Population persistence in the face of climate change and competition: A battle on two fronts

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A B S T R A C T

Many species undergo significant shifts in population distribution in response to changes in climate. This response can introduce a species to new competition from invasive organisms, or influence the dynamics of an otherwise balanced ecosystem. How can a species ensure its own survival while dealing with both interspecific competition and the effects of climate change? We examine a two-species discrete-time, continuous-space population model to determine conditions for coexistence and criteria for persistence in a changing climate. Our analysis suggests that the cost of keeping pace with climate change can weaken the ability of a species to compete with others, and that climate change has the capacity to shift the stable-state solution of the population model. These effects are somewhat mitigated by niche differentiation, with the potential for habitat considered inhospitable to one species to provide refuge for the other.

Using this model we simulate a hypothetical population of native bull trout *Salvelinus confluentus* experiencing competition from invasive brook trout *S. fontinalis* as their river habitat warms due to climate change. Based on current climate projections, we find that bull trout are likely to disappear from the study area by 2080, with brook trout expanding their range in the absence of competition.

1. Introduction

Climate change is having substantial impacts on species around the globe, and these impacts are expected to increase dramatically over the coming century (Thomas et al., 2011; Field et al., 2014). The effects can be seen at virtually every scale, from the individual and micro-habitat (Broitman et al., 2009) to the population level (Pearson and Dawson, 2003). Dispersal is a common species adaptation to climate change (Dawson et al., 2011). Poleward shifts have been observed in many species distributions in response to warming temperatures (Parmesan et al., 1999; Hickling et al., 2006; Sorte and Thompson, 2007), and shifts to higher elevations have been observed in others (Wilson et al., 2005; Chen et al., 2011).

Interspecific competition can curtail the movement and spread of populations, however, as shifting into new habitat often involves competing with species that are already established (Dunson and Travis, 1991; Davis et al., 1998). Although the importance of accounting for biotic interactions when modeling the effects of climate change on species has been well documented (Araújo and Luoto, 2007; Van der Putten et al., 2010; Urban et al., 2012), there is a notable deficit of modeling tools available to accomplish this, in part due to a lack of theoretical foundation on which to build (Gilman et al., 2010). Recent advances in modeling techniques have begun to address the gap

between the assumptions of species distribution models and community ecology theory (Pollock et al., 2014; Harris, 2015; Thorson et al., 2015), but these methods all use statistical approaches that ignore how biological traits and processes such as dispersal ability, growth rate, and niche breadth contribute to population survival.

Here we describe a spatially-explicit, mechanistic competition model that incorporates aspects of climate change, while explicitly accounting for population growth, dispersal ability, and competition. We derive approximations of persistence criteria for each species, and demonstrate the accuracy of the approximations. Finally, we illustrate the model with two species of competing trout, using observed stream temperature data and future climate projections for the Salmon River in central Idaho.

2. Methods

2.1. Modeling competition

Interspecific competition in a static environment has been well-studied through deterministic models such as the continuous-time, continuous-space Lotka-Volterra competition model (Cosner and Lazer, 1984; Kan-On, 1997), or its discrete-time analogue, the Leslie-Gower model (Leslie and Gower, 1958; Cushing et al., 2004), and the dynamics

of these systems have been thoroughly described. The Lotka-Volterra model has been used to study the effects of climate change on vegetation patterns (Jesse, 1999; Svirezhev, 2000). The Leslie-Gower model has been used to model a variety of competitive systems, including flour beetles (Park, 1948), plant assemblages (Levine and Rees, 2002; Adler et al., 2007), and fish (AlSharawi and Rhouma, 2009), but we are unaware of any examples in the literature that explicitly incorporate climate change into the modeling framework.

The Leslie-Gower model quantifies the populations of two univoltine species, M and N, given by

$$M_{t+1} = \frac{\lambda_m M_t}{1 + \alpha_m M_t + \beta_m N_t}, \tag{1}$$

$$N_{t+1} = \frac{\lambda_n N_t}{1 + \alpha_n N_t + \beta_n M_t}, \tag{2}$$

with $\alpha_m = (\lambda_m - 1)/K_m$, $\alpha_n = (\lambda_n - 1)/K_n$, where K_m and K_n represent the carrying capacities of species M and N, and β_m, β_n correspond to the strengths of competition between M and N.

