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Note

The Mismatch between Range and Niche Limits due to Source-Sink Dynamics Can Be Greater than Species Mean Dispersal Distance

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ABSTRACT: Species distribution models assume that at broad spatial scales, environmental conditions determine species ranges and, as such, source-sink dynamics can be ignored. A rationale behind this assumption is that source-sink dynamics manifest at length scales comparable to species mean dispersal distance, which is much smaller than length scales of species distribution and variation in climate. Using a two-dimensional reaction-diffusion model, we show that species can use sink habitats near the niche limit as stepping-stones to occupy sink habitats much further than the mean dispersal distance, thereby extending the distribution far beyond the environmental niche limit. This mismatch between range and niche limits is mediated by the shape (local curvature) of the niche limit. These curvature effects may be significant for a highly dispersive species with low per capita growth rate sensitivity to changes in the environment. These findings underscore the potential importance of stepping-stone dispersal in determining range limits.

Keywords: source-sink dynamics, range limit, reaction-diffusion models, stepping-stone, curvature.

Introduction

All species are geographically limited (Sexton et al. 2009). Understanding the mechanisms limiting species distributions is a central challenge in the biogeography theory (Gaston 2003; Holt and Keitt 2005). Traditionally, demographers argue that as a first approximation, range limits are formed by physiological limits on population growth imposed by the environment (Hargreaves et al. 2014). As such, the range limits are determined by scenopoetic environmental conditions (e.g., precipitation, temperature, and edaphic factors) for which the population per capita growth rate is zero (Holt et al. 2005). On the basis of this logic, in a landscape with a broadscale environmental gradient, the species range limit is aligned with the niche limit set by the environmental constraints (Peterson et al. 2011, chap. 2).

However, it has long been recognized that the match between the realized environment and species fundamental niche may be imperfect (Hutchinson 1957). For instance, dispersal from a high-quality source habitat can maintain the population in a sink that would otherwise become locally extinct (Pulliam 1988). Therefore, source-sink dynamics can generate a mismatch between range and niche limits (Pulliam 2000).

In practice, however, some species distribution modelers claim that the environment determines species ranges at broad spatial scales (Pearson and Dawson 2003), and biogeographers can ignore mismatches between range and niche limits due to dispersal (see Phillips et al. 2006). One possible theoretical justification of this idea is that occupied sink habitats must be linked to source habitats at a length scale comparable to the species' mean dispersal distance (Shmida and Wilson 1985; Holt and Gaines 1993; Tittler et al. 2006; Boulangeat et al. 2012). Since most species distributions span regions much larger than their typical dispersal distance, the mismatch between range and niche limits due to source-sink dynamics can be neglected.

This view may be overly conservative regarding the potential for dispersal to expand range limits. Several studies indicate that sink patches near the niche limit can export immigrants to other sink patches. Kanda et al. (2009) showed that Virginia opossum (*Didelphis virginiana*) in central Massachusetts used sink habitats near the niche limit as stepping-stones to occupy sink habitats at a distance much greater than the mean dispersal distance (see also Zawadzki et al. 2019). Over multiple generations, dispersal and subsequent

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reproduction in these stepping-stone sinks can extend the range limit far beyond the region where the species have a positive per capita growth rate. As well as maintaining range limits, dispersal from sinks can also facilitate invasion via transportation hubs (Apte et al. 2000), stabilize marine reserves (Gaines et al. 2010), and extirpate populations by draining source habitats (Skellam 1951; Hoopes and Harrison 1998).

These studies highlight that repeated, intergenerational dispersal and reproduction can sustain chains of sink patches, which we refer to as stepping-stone dynamics (Baum et al. 2004; Saura et al. 2014). Yet we lack an understanding of how demographic processes—such as birth, death, immigration, and emigration—interact at species boundaries to drive the mismatch between the range and niche limits. The lack of a mechanistic model prevents us from understanding when stepping-stone dynamics are important.

