

1 **Source-sink dynamics can maintain mismatched range and**
2 **bioclimatic limits even at large spatial scales**

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21 **Abstract**

22 Bioclimatic models assume that at broad spatial scales, climate is the primary determinant of
23 species distribution. Meanwhile, processes such as source-sink dynamics can be ignored because
24 they are thought to manifest at length scales comparable to species mean dispersal distance. We
25 present a reaction-diffusion model to show species can use sink patches near the bioclimatic (or
26 niche) limit as stepping-stones to occupy sinks much further than the mean dispersal distance,
27 thereby extending the distribution far beyond the bioclimatic envelope. This mismatch between
28 geographical and bioclimatic limits is mediated by the shape of the bioclimatic limit and may be
29 significant for low growth sensitivity and fast dispersal life strategy. These findings challenge one
30 of the core assumptions of the bioclimatic models. Therefore, we advocate that biogeographers
31 consider the role of dispersal when using bioclimatic models to generate inferences about the
32 ecological and evolutionary processes that determine the distribution of biota.

33

Introduction

34 All species are geographically limited. Understanding the mechanism that limits species
35 distributions is a central challenge in biogeography theory (Gaston 2003, Holt and Keitt 2005).
36 Traditionally, biogeographers have argued that geographical limits are formed by physiological
37 limits on population growth imposed by the environment. And as such, the range limits are
38 determined by bioclimatic conditions for which the population replacement rate is zero (Holt et al.
39 2005). Based on this logic, in a landscape with a broadscale environmental gradient, the species
40 range limit is aligned with the bioclimatic limit (von Humboldt and Bonpland 1807). Hence, the
41 bioclimatic theory of species distribution is, in essence, a framework on how to project
42 Hutchinson's (1957) fundamental niche onto the geographical space (Pearson and Dawson 2003).

43 However, it has long been recognized that the match between the realized environment and
44 fundamental niche may be imperfect. For instance, dispersal from a high-quality source habitat
45 can maintain the population in a sink that would otherwise go locally extinct (Pulliam 1988).
46 Therefore, source-sink dynamics can generate a mismatch between geographical and bioclimatic
47 limits (Pulliam 2000). These observations stand in sharp contrast to the assertions of bioclimatic
48 modelers who claim that at broad spatial scales, the climate is the primary determinant of species
49 distribution (Pearson and Dawson 2003) and, as such, biogeographers can ignore potential
50 mismatches between geographical and bioclimatic limits due to dispersal (Phillips et al. 2006).
51 The main justification of this idea is that—occupied sink patches must be linked to source patches
52 at a length scale comparable to the mean dispersal distance of an organism (Shmida and Wilson
53 1985, Tittler et al. 2006). And since mean dispersal distance is typically orders of magnitude
54 smaller than distribution length scales, the mismatch between range and bioclimatic limits due to
55 source-sink dynamics is small and can therefore be neglected (also see Boulangeat et al. 2012).

56 This argument, however, has a significant limitation because it assumes sink patches do
57 not produce migrants despite several studies indicating otherwise. For example, Kanda et al.
58 (2009) noted that Virginia opossum (*Didelphis virginiana*) in Massachusetts used sink habitats
59 near the bioclimatic limit as stepping-stones to occupy sink patches at a distance much greater than
60 mean dispersal distance, thereby extending the range limit far beyond the bioclimatic envelope. In
61 another study, Goel et al. (2020) showed that stepping-stone dispersal, coupled with bistable
62 dynamics, could explain the climatic deviation of the continental-scale savanna-forest boundary
63 from its bioclimatic limit.