Eqs. (1) and (2) have four fixed points, denoted as

$$L_0 = (0, 0), \tag{3}$$

$$L_M = \left(\frac{\lambda_m - 1}{\alpha_m}, 0 \right), \tag{4}$$

$$L_N = \left(0, \frac{\lambda_n - 1}{\alpha_n} \right), \tag{5}$$

$$L_B = \left(\frac{\alpha_n(\lambda_m - 1) - \beta_m(\lambda_n - 1)}{\alpha_m \alpha_n - \beta_m \beta_n}, \frac{\alpha_m(\lambda_n - 1) - \beta_n(\lambda_m - 1)}{\alpha_m \alpha_n - \beta_m \beta_n} \right). \tag{6}$$

L_B is asymptotically stable (Leslie and Gower, 1958) when

$$\frac{\lambda_n - 1}{\alpha_n} < \frac{\lambda_m - 1}{\beta_m} \tag{7}$$

and

$$\frac{\lambda_m - 1}{\alpha_m} < \frac{\lambda_n - 1}{\beta_n}, \tag{8}$$

Integrodifference equations (IDEs), by contrast, offer a spatially-explicit approach to population modeling, describing a population density $N_t(x)$ as a function of the cumulative effects of growth and dispersal at the previous time step, written as

$$N_{t+1}(x) = \int_\Omega k\left(x, y\right) f\left[N_t(y)\right] dy, \tag{9}$$

where $N_t(x)$ is the population density in generation t at location x, Ω is the spatial domain, f is the recruitment or growth function, and $k(x, y)$ is the dispersal kernel of the species that reflects the likelihood of moving from a location y to a location x. When Ω is finite, the population that disperses outside the domain does not survive. IDEs have recently been used to describe the effects of climate-related habitat shifts (Zhou and Kot, 2011; Kot and Phillips, 2015; Bouhours and Lewis, 2016).

Using the Leslie-Gower competition model to describe the growth phase of our two species yields a system of integrodifference equations, given by

$$M_{t+1}(x) = \int_{\Omega_m} \frac{k_m(x, y) \lambda_m M_t(y)}{1 + \alpha_m M_t(y) + \beta_m N_t(y)} dy, \tag{10}$$

$$N_{t+1}(x) = \int_{\Omega_n} \frac{k_n(x, y) \lambda_n N_t(y)}{1 + \alpha_n N_t(y) + \beta_n M_t(y)} dy, \tag{11}$$

where $k_m(x, y)$, $k_n(x, y)$ are the dispersal kernels of species M and N as in Eq. (9), the parameters $\lambda_m, \lambda_n, \alpha_m, \alpha_n, \beta_m, \beta_n$ are as in Eqs. (1) and (2). We define the domains Ω_i such that $\Omega_i = [L_{i_1} + ct, L_{i_2} + ct]$ is a one-

dimensional length of climatically suitable habitat for species i, and c represents the speed at which the habitat is shifting due to climate change (Zhou and Kot, 2011), which we assume here is constant. We further assume that dispersal probability depends only on the distance between locations x and y, which allows us to write the dispersal kernels as difference kernels, i.e., $k_i(x, y) = k_i(x - y)$. Finally, we will only consider cases in which $\Omega_m \cap \Omega_n \neq \varnothing$, so that interaction between the two populations is possible.

2.2. Habitat

We outline two different representations of habitat. In the first, two competing species occupy the same shifting patch. In the second, each species has its own separate patch, but the habitats partially overlap one another.

2.2.1. Model 1: A shifting patch of habitat

Representing the domain as a patch of length L moving at a constant speed c yields the system

$$M_{t+1}(x) = \int_{ct}^{L+ct} k_m\left(x - y\right) f\left[M_t(y), N_t(y)\right] dy, \tag{12}$$

$$N_{t+1}(x) = \int_{ct}^{L+ct} k_n\left(x - y\right) g\left[M_t(y), N_t(y)\right] dy, \tag{13}$$

with f and g representing the Leslie-Gower growth functions in (10) and (11).

If we wish to discuss persistence of the populations in the patch, it is useful to reparameterize our model to the reference frame of the moving patch rather than absolute location. Substituting $\hat{x} = x - ct$, $\hat{y} = y - ct$ into (12) and (13) and shifting by c gives us

$$M_{t+1}(\hat{x}) = \int_0^L k_m\left(\hat{x} + c - \hat{y}\right) f\left[M_t(\hat{y}), N_t(\hat{y})\right] d\hat{y}, \tag{14}$$

$$N_{t+1}(\hat{x}) = \int_0^L k_n\left(\hat{x} + c - \hat{y}\right) g\left[M_t(\hat{y}), N_t(\hat{y})\right] d\hat{y}. \tag{15}$$

For the remainder of this paper we will drop the hats on $\hat{x}$ and $\hat{y}$ for notational convenience when referring to a shifting patch of habitat, with the understanding that x and y refer to locations in the shifting domain.