In this paper, we develop a model to study the role of stepping-stone dispersal at the niche limit in determining species distribution. Although there are multiple theoretical approaches to study range limits (for various modeling approaches, see Case et al. 2005; Holt et al. 2005), we use a reaction-diffusion model for two reasons. First, the diffusion model is analytically tractable, offering general and deeper insights. Second, space is explicitly incorporated in diffusion models, allowing us to include large-scale environmental gradients on a two-dimensional landscape. Our results have important implications for relating an organism's niche to its distribution, or Hutchinson's duality. This duality conceptually links range limit and niche theory and underlies our efforts to predict species distributional patterns, draw biogeographic inferences, and formulate conservation actions (Colwell and Rangel 2009).

Methods

Consider a species in a two-dimensional landscape whose growth is limited by environmental conditions, such that at low density, the population grows exponentially at a rate r that depends on the local environment e (for notation, see table 1). As density increases, the population saturates to the carrying capacity, K, as a result of intraspecific competition. Although most species are limited by multiple environmental variables in reality, we present results for a single limiting environment for simplicity. In the supplemental PDF, we provide results for a species limited by multiple environmental variables.

Table 1: Symbology

Symbol	Interpretation
r	Per capita growth rate (time^{-1})
K	Carrying capacity
N	Population size
D	Dispersal rate (distance^2 time^{-1})
∇^2	Two-dimensional diffusion operator ($\partial^2/\partial x^2 + \partial^2/\partial y^2$) (distance^{-2})
e	Environmental variable that regulates species growth
e^*	Environmental conditions at niche limit, such that $r(e^*) = 0$
σ	Mean dispersal distance ($\sqrt{Dt_g}$) (distance)
t_g	Generation time (time)
ε	Environmental conditions at range limit
γ	Dimensionless constant of order unity, which does not depend on species characteristics
$\kappa = 1/r_c$	Curvature of niche limit, where r_c is the radius of curvature (distance^{-1})
$\tilde{E}$	Ratio of local environmental conditions at range limit and niche limit (ε/e^*)
$\tilde{A}$	Dimensionless area (($e^*/D\kappa^2$)($\partial r/\partial e$))
G	Change in environmental conditions per unit distance or environmental gradient (distance^{-1})

We consider a two-dimensional landscape with an environmental gradient (e.g., precipitation or temperature) along the x direction such that when $e < e^*$, the local growth rate is positive, and when $e > e^*$, the local growth rate is negative. Here, e^* is the niche limit of the species. More precisely, in two spatial dimensions, the niche limit forms a contour corresponding to $r(e^*) = 0$. Therefore, in the absence of dispersal, the species will be present in source locations where the population is above the replacement rate (i.e., $r > 0$) and will be absent in sink locations where the population is below the replacement rate (i.e., $r < 0$).

Next, we incorporate dispersal via the diffusion approach, which assumes that the dispersal kernel is a standard bivariate Gaussian distribution. However, a Gaussian kernel may be inappropriate for species that disperse long distances (Kot et al. 1996; Clark et al. 1998). For such species, one can investigate stepping-stone dynamics using integro-differential equations with leptokurtic kernels that have fatter tails, for example, Cauchy or Student's t distribution. Nevertheless, here we focus on the diffusion approach for simplicity (Holmes et al. 1994). Mathematically, we can express the joint contribution of growth and dispersal as a partial differential equation that captures variation in the population (N) in both space and time:

$$\frac{\partial N}{\partial t} = r(e)\,N\left[1 - \frac{N}{K}\right] + D\nabla^2 N, \tag{1}$$

where D is the dispersal rate of the species and $\nabla^2 (= \partial^2/\partial x^2 + \partial^2/\partial y^2)$ is the diffusion operator that approximates the dispersal process in a two-dimensional landscape. In a simple diffusion model, dispersal is assumed to be isotropic. On the basis of this model formalism, the typical length scale of species dispersal (σ) is $\sim\sqrt{Dt_g}$, where

t_g is the generation time of the species (see supplemental PDF). Although we consider a logistic growth model as the reaction term, our results are robust to nonlinearities in the per capita growth rate, as the boundary dynamics depend on $r(e)$; one can replace $r[1 - N/K]$ with $\partial f(N, e)/\partial N|_{N=0}$ in the derivations, where $f(N, e)$ is the density-dependent per capita growth rate.