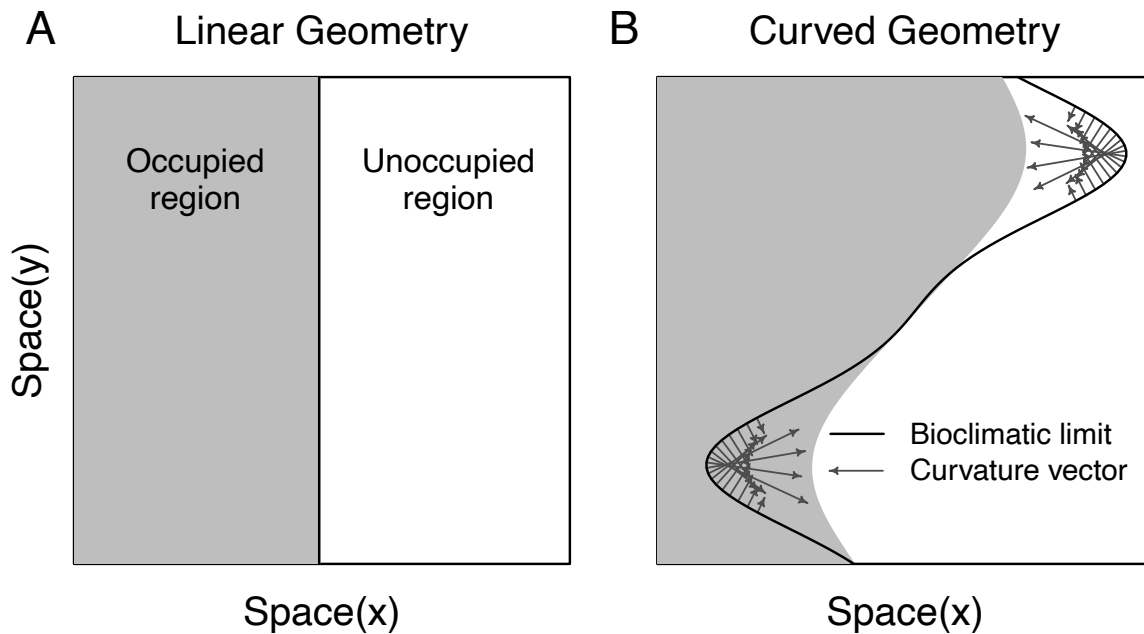
64 These studies highlight that interlinkage of population dynamics of faraway populations
65 by intermediate patches through dispersal, here referred to as stepping-stone dynamics, for short,
66 could be an important determinant of distribution limits. However, we lack an understanding of
67 how demographic processes—such as birth, death, immigration, and emigration—interact at
68 species boundary to drive the mismatch between the geographical and bioclimatic limits.
69 Furthermore, the lack of a mechanistic model renders us unable to ascertain when and where
70 stepping-stone dynamics may be important. Here we address this gap by considering a two-
71 dimensional reaction-diffusion model that combines environment-dependent growth and dispersal
72 characteristics of the species. We discuss the implications of our findings on relating an organism's
73 niche to distribution, which conceptually links range limit and bioclimatic theory, and underlies
74 our efforts to predict the distribution patterns and make biogeographic inferences (Colwell and
75 Rangel 2009, Peterson et al. 2011).

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Methods

78 We consider a species whose growth is limited by climate, such that the per-capita growth rate, r ,
79 is a scalar function of the local environment, e . Although, in reality, most species are limited by
80 multiple environmental variables, to build intuition, we present results for a single limiting
81 environment. In Appendix S1 in Supporting Information, we provide results for a species limited
82 by multiple environmental variables.



83

84 **Figure 1:** Distribution of species in a landscape with a increasing gradient in environment along x direction for (A)
85 linear and (B) curved shapes of the bioclimatic limit (black line). When the bioclimatic limit is a straight line (A), the
86 range limit aligns with the bioclimatic limit because of immigration balances emigration. However, when the
87 bioclimatic limit is curved (B), immigration and emigration rates may differ. As a result, the range limit deviates from
88 the bioclimatic limit in the direction of the curvature vector (grey arrow), with magnitude determined by the growth
89 and dispersal characteristics of the species (see Eq. 3). The length of grey arrows is proportional to the environmental
90 mismatch at the bioclimatic limit and the range limit. The grey region indicates occupied patches. The simulations
91 were performed on a 2D lattice of size 150x150 using Euler forward-time scheme with parameters $\partial r/\partial e|_{e=e^*} =$
92 0.1, $e^* = 5$, $D = 25$, $\Delta x = 1$, and $\Delta t = \Delta x^2/5D$.

