

spatial context, even if the technical details of their calculation change. By not making the explicit connection between invasion growth rates and the niche- and fitness-difference framework, we believe that Godsoe *et al.* [4] miss an opportunity to connect range theory to the mechanisms determining the outcome of species interactions.

The integration of coexistence theory and biogeography will allow a better understanding of how biotic interactions shape species' range limits. Invasion growth rates yield the primary answer of interest – whether a species can persist in a location in the presence of its competitors – and to this end we join Godsoe *et al.* [4] in advocating experiments that estimate species' intrinsic growth rates and interaction strengths across environmental gradients. However, parsing out niche and fitness differences provides additional power to resolve the underlying mechanisms structuring ranges. In particular, we believe that this is the best way forward for multiple research agendas, including the ability to link coexistence to specific traits [11] or use coexistence theory to forecast interaction outcomes as environments change [12].

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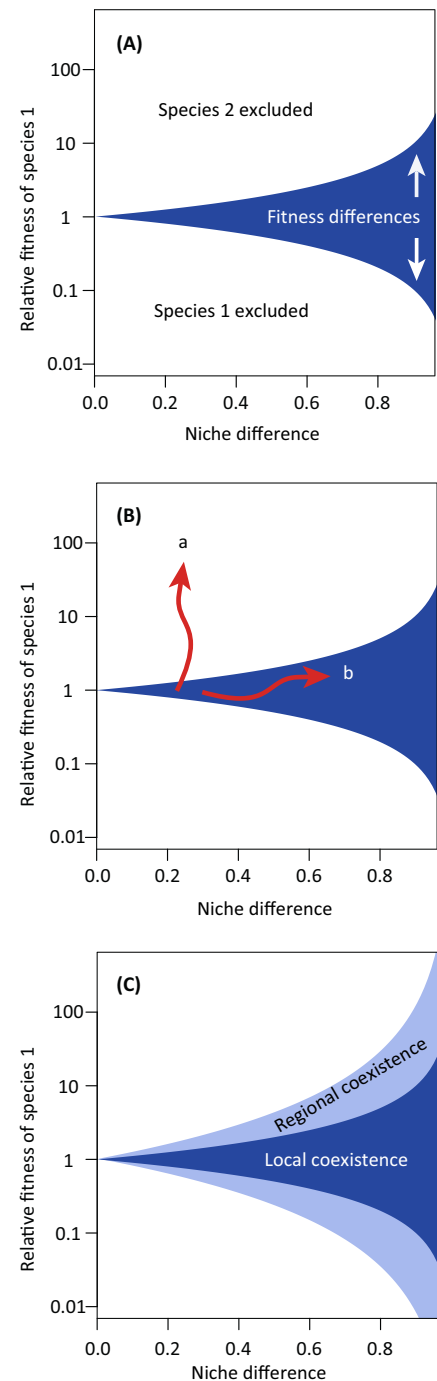
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Letter

Which Coexistence Mechanisms Should Biogeographers Quantify? A Reply to Alexander *et al.*

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An important challenge is the integration of biogeography and community ecology. This challenge is exemplified by controversies over the role of biotic interactions in shaping species' range limits. In a recent paper [1], we argued that a key avenue for this integration is the explicit focus on the ability of a species to increase when rare, which is central to the use of ecological niche models in single-species biogeography (e.g., [2]) as well as coexistence theory in community ecology [3–6]. Alexander *et al.* [7] suggest that additional insights may come from distinguishing species' 'average fitness differences' and 'niche differences'. When studying the presence of a single species (the problem we discuss



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Figure 1. Coexistence Mechanisms and the Impact of Biotic Interactions on Range Limits. (A) The Lotka–Volterra model with symmetric competitive interactions.

(See figure legend on the bottom of the next page.)

in [1]), it may typically be unnecessary to characterize fitness differences and niche differences, but for other biogeographic problems focusing on multiple species simultaneously, we see promise in Alexander *et al.*'s suggestion, although, as we note below, implementing it will be challenging.

Consider a simplified real-world example: the shrinkage of the altitudinal range of Hawaiian honeycreepers (such as the 'iwi *Drepanis coccinea*) towards the cool highlands because malaria-carrying mosquitoes colonized the lowlands [8]. To a first approximation, the 'iwi's growth rate, when it is rare, at position x along the altitudinal gradient may be an expression like

$$r_g = r_0(x) - \beta(C, x)M(C, x). \quad [1]$$

Each term in Equation 1 has a clear mechanistic interpretation. The first term is intrinsic growth rate, the second mortality from malaria; M is malarial mosquito density and β is *per capita*, per mosquito rate of bites. C is the resident community influencing mosquito abundance and behavior (e.g., alternative hosts for

$$\frac{dN_1}{dt} = N_1(r_1 - N_1 - \alpha N_2)$$

(and a similar equation for species 2), [1]

leads to the condition for coexistence:

$$\frac{1}{\alpha} > \frac{r_1}{r_2} > \alpha. \quad [1]$$

The figure sketches the conditions leading to species' coexistence in a plot of the log relative fitness (r_1/r_2) of species 1 versus the niche difference ($1 - \alpha$). Fitness is equal when $r_1/r_2 = 1$. As we move away from this point, fitness differences increase. Species coexist (blue) when niche differences are strong enough to overcome fitness differences. (B) Environmental gradients (red) change the strength of each coexistence mechanism, which can impact individual species' distributions and the overall effects of competition across the community. (C) Regional-scale processes may alter the strength of coexistence mechanisms, potentially altering the impact of biotic interactions on distributions.

malaria). Range limits could arise because of spatial variation in any of the ingredients in Equation 1; for the 'iwi at low altitudes, $r_0 > 0$ but $r_g < 0$, because mosquitoes there bear lethal malaria; mosquitoes are rare and sluggish at high altitudes, permitting 'iwi persistence. In [1] we argued that expressions like Equation 1 are essential for studying the range limit of a single species. In the absence of Allee effects, density-dependent feedback of the 'iwi on itself does not enter into the criterion for where it can increase when rare.