Results

Population change is regulated by four processes: birth and death (captured by the reaction term) and immigration and emigration (captured by the diffusion term). By definition, at the niche limit, the birth and death rates balance each other. Nonetheless, the boundary location may still deviate from the niche limit because of an imbalance between immigration and emigration. Instead, the boundary stabilizes in space where the ecological processes that increase boundary population—birth and immigration—balance the ones that decrease the boundary population—death and emigration (Pulliam 1988; Holt et al. 2005).

Balance of these four processes is met when dispersal and growth rates at the range limit are related as

$$|r(\varepsilon)| \approx \frac{\gamma^2}{4} D\kappa^2, \tag{2}$$

where $|r(\varepsilon)|$ is the absolute value of per capita growth rate when the local environment at the range limit is ε. Here, γ is a constant (with order of magnitude 1) independent of species characteristics, and κ is the curvature of the niche limit (for details, see supplemental PDF; Brazhnik and Tyson 1999*a*, 1999*b*; Tyson and Brazhnik 2000). Mathematically, the curvature at a point on a contour is the reciprocal of the radius of the circle that best approximates the local curve at the contour (see fig. 1; Rutter 2000, chap. 7). Intuitively, κ measures the roundness of the niche limit. The arc of a sharply curved niche contour can be approximated by a circle with small radius, which yields a high curvature value.

By Taylor expanding $|r(\varepsilon)|$ around e^*, we show that the mismatch between range and niche limits in niche space is

$$|\Delta E| \approx \frac{\gamma^2}{4}\left(\frac{D\kappa^2}{|\partial r/\partial e|}\right), \tag{3}$$

where $\Delta E = \varepsilon - e^*$ is the difference between the environment at the range and niche limits and $|\partial r/\partial e|$ tells us how sensitive the growth rate is to small changes in environmental conditions at the niche limit (e^*). To interpret these theoretical results, we consider three environmental gradient scenarios. In each scenario, we start with the boundary initially aligned with the niche limit. Thus, any deviation of the boundary from the niche limit is solely due to source-sink dynamics.

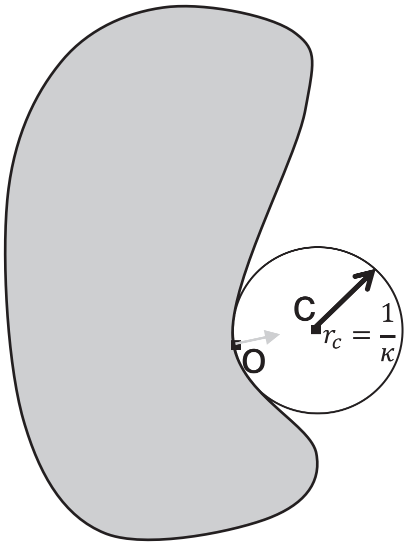

Figure 1: Consider a species whose per capita growth rate r is positive in the gray region. Accordingly, the solid black line bounding the gray region denotes the niche limit of the species. The radius of curvature at point O on the niche limit is defined as the radius of the circle (r_c) that passes through two arbitrarily close points on the niche limit near O. Intuitively, r_c is the radius of the circular arc that best approximates the curve at point O. On the basis of this logic, the curvature of a straight line is 0. The curvature vector at point O (gray arrow) has magnitude proportional to $\kappa = 1/r_c$ and direction from point O to C.

First, we consider a linear geometry of the niche limit (i.e., $\kappa = 0$; fig. 2*A*). For this geometry, locally, the areas of the sink and source habitats on either side of the species boundary are equal. As a result, immigration and emigration rates cancel each other to yield net zero dispersal flux at the boundary. In this trivial case, the range limit aligns with the niche limit ($\Delta E = 0$; fig. 2*A*; solid line in fig. 3), consistent with our theoretical prediction in equation (3).