93
94 We assume an increasing gradient in the environment along the x direction on a 2D
95 landscape, such that when $e < e^*$, the local growth rate is positive, and when $e > e^*$, the local
96 growth rate is negative. Here, e^* is the bioclimatic limit of the species. More precisely, in two
97 spatial dimensions, the bioclimatic limit forms a contour corresponding to $r(e^*) = 0$ (black
98 contour in Fig. 1), bounding where the species exhibits a positive growth rate. Therefore, in the
99 absence of dispersal, the species is present in source locations where the population is above the
100 replacement rate (*i.e.*, $r > 0$) and is absent in sink locations where the population is below the
101 replacement rate (*i.e.*, $r < 0$).

102 Next, we incorporate dispersal via the diffusion approach. The diffusion model has an
103 advantage in that it is analytically tractable (Holmes et al. 1994) and emulates observed dispersal
104 patterns among plants and animals (Okubo and Levin 2001). Mathematically, we can express the
105 joint contribution of growth and dispersal as a partial differential equation that captures variation
106 in the population (N) in both space and time:

$$\frac{\partial N}{\partial t} = r(e) N + D \nabla^2 N, \quad (1)$$

107 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
108 that approximates the spatially structured dispersal process in a 2D landscape. Based on this model
109 formalism, the mean dispersal distance (σ) of the species is $\sim \sqrt{Dt_g}$, where t_g is the generation time
110 of the species. Although we consider an exponential growth term, our results are robust to non-
111 linearities in growth rate; one can simply replace r with $\partial f(N, e)/\partial N|_{N=0}$ in the derivations to
112 account for non-linearities, where $f(N, e)$ is the density-dependent growth rate.

113

114

Results

115 Population change, including at species ecotone, is regulated by four processes: birth and
116 death (captured by the exponential growth term), and immigration and emigration (captured by the
117 diffusion term). Although the growth rate at the bioclimatic limit is zero, the boundary location
118 may still deviate from the bioclimatic limit due to immigration and emigration. The boundary
119 stabilizes where the ecological processes that increase boundary population—birth and
120 immigration—balance the ones that decrease the boundary population—death and emigration.

121 Using a traveling wave solution (Brazhnik and Tyson 1999) for equation (1), we show the
122 above ecological condition is met when dispersal and growth rates at the range limit are related as

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

123 where ε is the local environment at the range limit, γ^2 is a positive constant that is independent of
124 species characteristics, and κ is the curvature of the bioclimatic limit (see Appendix S1).

125 When κ is small, the mismatch between range and bioclimatic limits in niche space is

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

126 where $\Delta E = \varepsilon - e^*$ is the difference between the environment at the range and bioclimatic limits,
127 and $\partial r / \partial e$ is the sensitivity of species growth rate to changes in the environment at the bioclimatic
128 limit. To interpret these theoretical results, we consider three environmental gradient scenarios. In
129 each scenario, we start with the boundary initially aligned with the bioclimatic limit. Thus, any
130 deviation of the boundary from the bioclimatic limit is solely due to source-sink dynamics.

131 First, we consider a linear geometry of the bioclimatic limit (*i.e.*, $\kappa = 0$, Fig. 1A). For this
132 geometry, the number of sink and source patches on either side of the species boundary are equal.
133 As a result, immigration and emigration rates cancel each other to yield net-zero dispersal flux at
134 the boundary. In this trivial case, the range limit aligns with the bioclimatic limit (*i.e.*, $\Delta E = 0$,
135 Fig. 1A), which is consistent with our theoretical prediction in equation (3).

136 However, in reality, the bioclimatic limit rarely assumes a linear geometry (*i.e.*, $\kappa \neq 0$).
137 For instance, when the bioclimatic limit is bent with the convex side facing source habitats (bottom
138 half of Fig. 1B), immigration exceeds emigration due to a relatively higher proportion of sources
139 than sinks. Consequently, the boundary population increases and the boundary transgresses
140 slightly into the sink region (grey arrows in Fig. 1B show the direction of movement). Because the
141 shape of the range limit is still convex after a slight shift in the boundary position, immigration at

142 the boundary from these newly occupied sinks still exceeds emigration. As a result, the boundary
143 will continue to encroach sink habitats due to net positive dispersal flux.

