niche.

The second step is to determine whether the focal species can increase in density when rare, while other species are present. This is a straightforward application of protocols already used to study the coexistence of species. For example, Shinen and Navarette [60] tested for coexistence between two barnacle species, *Jehlius cirratus* and *Notochthamalus scabrosus*. In another example, Burns and Brandt [61] tested the effect of soil conditions on whether competing species of dock (*Rumex* spp.) coexisted. Figure I shows a treatment that tested whether *Rumex crispus* (red tag) was able to establish in plots where *Rumex obtusifolius* was already present (blue tag). A nice experiment with predation was conducted by McKinnon *et al.* [62] in their investigation of predation risk across the Canadian Arctic (Figure II). Using a mix of surveys of natural and artificial nests, they documented that predation risks of shorebirds declined by 3.6% per degree relative to the southernmost site, which can explain why many of these birds are restricted to northern latitudes. Much of this predation is due to Arctic foxes (*Vulpes lagopus*).



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Figure I. Experimental Determination of the Ability of *Rumex crispus* (Red Tag) to Establish in Environments where *Rumex obtusifolius* (Blue Tag) Was Present. Photo provided by A. Brandt.



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Figure II. Surveys Reveal Broad-Scale Variation in Biotic Interactions. (A) shorebird nest predation decreases with increasing latitude across the Canadian arctic. [62]. (B) A golden plover (*Pluvialis dominica*) and its nest exposed to predation. Photos provided by D. Gravel. Reproduced from [62] (A).

where S is species richness. Following the approach developed in [35], we can decompose $I_i(\mathbf{E}, \mathbf{C})$ into two terms describing the effect of a community on a focal species (omitting dependence on \mathbf{E} for clarity), giving us Equation 4:

$$I_i(\mathbf{E}, \mathbf{C}) = S \left(\overbrace{\bar{\alpha} N^*}^{\text{average interaction}} + \overbrace{\text{COV}(\alpha_{ij}, N_j^*)}^{\text{interaction–density covariance}} \right) \quad [4].$$

A community of negatively interacting species could set the range limit of a focal species if the average total interaction strength is large (e.g., competitors are abundant), either because average per capita interactions are strong or because the average abundance of those species is large. The covariance term indicates that the effect of interactions on range limits is magnified if more abundant species also exert stronger per capita interactions. In many communities, it will not be feasible to empirically investigate per capita effects of each species on each other (there are, after all, $S^2 - S$ such effects). Equation 4 suggests that this problem can be addressed by answering two questions about the community: what is the average strength of biotic interactions in the community? And, are the species in the community that are particularly harmful to the focal species abundant or rare? These are wide-open research questions.

Toward Ecological Networks

MacArthur showed how the ability of species to coexist depends on indirect interactions mediated by resource competition [4]. Persistence requires species to both utilize resources differentially from each other (niche differentiation) and differ significantly in how they impact those resources. Chesson and Kuang [36] revisited MacArthur's insights [37,38] to consider indirect interactions mediated by shared predators (apparent competition). Species can differentiate in either the resources they consume, the predators they share, or both. The Chesson–Kuang framework potentially provides operational tools to predict range limits of species embedded in more complex interaction networks than just guilds of competitors (see also [39]). The theory articulates how the impact of the focal ensemble of competing and predating species on the intrinsic growth rate of a focal species is proportional to niche overlap, which can be estimated by quantifying interactions among resources, consumers, and predators [40].

The computation of niche overlap from network structure opens niche theory to begin to embody more complex interaction networks. One quantity to document is the amount of overlap of resources and enemies (and potentially mutualists, although existing theory is restricted to trophic interactions) between the focal species and the focal ensemble. Species that rarely share interactions with other members of the same trophic level should, on average, be the least sensitive to indirect biotic interactions, such as apparent competition, at range limits, and might be candidates for species whose range limits are largely determined by abiotic conditions and the availability of their resources. Network metrics, such as the contribution to network nestedness, could be used to approximate niche overlap. The key question is then to understand if there is systematic variation in network structure and, consequently, in niche overlap over environmental gradients. For example, a focal plant species might experience intense indirect competition at range limits, given significant overlap in the herbivores and pathogens experienced by itself and other community members. A recent meta-analysis suggested that such effects are stronger in higher precipitation environments [41].