However, for real species, the niche limit may be curved (i.e., κ is not equal to 0). When the niche limit bends such that the proportion of source habitats exceeds the sink habitats near the niche limit (bottom half of fig. 2*B*), immigration exceeds emigration. Consequently, the boundary population increases and the boundary transgresses slightly into the sink habitats (arrows in fig. 2*B* show the direction of movement). Because the proportion of sources at the boundary is still higher than sinks after a slight shift in the boundary position, immigration from these newly occupied sinks still exceeds emigration. As a result, the boundary will continue to encroach sink habitats because of net positive dispersal flux.

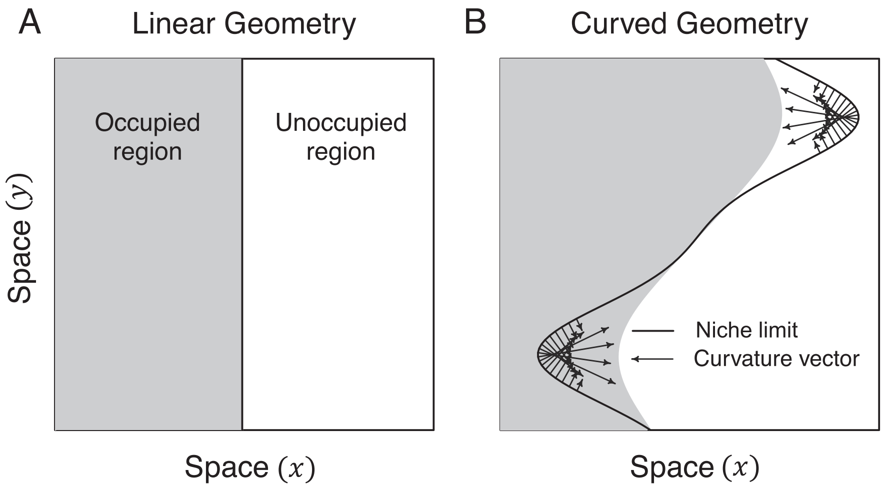

Figure 2: Distribution of species in two-dimensional landscape with increasing gradient in environment along x direction for linear (A) and curved (B) shapes of niche limit (black line). When the niche limit is a straight line (A), the range limit aligns with the niche limit because immigration balances emigration. However, when the niche limit is curved (B), immigration and emigration rates may differ. As a result, the range limit deviates from the niche limit in the direction of the curvature vector (arrow), with magnitude determined by the growth and dispersal characteristics of the species (see eq. [3]). The length of arrows is proportional to the environmental mismatch at the niche and range limits. The gray region indicates an occupied landscape. The simulations were performed by discretizing the two-dimensional landscape with a lattice of size 150 × 150. We used the Euler forward-time scheme with parameters $\partial r/\partial e|_{e=e^*} = 0.1$, $e^* = 5$, $D = 25$, $K = 10$, $\Delta x = 1$, and $\Delta t = \Delta x^2/5D$.

So, how far will the species boundary move before it comes to a halt? That depends on the growth and dispersal characteristics of the species. In the above scenario, the population in sinks near the niche limit increases because of dispersal influx from sources and decreases because of inferior habitat quality. If the dispersal rate D is high, and the quality of sinks slowly declines as one moves away from the niche limit (i.e., $\partial r/\partial e$ is small), the sink populations will increase rapidly. As a result, sink habitats near the niche limit become exporters of individuals to adjacent sink habitats. Eventually, the boundary stabilizes when the positive dispersal flux is offset by decreased growth due to declining habitat quality (dashed line in fig. 3). The species uses sink habitats near the niche limit as stepping-stones to occupy neighboring sinks, thereby extending the range limit far beyond where it would occur in the absence of dispersal (i.e., $\Delta E \neq 0$; see eq. [3]).