144 So, how far will the species boundary move before it comes to a halt? That depends on the
145 growth and dispersal characteristics of the species. For the convex shape bioclimatic limit, the
146 population in sinks near the bioclimatic limit increases due to dispersal influx from sources and
147 decreases due to inferior patch quality. If the dispersal rate D is high, and the quality of sinks
148 declines slowly as one moves away from the bioclimatic limit (*i.e.*, $\partial r/\partial e$ is low), the sink
149 populations will increase rapidly. As a result, sinks near the bioclimatic limit become an exporter
150 of individuals to adjacent patches. Eventually, the boundary will equilibrate when the positive
151 dispersal flux is balanced by a decrease in growth due to declining patch quality. In this way, the
152 species can use sink patches near the bioclimatic limit as stepping stones to occupy neighboring
153 sinks, thereby extending the distribution far beyond the bioclimatic limit (*i.e.*, $\Delta E \neq 0$; see Eq. 3).

154 For the third scenario, we consider a bioclimatic limit with its concave side facing source
155 habitats (upper half of Fig. 2B). In contrast to the previous scenario, emigration exceeds
156 immigration and, as a result, the boundary moves backward into source habitats (grey arrows in
157 the upper half of Fig. 2B). Here, too, the magnitude of mismatch between range and bioclimatic
158 limits is determined by dispersal and growth. If the quality of source patches increases slowly and
159 the dispersal outflux is high, the source populations near the bioclimatic limit decrease rapidly to
160 local extinction. This local extinction event creates a domino effect, wherein the boundary
161 continues to encroach source patches until the negative dispersal flux is balanced by an increase
162 in growth rate. Although this scenario may seem counterintuitive as the species range contracts
163 even though source patches are accessible to the species, local extinction due to curved geometry
164 is widely studied in range limit theory (see critical patch size in Okubo and Levin 2001).

165 Next, we synthesize our results by partitioning the relative contribution of climate and
166 dispersal in determining distribution limits in niche space. Dividing equation (3) by e^* we get

$$\tilde{E} \approx \underbrace{1}_{\text{climatic control}} \pm \underbrace{\frac{\gamma^2}{4\tilde{A}}}_{\text{source-sink dynamics}}, \quad (4)$$

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

$$\tilde{A} = \underbrace{\frac{1}{D} \frac{\partial r}{\partial e}}_{\text{life-history effects}} \times \underbrace{\frac{e^*}{\kappa^2}}_{\text{curvature effects}} \quad (5)$$

168 is defined as a dimensionless area that depends on species growth and dispersal and on the
169 curvature of the bioclimatic limit. Rescaling the environment at the range limit offers two
170 important insights. First, we can partition the environment at a range limit for any species into
171 niche constraints imposed by the environment and local source-sink dynamics (see Eq. 4). Second,
172 we can interpret \tilde{A} as a measure of scale to infer the relative importance of environment and
173 dispersal. When \tilde{A} is large, the local environment at range limit approaches the bioclimatic limit
174 ($\tilde{E} \approx 1$). However, when \tilde{A} is small, the environment at the range limit deviates substantially from
175 the bioclimatic limit.

176 Although in our derivations, we show the mismatch between range and bioclimatic limits
177 in niche space, we can also express the mismatch in the geographical space. For instance, consider
178 a landscape with an environmental gradient, G , in the radial direction. Using equation (3), we can
179 show the mismatch between range and bioclimatic limits in the geographical space is

$$\frac{\gamma^2}{4} \left(\frac{G}{t_g} \frac{\kappa^2}{\partial r / \partial e} \right) \sigma^2. \quad (6)$$

180 Equation (6) suggests that depending on the species life-history traits, the shape of the bioclimatic
181 limit, and the environmental gradient, the local mismatch in geographical space can be much
182 greater than the species' mean dispersal distance, σ , as illustrated in Fig. 1.

183

184

Discussion

185 We develop a reaction-diffusion model that mechanistically combines dispersal and growth
186 to examine the role of stepping-stone dynamics in determining distribution limits. We find that
187 species distribution is not only determined by local environmental conditions (niche requirements)
188 but also by source-sink dynamics, which are mediated by the geometrical shape of the bioclimatic
189 limit (Fig. 1 and Eq. 3). For species with high dispersal rate and low growth sensitivity, the
190 mismatch between geographical and bioclimatic limits may be substantial even at large spatial
191 scales (Eq. 6). Based on our analytical results, we propose a dimensionless area, \tilde{A} , that can be
192 used as a measure of scale to infer the relative importance of dispersal and climate in determining

193 range limits (Eq. 4). Our findings raise conceptual and practical challenges for using bioclimatic
194 models in predicting the distribution of biota and generating biological insights.

