Letter

Species’ Distributions as a Coexistence Problem: A Response to Godsoe et al.

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Ecologists are seeking increasingly sophisticated ways to understand how biotic interactions influence species’ distributions, range limits, and range dynamics [1–3]. A recent article by Godsoe et al. [4] aims to integrate coexistence theory into more traditional range theory, arguing that coexistence theory might guide a general understanding of when and how biotic interactions impact species’ range limits. This is a plausible and compelling idea because a species’ distribution can be conceptualized as the outcome of a geographic-scale coexistence problem [5]. However, we feel that it is important to point out how other insights from coexistence theory that are not highlighted by Godsoe et al. [4] could provide deeper understanding of the mechanisms setting range limits.

Coexistence can be understood in terms of only two sets of forces: differences between species in their competitive ability (referred to in the coexistence literature as species’ average fitness differences) promote competitive exclusion, while coexistence is promoted by differences between species that reduce the intensity of interspecific relative to intraspecific competition (i.e., niche differences). Together, average fitness differences and niche differences determine whether a species can increase from low density when in the presence of a competitor that is near its equilibrium abundance (also known as the ‘invasion growth rate’ in the coexistence literature) [6]. As emphasized by Godsoe et al. [4], the invasion growth rate is a key metric for understanding the outcome of species interactions and has already served as a useful tool in numerous empirical investigations (e.g., [7,8]).

Although the invasion growth rate is itself often enough to reveal whether a species can persist with competitors, parsing it into niche and fitness differences could have value for our basic understanding of the mechanisms underlying range margins. In particular, it could reveal whether competitive exclusion at range margins is driven mainly by declines in the competitive ability of a focal species relative to its competitor or by increasing niche overlap between competitors, when approaching range limits. For example, in the first case a range limit can emerge because a species’ intrinsic growth rate (i.e., population growth in the absence of competition) declines towards the edges of the fundamental niche, as predicted by range theory [9], because its sensitivity to competition increases, or because the competitive ability of its competitor increases; in the second case, competitive exclusion becomes more likely, even in the absence of any change in species’ relative competitive ability, as niche differences become smaller. In the many examples of closely related species that replace each other across environmental gradients (e.g., the example of the red and grey squirrels cited by Godsoe et al. [4]), this latter scenario would ultimately mean that replacement is due to encounters with species that have similar niches (e.g., that consume similar resources), while the first scenario suggests that one species replaces another due to increasing differences in their relative competitive abilities.

Our discussion of the niche- and fitness-difference framework thus far treats invasion growth rates at range edges as if they were spatially independent quantities. This is not true, given that spatial structure is introduced by processes such as dispersal limitation, spatially structured competition (e.g., competition that is limited to nearest neighbors), and spatially varying environments. As Godsoe et al. [4] suggest, scale-transition theory [10] provides the quantitative framework to scale from local to regional invasion growth rates in a way that explicitly accounts for spatial processes. However, the conceptualization of coexistence in terms of niche and fitness differences remains valid within a 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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References