If the populations are able to coexist over time, then we might reasonably expect each population to eventually settle at a stable distribution. Indeed, such behavior is readily observable in numerical simulations. We will denote these limiting distributions of M and N as $M^*(x)$ and $N^*(x)$, respectively. Without specifying kernels k_m and k_n, it is not possible to find an explicit solution for this system. Instead, we will derive approximations of the average population densities M^* and N^* of $M^*(x)$ and $N^*(x)$, which we will in turn use to approximate persistence criteria.

Van Kirk and Lewis (1997) defined the average dispersal success S of a population on a domain Ω as

$$S = \frac{1}{|\Omega|} \int_\Omega \int_\Omega k\left(x - y\right) dx \, dy, \tag{16}$$

where $|\Omega|$ represents the length of Ω. This approximation averages across the spatial aspects of the kernel to give a number that reflects the proportion of propagules that stay inside the domain after a single dispersal event. From the perspective of the patch, however, it is apparent that kernels k_m, k_n become increasingly asymmetric with increasing c. Unfortunately, S does not translate well to asymmetric kernels (Reimer et al., 2015). Rinnan (2018) generalized S for asymmetric kernels, defining the quantity

$$GS = \frac{1}{|\Omega|} \int_\Omega \int_\Omega \sqrt{k(x + c - y)k(y + c - x)} \, dx \, dy, \tag{17}$$

which reflects the proportion of individuals staying in the patch after several dispersal events. Rinnan (2018) demonstrated that an IDE with kernel $k(x + c - y)$ has many similar characteristics to an IDE with the symmetric kernel $\sqrt{k(x + c - y)k(y + c - x)}$. In particular, GS can be used in place of S to more accurately determine the persistence criteria of populations modeled with asymmetric dispersal. (It is worth noting that $GS = S$ when $c = 0$.)

We will use (17) to simplify (14) and (15), reducing the spatial population densities to their means. We begin by averaging the populations $M_t(x)$, $N_t(x)$ over the patch of habitat, which we denote as

$$\overline{M}_t = \frac{1}{L} \int_0^L M_t(x) \, dx, \tag{18}$$

$$\overline{N}_t = \frac{1}{L} \int_0^L N_t(x) \, dx. \tag{19}$$

Applying this average to both sides of (14) and (15) yields

$$\frac{1}{L} \int_0^L M_{t+1}(x) \, dx = \frac{1}{L} \int_0^L \int_0^L k_m\left(x + c - y\right) f\left[M_t(y), N_t(y)\right] dy \, dx, \tag{20}$$

$$\frac{1}{L} \int_0^L N_{t+1}(x) \, dx = \frac{1}{L} \int_0^L \int_0^L k_n\left(x + c - y\right) g\left[M_t(y), N_t(y)\right] dy \, dx. \tag{21}$$

If the respective differences between $M_t(x)$, $N_t(x)$ and their spatial averages $\overline{M}_t$, $\overline{N}_t$ are small, then the first terms of the Taylor expansions of f and g about $\overline{M}_t$, $\overline{N}_t$ suggest that

$$f[M_t(y), N_t(y)] \approx f[\overline{M}_t, \overline{N}_t], \tag{22}$$

$$g[M_t(y), N_t(y)] \approx g[\overline{M}_t, \overline{N}_t]. \tag{23}$$

Substituting these into (20) and (21) yields

$$\frac{1}{L} \int_0^L M_{t+1}(x) \, dx \approx f[\overline{M}_t, \overline{N}_t]\frac{1}{L} \int_0^L \int_0^L k_m(x + c - y) \, dy \, dx, \tag{24}$$

$$\frac{1}{L} \int_0^L N_{t+1}(x) \, dx \approx g[\overline{M}_t, \overline{N}_t]\frac{1}{L} \int_0^L \int_0^L k_n(x + c - y) \, dy \, dx, \tag{25}$$

which can be approximated as

$$\overline{M}_{t+1} \approx GS_m \cdot f[\overline{M}_t, \overline{N}_t], \tag{26}$$