Scaling of the Niche

Previous sections present criteria for characterizing fundamental and realized niches at a local spatial scale, assuming that the local environment (including resources and resident abundances) is spatially homogeneous. This is an approximation that can be expanded to consider

Box 3. An Example of Scale Transition Theory

For a given species to persist in a region, it must have a positive growth rate (at the regional scale) when it is rare and other species in the region are at equilibrium. To scale up to the regional growth rate from local growth can be challenging, but a flavor of the key issues can be illustrated using an example from Chesson *et al.* [42].

Consider a region (Figure 1) where, in each local site, interactions between two species are described by a Lotka-Volterra competition model. If we ignore dispersal, species i can invade provided (inequality I):

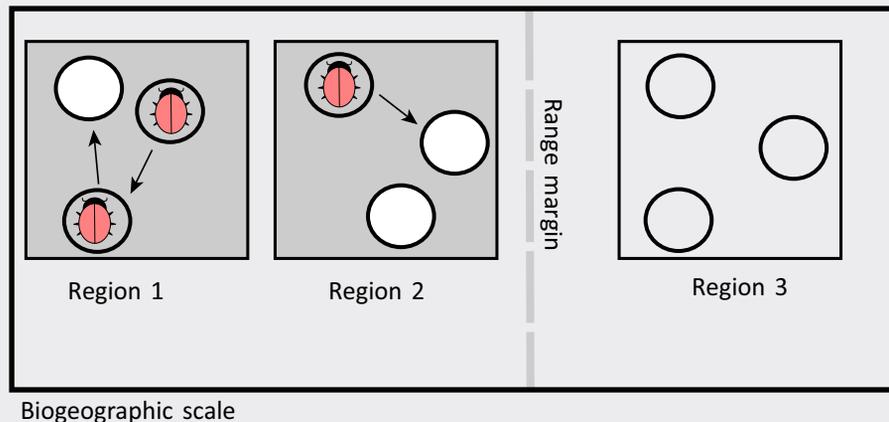
$$r_i - \alpha_{ij}N_j^* > 0 \quad [I].$$

This expression is a special case of inequality 2 based on local processes, a range limit is predicted if the intrinsic growth rate of species i does not surmount the negative impact of the resident [which can be large if either the equilibrium density of the nonfocal species (N_j^*) or its per capita impact (α_{ij}) are large]. For simplicity, we assume that the environment in each site is identical.

What happens given regional-scale processes, such as dispersal? Consider the regional growth rate. Chesson *et al.* [42] examined a tractable model where individuals disperse rapidly and asymmetrically among sites, driven by physical transport processes generating heterogeneity in abundance among locations, but with homogeneity in local growth rates. The regional growth rate of the focal species is influenced by both the average abundance of the nonfocal resident species, and a covariance term (σ) that reflects whether the two species primarily disperse to the same or different patches. The regional average growth rate is then the left side of inequality II:

$$r_i - \alpha_{ij}\bar{N}_j^* - \alpha_{ij}\sigma\bar{N}_j^* > 0 \quad [II].$$

This expression generalizes inequality 2 to include effects of among-patch dispersal. A range limit arises when this regional growth rate is positive in some regions, but negative in others. This could be because there is coarse-scale heterogeneity in the intrinsic growth rate, in the strength of competition, or in the dispersal pattern underlying σ . Fixed, asymmetric dispersal within a region has two consequences: it creates a source-sink structure for the resident, which lowers its abundance averaged over the entire region (\bar{N}_j^*). Dispersal also changes how the focal species experiences competition. The focal species experiences lowered competition when both species tend to disperse to different patches. Thus, biotic interactions are less important at shaping range limits; this exemplifies the Eltonian noise hypothesis [63], where biotic interactions are less important at the regional scale than expected given observations at the local scale. Conversely, biotic interactions can become more important at a regional scale when both species disperse to the same patches.