For the third scenario, we consider the region of the niche limit that is surrounded by a higher proportion of sink habitats than source habitats (top half of fig. 2*B*). In contrast to the previous scenario, emigration exceeds immigration, and as a result, the boundary moves backward into source habitats (arrows in the upper half of fig. 2*B*). Here, too, the magnitude of mismatch between range and niche limits is determined by dispersal and growth. If the quality of source habitats increases slowly and the dispersal outflux is

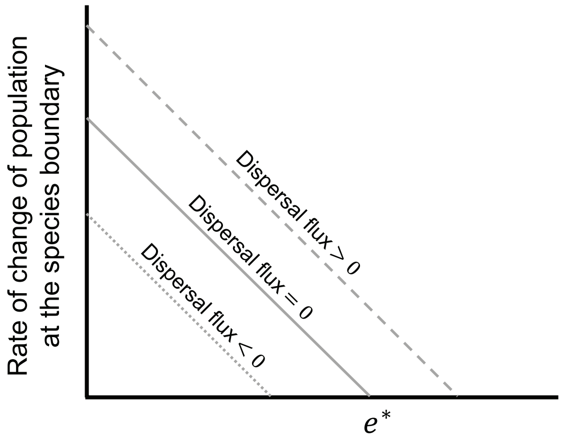

Figure 3: Deviation of the range limit from the niche limit is mediated by the dispersal flux (immigration minus emigration) at the boundary. For the linear geometry of the niche limit, the dispersal flux at the species boundary is zero (solid line). Consequently, the range limit matches the niche limit (e^*). In contrast, when the niche limit is curved, as shown in figure 2*B*, dispersal flux can be positive (dashed line) or negative (dotted line). As a result, the boundary deviates from the niche limit. In the plot, the environmental conditions at the range limit correspond to the point where the lines intersect the x-axis.

high, the source populations near the niche limit decrease rapidly to local extinction. This local extinction event creates a domino effect, and as a result, the boundary continues to encroach source habitats. Eventually, the boundary ceases to move when the rate of change of population at the boundary is zero (dotted line in fig. 3). Although this scenario may seem counterintuitive, local extinction due to curved geometry is widely studied in the invasion theory (see discussion of critical patch size in Okubo and Levin 2001).

Next, we partition the relative contribution of environment and dispersal in determining range limit in niche space. Dividing equation (3) by e^* and rearranging, we get

$$\tilde{E} \approx 1 \pm \frac{\gamma^2}{4}\frac{1}{\tilde{A}}, \tag{4}$$

where $\tilde{E} = \varepsilon/e^*$ is the rescaled environment at the range limit and

$$\tilde{A} = \frac{e^*}{D\kappa^2}\frac{\partial r}{\partial e} \tag{5}$$

is defined as a dimensionless area that depends on species growth and dispersal and the curvature of the niche limit. When dispersal rate is low, $\tilde{A}$ is very large and $\tilde{E} \approx 1$, implying that the environment at range limit (ε) matches the niche limit (e^*). This rescaling of the environmental index at the range limit offers an important insight: equation (4) suggests that when $\tilde{A}$ is small, the environment at the range limit will deviate substantially from the niche limit. From $\tilde{A}$ (eq. [5]) we can infer that source-sink dynamics may be substantial for a highly dispersive species with low growth sensitivity at niche limit.

Although we show the mismatch between range and niche limits in niche space, we can also express the mismatch in geographical space. For instance, consider a landscape with a circular environmental gradient, G, with increasing e as one moves away from the origin. Dividing equation (3) by G, we can show that the magnitude of the mismatch between range and niche limits in the geographical space is (recall that t_g and σ are the generation time and species mean dispersal distance)

$$\frac{\gamma^2}{4}\left(\frac{1}{Gt_g}\frac{\kappa^2}{\partial r/\partial e}\right)\sigma^2. \tag{6}$$

The above expression states that under appropriate conditions, the realized range limit can extend a distance beyond the niche limit much greater than the species' mean dispersal distance.

Let us consider a long-lived plant species limited by temperature to make this point clear. Using seed trap and pollen data from Clark (1998) and Clark (1993), respectively, we can do a back-of-the-envelope calculation to estimate the magnitude of mismatch between range and niche limits. The constant γ is of the order 1 (see sec. 3.5 in Lewis et al. 2016). If we assume that $1/\kappa$ is an order of magnitude smaller than the distribution length scales (~10^2–10^3 km), κ^2 varies between 10^{-2} and 10^{-4} km^{-2}. Climate data suggests that G is of the order 10^{-2} °C km^{-1}. Using seed traps, Clark (1998) estimated D between 10^2 and 10^3 m^2 year^{-1}. From pollen accumulation rates, Clark (1993) estimated r between 10^{-2} and 10^{-3} year^{-1}. If we assume that r changes by a few percent at the range margins per 1°C, $\partial r/\partial e$ varies between 10^{-4} and 10^{-5} year^{-1} °C^{-1}. Putting these parameters together in equation (3), we estimate that the mismatch between range and niche limits ($|\Delta E|/G$) is between 10 m and 100 km. Despite wide variation in our estimate, this rough calculation shows that the mismatch between range and niche limits could be orders of magnitude greater than the species mean dispersal distance (~10–30 m).