$$\overline{N}_{t+1} \approx GS_n \cdot g[\overline{M}_t, \overline{N}_t], \tag{27}$$

where GS_m and GS_n represents the generalized average dispersal success of species M and N, respectively. (See Rinnan (2018) for a more thorough treatment of this approximation for a single-species model.) More explicitly, we have

$$\overline{M}_{t+1} \approx \frac{GS_m \lambda_m \overline{M}_t}{1 + \alpha_m \overline{M}_t + \beta_m \overline{N}_t}, \tag{28}$$
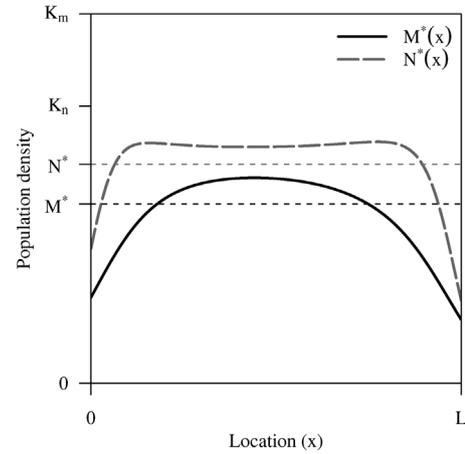
$$\overline{N}_{t+1} \approx \frac{GS_n \lambda_n \overline{N}_t}{1 + \alpha_n \overline{N}_t + \beta_n \overline{M}_t}. \tag{29}$$

This system has four fixed points at

$$P_0 = (0, 0), \tag{30}$$

$$P_M = \left(\frac{S_m \lambda_m - 1}{\alpha_m}, 0\right), \tag{31}$$

$$P_N = \left(0, \frac{S_n \lambda_n - 1}{\alpha_n}\right), \tag{32}$$

Fig. 1. Equilibrium distributions $M^*(x)$ (black) and $N^*(x)$ (grey) of (12) and (13) with $\lambda_m = 2.2$, $\lambda_n = 2.5$, $K_m = 80$, $K_n = 60$, $\beta_m = 0.1$, $\beta_n = 0.005$, and assuming Gaussian dispersal kernels for $k_m(x + c - y)$, $k_n(x + c - y)$ with $\sigma_m = 1$, $\sigma_n = 0.5$, and $c = 0.1$. Approximations M^* and N^* in (33) provide estimates of the average population densities.

$$P_B = (M^*, N^*) = \left(\frac{\alpha_n(GS_m\lambda_m - 1) - \beta_m(GS_n\lambda_n - 1)}{\alpha_m\alpha_n - \beta_m\beta_n}, \frac{\alpha_m(GS_n\lambda_n - 1) - \beta_n(GS_m\lambda_m - 1)}{\alpha_m\alpha_n - \beta_m\beta_n}\right) \tag{33}$$

P_B is asymptotically stable when

$$\frac{GS_n\lambda_n - 1}{\alpha_n} < \frac{GS_m\lambda_m - 1}{\beta_m} \tag{34}$$

and

$$\frac{S_m\lambda_m - 1}{\alpha_m} < \frac{S_n\lambda_n - 1}{\beta_n}, \tag{35}$$

which is similar in form to the conditions of stability for the nontrivial fixed point L_B of the Leslie-Gower model described in (7) and (8), but with the addition of the dispersal success parameters GS_m and GS_n. A proof of the stability of P_B is offered in A.

Following Leslie and Gower (1958), we find it helpful to define some parameters to simplify our notation a bit. First, let p, q be given by

$$p = \frac{GS_m\lambda_m - 1}{\alpha_m}, \tag{36}$$

$$q = \frac{GS_n\lambda_n - 1}{\alpha_n}, \tag{37}$$

which can be thought of as penalized carrying capacities that account for population loss due to dispersal. Note that if $GS_m = 1$, for example, indicating all individuals staying inside the patch after dispersal, then $p = (\lambda_m - 1)/\alpha_m = K_m$. Second, we define u and v such that

$$u = \frac{\beta_m\beta_n}{\alpha_m\alpha_n}, \tag{38}$$

$$v = \frac{\beta_m(GS_n\lambda_n - 1)}{\alpha_n(GS_m\lambda_m - 1)}. \tag{39}$$

u is the ratio of interspecific competition parameters to intraspecific competition parameters, and can be interpreted as a measure of the strength of interspecific competition. v is a function of the speed of climate change c, since GS_m and GS_n are themselves functions of c, as shown in (17).