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Figure 1. Range Limits Emerge through the Interactions of Processes at Multiple Spatial Scales. Each of these can affect the realized niche of a species. The circles represent habitat patches (the local scale) where the species of interest can be present (gray) or absent (white). The regional scale (squares) comprises an amalgam of patches. The species (pink beetle) is present in some regions (gray squares) but not others (white squares). Local persistence can depend on dispersal among patches (arrows), as can abundances within occupied patches. Dispersal is sufficiently rare among regions, however, that to examine coexistence at the broader biogeographic scale (rectangle), one assumes that the regions are spatially closed.

dispersal at different spatial scales, [42,43] and landscapes with mosaics of different habitat types [44]. As a start towards this challenge, we suggest that it can be useful to distinguish three spatial scales (Box 3, Figure 1), the 'local', the 'regional', and the 'biogeographic', because this simplifies the mathematical presentation. The local scale comprises individual patches. Direct interactions within and among species occur at that scale. The regional scale comprises an amalgam of 'local' patches. Dispersal is important at the regional scale and many types of spatial dynamics, including metapopulation processes and source–sink dynamics, can influence the regions where a species persists, and the specific locations harboring it. At the regional scale, landscape configuration can also strongly influence the success of the species. So long as regions are sufficiently large, we can, to a first approximation, ignore dispersal among regions. At the biogeographic scale, the distribution of a species is the set of regions where a species is present. Dispersal among regions can facilitate the arrival of individuals to a region of interest, but we assume that it does not govern within-region persistence. Broad dispersal barriers create historical contingencies that can prevent a species from occupying suitable regions. We are now ready to use an approach known as '**scale transition theory**' to link population growth rates across scales [45]. This approach is mathematical, but community ecologists have already articulated how to empirically estimate the strength of this link [46,47].

In location k , the population growth rate is the birth rate minus the death rate, augmented by immigration (S_k), and depleted by emigration or outflow (O_k), as follows (Equation 5):

$$\begin{aligned} \frac{dN_k}{dt} &= (b_k(\mathbf{E}, \mathbf{R}) - d_k(\mathbf{E}))N_k + S_k - O_k \\ &= r_k N_k + S_k - O_k \end{aligned} \quad [5].$$

Different locations can have different growth rates because of spatial variation in abiotic conditions and resources. Landscape configurations change the immigration and emigration of individuals at patch k . We examine population growth over the entire region by adding up growth across all locations. Given that we assume that dispersal among regions is negligible, the immigration and emigration terms across locations cancel out. One can then obtain the regional intrinsic growth rate as follows [18] (Equation 6):

$$d \frac{\bar{N}}{dt} = \bar{r} \bar{N} = [\bar{r} + \text{cov}(r, v)] \bar{N} \quad [6].$$

The overbar refers to a spatial average; v measures the relative abundance of the focal species across space; and cov is the covariance between local growth rates and local abundances. The regional intrinsic growth rate (the expression in brackets on the right side of Equation 6) cleaves into two terms: an average intrinsic growth rate, averaged across locations, and a term expressing how movement alters the exposure of individuals to those different locations (the covariance term). A region has environmental conditions within the regional fundamental niche of a species if the regional growth rate is greater than 0. If local intrinsic growths are all positive, the regional growth rate will be as well. Likewise, a species cannot persist in a region if all growth rates across the region are negative (in a constant environment, [22]). In these cases, dispersal merely shuffles individuals, without affecting the regional fundamental niche.

Spatial dynamics shape the regional fundamental niche when the region contains a mix of localities, some within the (local) fundamental niche, and some outside. For example, if individuals can move to locations to maximize their individual fitness, a positive covariance term results, and a species might persist at the regional scale even if most localities in the region are outside its local fundamental niche; the same is true if dispersal rates are low, because populations tend to build up where growth rates are locally high. Conversely, when dispersal is rapid and uniform, the species becomes roughly equally dense everywhere; the covariance term approaches zero and the regional average growth rate defines the range limit. In this case,

dispersal from source to sink habitats can so depress the growth rate of a species that it goes regionally extinct.