Discussion

We develop a two-dimensional reaction-diffusion model that mechanistically combines dispersal and growth to examine the role of stepping-stone dynamics in determining range limits. As expected, we find that the range limit is determined by local environmental conditions via niche requirements and by source-sink dynamics, which are mediated by the geometrical shape of the niche limit (fig. 2; eq. [3]). However, in contrast to previous studies (Shmida and Wilson 1985; Holt and Gaines 1993), we find that the mismatch between range and niche limits may be much greater than the mean dispersal distance for species with high dispersal rate and low growth sensitivity (eq. [6]). Our findings highlight the importance of stepping-stone dispersal in determining the reciprocal relationship between ecological niches and species ranges (Hutchinson 1978).

Conceptually, niche-based range models work in two steps. First, the species niche is estimated either by biophysical experiments (Crozier and Dwyer 2006) or by a correlative approach that maps species occurrence to prevailing environmental conditions (Phillips et al. 2006). Next, the constructed niche is transferred onto geography at either a different time or different space (Randin et al. 2006). The predicted distribution patterns are then used to make a wide range of biogeographic inferences (Elith and Leathwick 2009; Peterson et al. 2011). Naturally, the robustness of these inferences depends on how reliably we can construct niches and reproject them onto geographical space.

The diffusion model suggests that for some species, the mismatch between range and niche limits due to curvature-driven stepping-stone dynamics can be much greater than the mean dispersal distance (eq. [6]). As a result, neglecting dispersal may lead to significant over- or underestimation of species distribution when projecting the niche envelope onto geographical space (Pagel and Schurr 2012; Gilroy and Edwards 2017). When estimating the niche envelope using occurrence data, the model may include the environment from occupied sinks and fail to capture the environment in empty sources. Even if the niche envelope is known (e.g., via biophysical experiments), transferring the envelope to a different region may still lead to projection errors. Near the niche limit, the model may fail to predict occupied sinks and empty sources accessible through local dispersal. These errors arising from the interactions between growth and dispersal at the population margins can thwart forecasting efforts and yield biased inferences.

It is therefore prudent to ask: is source-sink dynamics just a minor nuisance (as traditionally assumed) or a major determinant of range limits of species? And, if so, which statistical procedures can allow us to detect and quantify the effects of stepping-stone dispersal on species distributions? Unfortunately, there is little direct empirical evidence at present to evaluate the importance of curvature-mediated source-sink dynamics at large spatial scales. In a recent study, Goel et al. (2020) showed that stepping-stone dispersal at the savanna-forest boundary could explain the continental-scale mismatch between biome and climate. In particular, the researchers found that the variation in precipitation at the savanna-forest boundary in Africa was consistent with curvature dynamics predicted from theory. These source-sink dynamics resulted in up to ∼1,000 mm in variation in annual precipitation at the biome boundary and corresponding deviation of ∼500 km of biome boundary from its bioclimatic limit (see figs. 5 and 6 in Goel et al. 2020). This case study suggests that curvature effects could be prevalent even at large spatial scales.