Using these new parameters, we may now more succinctly write the fixed points as

$$P_0 = (0, 0), \tag{40}$$
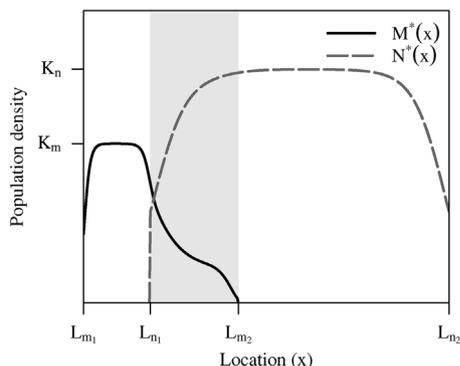
$$P_M = (p, 0), \tag{41}$$

Fig. 2. An illustration of equilibrium distributions $M^*(x)$ and $N^*(x)$ of Model 2 in Eqs. (48) and (49). The shaded area of the figure shows the region of habitat overlap where the two species interact. Outside of the shaded area, each species has patches of habitat that provide refuge from competition.

$$P_N = (0, q), \tag{42}$$

$$P_B = \left(p\left(\frac{1 - v}{1 - u}\right), q\left(\frac{1 - u/v}{1 - u}\right) \right). \tag{43}$$

2.2.2. Model 2: Overlapping patches of shifting habitat

In this scenario each species has its own specialized habitat niche with some degree of overlap, allowing for interaction between the two populations. We denote the patches of habitat by

$$\Omega_m = [L_{m_1} + ct, L_{m_2} + ct], \tag{44}$$

$$\Omega_n = [L_{n_1} + ct, L_{n_2} + ct], \tag{45}$$

with $\Omega_m \cap \Omega_n \neq \emptyset$. We further assume that both habitats are shifting at the same rate c. The locations where the habitats do not overlap can provide locations of possible refuge for the species, i.e., patches without competition from the other species (see Fig. 2).

Our growth functions f and g may now be written piecewise, so that

$$f[M_t(y), N_t(y)] = \begin{cases} \frac{\lambda_m M_t(y)}{1 + \alpha_m M_t(y)}, & L_{m_1} < y \leq L_{n_1}, \\ \frac{\lambda_m M_t(y)}{1 + \alpha_m M_t(y) + \beta_m N_t(y)}, & L_{n_1} < y \leq L_{m_2}, \end{cases} \tag{46}$$

$$g[M_t(y), N_t(y)] = \begin{cases} \frac{\lambda_n N_t(y)}{1 + \alpha_n N_t(y) + \beta_n M_t(y)}, & L_{n_1} < y \leq L_{m_2}, \\ \frac{\lambda_n N_t(y)}{1 + \alpha_n N_t(y)}, & L_{m_2} < y \leq L_{n_2}. \end{cases} \tag{47}$$

Our system may be rewritten as a disjoint sum of IDEs. In the example illustrated in Fig. 2, this takes the form

$$M_{t+1}(x) = \int_{L_{m_1}}^{L_{n_1}} \frac{k_m(x + c - y)\lambda_m M_t(y)}{1 + \alpha_m M_t(y)} dy \\ + \int_{L_{n_1}}^{L_{m_2}} \frac{k_m(x + c - y)\lambda_m M_t(y)}{1 + \alpha_m M_t(y) + \beta_m N_t(y)} dy \tag{48}$$

$$N_{t+1}(x) = \int_{L_{n_1}}^{L_{m_2}} \frac{k_n(x + c - y)\lambda_n N_t(y)}{1 + \alpha_n N_t(y) + \beta_n M_t(y)} dy + \int_{L_{m_2}}^{L_{n_2}} \frac{k_n(x + c - y)\lambda_n N_t(y)}{1 + \alpha_n N_t(y)} dy, \tag{49}$$

where once again x and y represent locations from the frame of reference of the moving habitats.