195 Conceptually, bioclimatic models work in two steps. First, the species' fundamental niche,
196 or the bioclimatic envelope, is estimated either by biophysical experiments (Crozier and Dwyer
197 2006) or by a correlative approach that map species occurrence to prevailing climatic conditions
198 (Phillips et al. 2006). Next, the constructed niche is transferred onto geography, either at a different
199 time or space (Randin et al. 2006). The predicted distribution patterns are then used to make a
200 wide range of biogeographic inferences, such as niche conservatism of invasive species (Liu et al.
201 2020) and sister taxa (Peterson et al. 1999), range shifts due to climate change (Araujo and Rahbek
202 2006), finding suitable habitats to introduce endangered species (Martinez-Meyer et al. 2006),
203 discovering new species (Raxworthy et al. 2003) or populations (Feria and Peterson 2002) in
204 unsampled regions, identifying historical refugia (Waltari et al. 2007), mapping risk potential of
205 disease vectors (Moffett et al. 2007), and many more. Naturally, the robustness of these inferences
206 depends on how reliably we can construct niches and reproject them onto geographical space.

207 The diffusion model suggests that, for certain life histories, the geographical limit may
208 deviate substantially from the bioclimatic limit due to stepping-stone dynamics (see Fig. 1). As a
209 result, ignoring dispersal can lead to systematic errors in constructing and transferring species
210 bioclimatic envelope (Gilroy and Edwards 2017) even at large spatial scales. First, when
211 estimating bioclimatic envelope using occurrence data, the model may include the environment
212 from occupied sinks and fail to capture the environment in empty sources. Second, even if the
213 bioclimatic envelope is known (e.g., via biophysical experiments), transferring the envelope to a
214 different region may lead to projection errors near the bioclimatic limit as the model may fail to
215 predict occupied sinks and empty sources that are accessible through local dispersal. These errors
216 arising from the interactions between growth and dispersal at the population margins can thwart
217 forecasting efforts and yield misleading inferences.

218 Although the evidence for large-scale source-sink dynamics is scant, in a recent study, Goel
219 et al. (2020) showed that stepping-stone dispersal at the savanna-forest boundary could explain the
220 continental-scale mismatch between biome and bioclimatic limits. In particular, the authors found
221 that the mismatch in local precipitation at the biome boundary in Africa and the bioclimatic limit
222 was consistent with curvature dynamics predicted from theory. However, these results should be
223 interpreted with caution as curvature dynamics have not been replicated on other tropical

224 continents, and it is always possible that latent variables could produce observed biome patterns.
225 Nevertheless, source-sink dynamics at the savanna-forest boundary in Africa raise two points.
226 First, source-sink dynamics may operate at length scales 10^3 to 10^4 times greater than typically
227 assumed (Shmida and Wilson 1985). Second, ignoring stepping-stone dispersal at bioclimatic limit
228 may bias biogeographic inferences about the mechanisms that maintain geographic limits.

229 It is, therefore, prudent to ask—is bioclimatic theory useful? We think it is. After all, there
230 is overwhelming evidence that the distribution of biota, both in the past (Davis and Shaw 2001)
231 and present (Walther et al. 2002), closely tracks climate, albeit the match is not always perfect
232 (Araujo and Peterson 2012). Instead, we advocate for the cautious use of bioclimatic theory to
233 project distribution patterns and make biological inferences. Our analysis (Eq. 3) suggests that
234 bioclimatic models may be suitable for species sensitive to changes in the environment and have
235 a low dispersal rate. In contrast, for species with fast dispersal and low growth sensitivity, stepping-
236 stone dynamics may be substantial and, therefore, a correlative bioclimatic model may yield
237 erroneous inferences—even at large spatial scales. For such species, one way forward would be to
238 develop Dynamic Range Models that statistically integrate both niche requirements and dispersal
239 based on observational data (see Schurr et al. 2012).

240

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247

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