The next step is to examine whether source-sink dynamics determine the range limits of other taxa in different biogeographical regions. For species that are limited by a single environmental variable, the mismatch between range and niche limits can be estimated using the geometrical approach presented in Goel et al. (2020; for a numerical example, see fig. S1). However, this method is not feasible for species with multidimensional niche. As discussed before, statistical approaches based on correlative species distribution models (Peterson et al. 2011; Guisan et al. 2017) are inappropriate for this task because they ignore source-sink dynamics altogether and, as a result, produce biased niche estimates. Recently developed process-based hybrid species distribution models (Keith et al. 2008; Thuiller et al. 2008) also suffer this problem. The hybrid models combine niche estimated from correlative species distribution models with spatial population dynamics in a piecemeal approach, which, again, biases projections due to underlying biases in the niche estimates (Gallien et al. 2010; Pagel and Schurr 2012; Schurr et al. 2012). Detecting source-sink dynamics at large is thus challenging and requires detailed knowledge of demographic rates (r and D) across the species range. One possibility is to use transplant and greenhouse experiments to obtain growth rates (Crozier and Dwyer 2006; Hargreaves et al. 2014) and propagule trapping (Nathan and Muller-Landau 2000; Bullock et al. 2017) and satellite tracking (Katzner and Arlettaz 2020) to obtain the dispersal kernel. However, such analysis can be done only for well-studied species for which demographic data are available at relevant spatial and temporal scales.

To circumvent these limitations, Pagel and Schurr (2012) proposed a hierarchical Bayesian statistical framework that allows modelers to explicitly link climate and species distribution data (e.g., presence-absence and species abundance) with a population dynamic model. This approach provides two major advantages. First, we can use observations from commonly available environment and species occurrence data repositories, which allows us to study the range dynamics of species across many taxa. Second, since the Bayesian approach jointly estimates growth and dispersal rates, we get unbiased estimates of the niche curve (i.e., $r(e)$) and dispersal kernel. As a result, we can disentangle the contribution of environment and source-sink dynamics in determining the range limits (Ehrlen and Morris 2015). Indeed, in a comparative analysis, Zurell et al. (2016) showed that the process-based Bayesian model in Pagel and Schurr (2012) outperforms simple correlative distribution models and its hybrid variants in tracking species boundaries under climate change scenario.

The two-dimensional reaction-diffusion model presented in this paper can be used as the spatial population dynamics model in Pagel and Schurr's (2012) statistical framework to study range dynamics of real species. A step in this direction was taken by Wikle (2003) to fit a two-dimensional reaction-diffusion model to the invasion history of house finches in the United States using a Bayesian framework. Such process-based statistical models can make better biodiversity change predictions and facilitate causal interpretation of the ecological mechanisms that limit species distributions.

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Statement of Authorship

N.G. conceived and designed the study and wrote the paper with feedback from T.H.K.

Data and Code Accessibility

This paper has no data. Code has been deposited in GitHub (https://github.com/nikunj410/Source-sink-dynamics-at-range-limits.git) and the Dryad Digital Repository (https://doi.org/10.5061/dryad.c59zw3r97; Goel and Keitt 2022).

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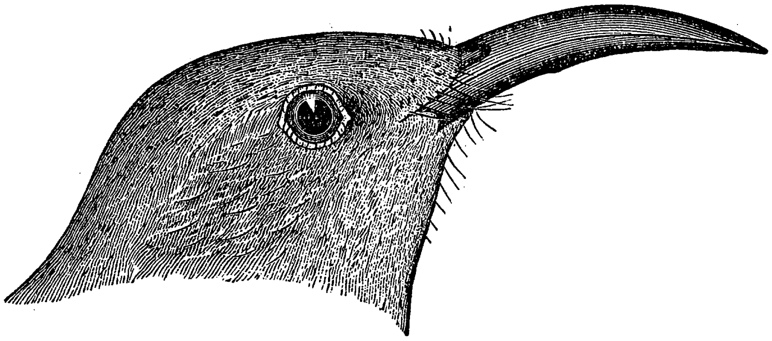

Next, we have the Californian Mocking-thrush (*H. redivivus* [figured]). Its points are—the long arcuate bill; dark olive-brown color, paler below, gradually changing to rusty-brown on the belly and to rusty-white on the throat; heavily streaked ear coverts, but no maxillary stripes nor spots on the breast; length eleven inches or more, wing four or less, tail five or more, bill and tarsus, each, about 1 1/3 inches." From "Some United States Birds, New to Science, and Other Things Ornithological" by Elliott Coues (*The American Naturalist*, 1873, 7:321–331).