Denoting the proportions φ_m, φ_n of L_m and L_n in which interaction between the two species is possible as

$$\varphi_m = \frac{L_{m_2} - L_{n_1}}{L_m}, \tag{50}$$

$$\varphi_n = \frac{L_{m_2} - L_{n_1}}{L_n}, \tag{51}$$

it can be shown (see Appendix B) that

$$\overline{M}_{t+1} \approx (1 - \varphi_m) \frac{GS_{m_1}\lambda_m \overline{M}_t}{1 + \alpha_m \overline{M}_t} + \varphi_m \frac{GS_{m_2}\lambda_m \overline{M}_t}{1 + \alpha_m \overline{M}_t + \beta_m \overline{N}_t}, \tag{52}$$

$$\overline{N}_{t+1} \approx \varphi_n \frac{GS_{n_1}\lambda_n \overline{N}_t}{1 + \alpha_n \overline{N}_t + \beta_n \overline{M}_t} + (1 - \varphi_n) \frac{GS_{n_2}\lambda_n \overline{N}_t}{1 + \alpha_n \overline{N}_t}, \tag{53}$$

where

$$GS_{m_1} = \frac{1}{(L_{n_1} - L_{m_1})} \int_{L_{m_1}}^{L_{n_1}} \int_{L_{m_1}}^{L_{m_2}} f_m\left(x, y\right) dx \, dy, \tag{54}$$

$$GS_{m_2} = \frac{1}{(L_{m_2} - L_{n_1})} \int_{L_{n_1}}^{L_{m_2}} \int_{L_{m_1}}^{L_{m_2}} f_m\left(x, y\right) dx \, dy, \tag{55}$$

$$GS_{n_1} = \frac{1}{(L_{m_2} - L_{n_1})} \int_{L_{n_1}}^{L_{m_2}} \int_{L_{n_1}}^{L_{n_2}} f_n\left(x, y\right) dx \, dy, \tag{56}$$

$$GS_{n_2} = \frac{1}{(L_{n_2} - L_{m_2})} \int_{L_{m_2}}^{L_{n_2}} \int_{L_{n_1}}^{L_{n_2}} f_n\left(x, y\right) dx \, dy, \tag{57}$$

and where $f_m(x, y) = \sqrt{k_m(x + c - y)k_m(y + c - x)}$ and $f_n(x, y) = \sqrt{k_n(x + c - y)k_n(y + c - x)}$. Unfortunately, the coexistence equilibrium of equations (52) and (53) is prohibitively arduous to compute, and we cannot derive an explicit formula for M^* and N^* as we did with Models 1 and 2. Instead, we will make a few qualitative observations about the nature of the fixed point of interest.

First, we can see that (52) and (53) are bound above by the case of no interaction and bound below by the case of interaction across the entire domain (Model 2). Specifically, we have

$$\frac{GS_m\lambda_m\overline{M}_t}{1 + \alpha_m\overline{M}_t + \beta_m\overline{N}_t} \leq \overline{M}_{t+1} \leq \frac{GS_m\lambda_m\overline{M}_t}{1 + \alpha_m\overline{M}_t}, \tag{58}$$

$$\frac{GS_n\lambda_n\overline{N}_t}{1 + \alpha_n\overline{N}_t + \beta_n\overline{M}_t} \leq \overline{N}_{t+1} \leq \frac{GS_n\lambda_n\overline{N}_t}{1 + \alpha_n\overline{N}_t}. \tag{59}$$

At equilibrium, (58) and (59) become

$$\frac{GS_m\lambda_m M^*}{1 + \alpha_m M^* + \beta_m N^*} \leq M^* \leq \frac{GS_m\lambda_m M^*}{1 + \alpha_m M^*}, \tag{60}$$

$$\frac{GS_n\lambda_n N^*}{1 + \alpha_n N^* + \beta_n M^*} \leq N^* \leq \frac{GS_n\lambda_n N^*}{1 + \alpha_n N^*}. \tag{61}$$

Rearranging (60) and (61), let us denote the upper and lower bounds of M^* and N^* by the equations

$$l_m : N = \frac{GS_m\lambda_m - \alpha_m M - 1}{\beta_m}, \tag{62}$$

$$u_m : M = \frac{GS_m\lambda_m - 1}{\alpha_m} = p, \tag{63}$$

$$l_n : M = \frac{GS_n\lambda_n - \alpha_n N - 1}{\beta_n}, \tag{64}$$

$$u_n : N = \frac{GS_n\lambda_n - 1}{\alpha_n} = q. \tag{65}$$

Plotting these bounds in M, N-space, we may visualize the regions of space that satisfy (60) and (61), corresponding to values of (M^*, N^*) that result in coexistence (see Fig. 3). In particular, we see that the two populations at equilibrium will never be larger than what each can obtain in the absence of interaction with the other.