Robust coexistence of multiple species requires each species to increase when rare, with others at their equilibrium abundances (setting aside complexities from unstable dynamics and multispecies interactions [5]). Density-dependent feedback controls these abundances. This criterion generates coexistence conditions involving the interplay of 'average fitness differences' and 'niche differentiation'. The fitness differences in coexistence theory often incorporate density-dependent feedback mediated indirectly through resources or natural enemies (e.g. [2], see expression 6) or direct interactions within and between species (e.g. [5], see expression 4), requiring empirical estimates of considerably more quantities than are required by expressions such as Equation 1.

When considering the biogeography of multiple interacting species, we agree that important insights could emerge by distinguishing niche and fitness differences; for instance, in gauging the overall impact of competition on the distributions of all species in a community simultaneously [9,10]. Figure 1 shows a simple example where average fitness differences do indeed match the relative intrinsic growth rate, r . Niche differences imply weaker competition among than within species (Figure 1A, right). Fitness differences emerge when species differ in r . The 'funnel' portrays conditions

permitting coexistence, defining localities where neither species affects the other's distribution (see caveats in [4]). Figure 1B shows two environmental gradients, with arrows indicating the direction in which coexistence mechanisms favor the presence of species 1. Across both gradients biotic interactions have little effect on the distribution of species 1. However, along the gradient with increasing fitness differences (a) biotic interactions have a strong impact on distributions across the community, because species 2 is excluded across most of the gradient. In the gradient where niche differences increase (b), biotic interactions have negligible impact on distributions across the community.

Similar issues emerge at broader spatial scales. Some broad-scale mechanisms expand the range of conditions where a focal species has a positive invasion growth rate. For example, a steep elevation gradient may permit both 'iwi and malaria-transmitting mosquitoes to have positive growth rates across Hawaii, considered as a whole. Understanding these processes is vital when investigating the range limit of a focal species. Some broad-scale mechanisms facilitate regional coexistence by increasing niche differences or reducing fitness differences (Figure 1C) [6,10], but broad-scale mechanisms can also hamper regional coexistence [11].

Analysis of stabilizing and equalizing mechanisms may not be needed to study individual species' range limits – one can sensibly focus on understanding a single species without unraveling the entire suite of interactions that govern abundances across entire communities – but we agree that a wholehearted fusion of biogeography and community ecology will eventually require an analysis of how stabilizing and equalizing mechanisms shift across space, aiming towards a community biogeography.

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Letter

Competition in the Historical Niche: A Response to Scheele *et al.*

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Scheele *et al.* [1] recently proposed the 'niche reduction hypothesis' to understand species declines and how to

manage them. This is an important advance demonstrating that threats often reduce the niche breadth of a species, and this has implications for conservation management. Scheele *et al.* [1] argue this approach 'can improve management of declining species by identifying where to focus resources and which interventions are most likely to be effective in a given environment'. However, an important factor not covered therein is the role that interspecific competition plays in niche expansion and contraction. We argue here that interspecific competition is key to understanding and improving the effectiveness of management interventions, especially within the historical niche of a species.

Competition between species is a dominant driver of community assembly and niche dynamics. Early work on niche theory predicted that species niche breadth [2] and overlap [3] should decrease with species richness, in other words that niche breadth and overlap are higher where there are fewer competitors. Indeed, there is empirical support for this in many communities, including forest plants [4] and passerine birds [5]. The corollary of this phenomenon is that if species richness is reduced as a result of local extinctions, then remaining species may expand their realised niche breadths as interspecific competition is reduced (ecological release) [6,7]. Alternatively, exotic species may invade the vacated niche space – a pattern often observed in plant communities [8]. This latter situation is distinct from that where the decline of a native species is driven by competition from an exotic.

Thus, if declining or locally extinct species are returned to areas of their former range, they may experience higher levels of interspecific competition than they did historically [9,10]. The consequences of this will depend on the competitive strengths of the resident and returning

species, as well as on the drivers of competitive dominance. Returning species that are poor competitors or have very specific habitat requirements may struggle to re-establish in the face of elevated competition within their niche space. For example, red wolves (*Canis rufus*) were historically found throughout eastern USA, but now exist in a single managed population in North Carolina. Following the decline of both red and grey wolves (*C. lupus*), coyotes (*C. latrans*) expanded their range across much of North America. This includes the former range of the red wolf where coyotes act as a competitor, inhibiting recovery [11].

Stronger competitors may fare better, but reductions in local community size and increased importance of ecological drift can render them effectively neutral, thus disrupting traditional competition–colonisation trade-offs [12]. Similarly, if the competitive dominance of a returning species was previously driven by propagule pressure, a small reintroduced population may struggle to establish in a system now dominated by other species.

In summary, even if a threat causing niche contraction is removed, niche breadth may not expand as expected. Shifts in community dynamics can cause new limiting forces to emerge in the historical niche of a species following its local extinction. Extending the niche reduction hypothesis to consider changes in competitive dynamics will enhance its relevance to ecosystem restoration and biodiversity conservation. An increased focus on the role of competition in biodiversity models and plans more generally is timely given an increasing number of proposals to reintroduce or translocate species through rewilding, de-extinction, and assisted colonisation.

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