One can also define a regional realized niche. To do this, make local growth rates functions of the abundances of resident community members, and insert the resulting expression into the expression for regional growth. Spatial variation in community composition, possibly co-varying predictably with environmental variation, might imply spatial variance in local growth rates of the focal species. This can alter the spatial average of growth rates, as well as the realized distribution of the species at the local scale across localities. How this plays out depends on the biology of local interactions and dispersal [42]. **Box 3** uses this formulation as a starting point to describe how spatial processes can alter the impact of competition on range limits for one particular case. In some cases, Soberón's 'Eltonian noise' hypothesis holds, and biogeographic-scale distributions can just reflect a spatial averaging of the fundamental niche at local levels; however, this need not always be the case [42]. An important agenda for future work will be to use scale transition theory to rigorously test the link between community ecology and broad-scale range limits; although general guidelines are already available [46,47], more work is needed to adapt these methods for biogeography.

Concluding Remarks

Understanding the effects of biotic interactions on range limits is difficult because of the myriad ways species can interact. Some attempts have been made to provide general guidelines [18], but the theory remains opaque and difficult to apply. Species distribution models typically do not consider biotic interactions [27,48] and, despite promising work on joint species distribution models [49,50], general evidence supporting or rejecting the hypothesis that biotic interactions impact range limits is lacking. The framework we highlight here is promising because it clarifies some conceptual issues in niche theory, and suggests how one can relate niche concepts across different spatial scales. These could help highlight exciting avenues for empirical research (See Outstanding Questions).

Our approach emphasizes the effects of population dynamics within a geographic area (defined at either local, regional, or biogeographic scales). These dynamics can be used to demarcate the fundamental and realized niches of a species, which in turn influences its distribution. However, other processes can shape the distribution of a species [34]. These include: dispersal barriers at biogeographic scales [51]; strong dispersal among regions (such that some parts of a range might be demographic sinks); historical contingencies, such as priority effects [52]; nonequilibrium dynamics [53]; and regional-scale extinctions that occur for reasons not evident in present conditions. Each of these processes can change where a species is present, when biotic interactions matter and when they do not. It is our belief that the best way to study the consequences of these processes is to first articulate when population dynamics (including niche theory) predict that a species will be present, then contrast these predictions with the areas where species are in fact present [54]. This is a task that our framework is designed to facilitate by developing criteria to predict the effects of biotic interactions across a diverse range of mechanisms and spatial scales.

This framework also raises important technical challenges to meet in the field, such as measuring intrinsic growth rate, average interaction strength, and growth–density covariance. Some of these challenges have been recently addressed in empirical studies of the coexistence of species [55], suggesting that the framework we propose is feasible at least at times in the field. We suggest a clear answer to the fundamental question of the impact of biotic interactions on range limits will require contrasts between the effects of biotic interactions and the effects of the abiotic environment on the growth rate of a species at local scales, and aggregated

Outstanding Questions

Can we predict species range limits from population growth rates calculated at an appropriate scale? Modern coexistence theory claims that the effects of species interactions can be understood by studying population growth rates calculated over an appropriate spatial scale.

Does the variation of resource quality and availability over biogeographical gradients influence demography?

Resources can vary in both their quantity (e.g., productivity should increase with temperature), thus also contributing to local demography and, subsequently, to range limits.

Does per capita interaction strength vary along temperature gradients? There is considerable evidence that interactions such as predation and top-down control can vary over temperature gradients, but the underlying mechanisms remains unclear. Documentation of the variation of per capita interaction strength will be important.

Is there systematic variation in network structure along gradients? Niche overlap depends on the fine details of the structure of which species interact with others in networks. We are only now getting access to extensive data sets of networks in space and time. The investigation of species roles and trophic complementarity over large gradients will provide a more mechanistic understanding of the effect of biotic interactions on range limits.

Does per capita interaction strength covary with population size? Or, in other words, are the most abundant species also those with the strongest impact on other species? This critical quantity enters the equation used to approximate the total effect of interactions from a diverse community. Understanding this question would help us to determine how interactions with entire communities shape range limits.

How does the intrinsic growth rate and the strength of biotic interactions change with spatial scale? The persistence of a species in a region requires that the regional average growth rate is positive. This quantity might differ from the growth rate at a local community because of spatial processes. The

(appropriately) up to larger spatial scales. The next challenge for theoreticians and modelers will be to sit together and co-develop operational species distribution models from this theory [56].

issue of scaling the impact of biotic interactions on range limits is still controversial.

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