Second, since φ_m, $\varphi_n > 0$ by assumption, (52) and (53) at equilibrium can be arranged to get
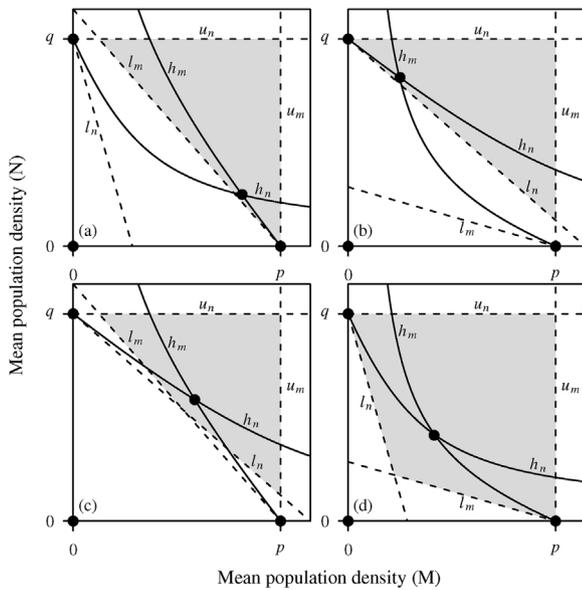
Fig. 3. Regions of potential stability of Model 2, assuming $p, q > 0$ and (a) $v < u, v < 1$; (b) $u < v, v > 1$; (c) $u < v < 1$; and (d) $1 < v < u$. Shaded regions of M, N-space correspond to values of M and N that satisfy inequalities (60) and (61). The fixed point (M^*, N^*) is given by the intersection of the hyperbolas h_m and h_n, defined in (66) and (67), and can be located anywhere inside the shaded regions, depending on the shapes of h_m and h_n.

$$h_m: N = \frac{(GS_m \lambda_m - 1 - \alpha_m M)(1 + \alpha_m M)}{\beta_m(1 + \alpha_m M - (1 - \varphi_m)GS_{m_1} \lambda_m)}, \tag{66}$$

$$h_n: M = \frac{(GS_n \lambda_n - 1 - \alpha_n N)(1 + \alpha_n N)}{\beta_n(1 + \alpha_n N - (1 - \varphi_n)GS_{n_2} \lambda_n)}, \tag{67}$$

where h_m and h_n define two hyperbolas in M, N-space that intersect at the fixed point (M^*, N^*) (see Fig. 3), and with asymptotes

$$a_m = \frac{(1 - \varphi_m)GS_{m_1} \lambda_m - 1}{\alpha_m}, \tag{68}$$

$$a_n = \frac{(1 - \varphi_n)GS_{n_2} \lambda_n - 1}{\alpha_n}. \tag{69}$$

## 3. Results

3.1. Persistence criteria

When $\Omega_m = \Omega_n$ (Model 1), there are four possible outcomes for our model: mutual extirpation, species M survives, species N survives, or mutual survival. These outcomes are summarized in Fig. 4.

3.1.1. Outcome I: Mutual extirpation

Survival of species M and N depends first and foremost on their respective abilities to keep pace with the speed of climate change. When $GS_i \lambda_i < 1$, the growth rate of species i will not be large enough to compensate for the population loss through dispersal and the speed of climate change, and species i will go extinct. Mutual extirpation will occur when $GS_m \lambda_m < 1$ and $GS_n \lambda_n < 1$, or equivalently, when $p < 0$ and $q < 0$, with p, q as defined in Eqs. (36) and 37)). In this sense, p and q reflect persistence ability in a moving habitat.

3.1.2. Outcome II: M outcompetes N

When $p > 0$ and $q < 0$, species N is unable keep pace with the speed of climate change and will die out. This will simplify to a one-dimensional shifting habitat IDE model in which species M will experience Beverton-Holt population growth in the absence of species N.
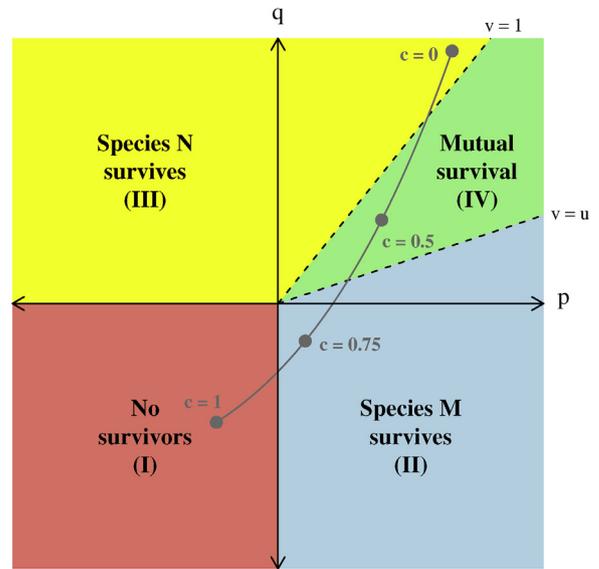
Fig. 4. A delineation of p, q-space, illustrating the approximated outcome for Models 1 and 2. If the growth rate of a species is sufficient to replace the population lost due to the speed of climate change, then the species can survive. Parameter values of $K_m = 80$, $K_n = 100$, $\beta_m = \beta_n = 0.005$, $\lambda_m = 1.5$, $\lambda_n = 2.5$ were used to illustrate the effects of varying the speed of climate change c (grey). When $c = 0$, N will outcompete M; when $c = 0.5$, mutual survival will occur; when $c = 0.75$, N will be unable to keep pace and M will survive; when $c = 1$, neither species will survive.

Assuming both species can keep pace with climate change (i.e., $p > 0$ and $q > 0$), species M will outcompete species N when either $u > v$ and $v < 1$ with u, v as defined in Eqs. (38) and (39). Depending on initial population densities, M may also outcompete N when $u > v$ and $v > 1$.

3.1.3. Outcome III: N outcompetes M

Similarly, when $p < 0$ and $q > 0$, species M will be unable to pace with the shifting habitat but species N will persist. If both $p > 0$ and $q > 0$, species N will outcompete species M either when $u < v$, $v > 1$, or when $u > v$ and $v > 1$ if initial conditions are favorable for N.

3.1.4. Outcome IV: Mutual survival

Mutual survival occurs when both $p > 0$ and $q > 0$ and when $u < v < 1$. In this situation, both species can keep pace with the speed of climate change, and there is a stable equilibrium for both populations at the fixed point in Eq. (43).

3.2. Effects of climate change on competition

The speed of climate change c has the capacity to change the longterm outcome of the system by shifting the equilibrium through a bifurcation. Holding all other parameters constant, as the value of c changes, the fixed point of the system may move through different stability regions of p, q-space. This result reflects the compounding effects of climate change and competition: even if a species is able to keep pace with a changing climate, its capacity to compete with other species may be weakened, which may lead to qualitatively different outcomes compared to competing with the same species in a static climate.

Fig. 4 illustrates this phenomenon using the same dispersal behavior as used in Fig. 1, and with $K_m = 80$, $K_n = 100$, $\beta_m = \beta_n = 0.005$, $\lambda_m = 1.5$, and $\lambda_n = 2.5$. When $c = 0$, species N will outcompete species M due in part to its higher reproductive rate. N has comparatively limited dispersal ability, however, and M is better equipped to keep pace with habitat changes. As such, when $c = 0.5$, N loses its competitive advantage and mutual survival will occur. When $c = 0.75$, N can

no longer keep pace and will go extinct, but M will continue to survive at a lower mean population density. When $c = 1$, neither species will be able to persist.

Expressing the criteria $u < v < 1$ for mutual survival in terms of p and q, we expect the interactive effects of climate change and competition to induce a bifurcation when there is some value of c such that

$$q = \frac{\alpha_m}{\beta_m} p \tag{70}$$

or

$$p = \frac{\alpha_n}{\beta_n} q. \tag{71}$$

3.3. Effects of refuge habitat

When a species has habitat in which they do not experience competition (Model 2), this habitat may act as a stable island for a source population, which can replenish losses incurred from competition in sufficiently nearby populations. If $\varphi_m = \varphi_n = 1$ (representing interaction between M and N across the entire domain, as in Model 1), (66) and (67) reduces to

$$M^* = \frac{GS_n \lambda_n - 1 - \alpha_n N^*}{\beta_n}, \tag{72}$$

$$N^* = \frac{GS_m \lambda_m - 1 - \alpha_m M^*}{\beta_m}, \tag{73}$$

which can be solved to get the coexistence fixed point P_B of Model 1, as expected. As the amount of refuge for species M increases (i.e., as φ_m decreases), the value of the asymptote a_m in (68) increases, which in turn increases the average population density at equilibrium of M. A similar pattern of behavior can be seen in N.

Fig. 3(a) shows us that in conditions that lead to M outcompeting N in Model 1 ($u > v$, $v < 1$), it is possible for M and N to coexist if there is sufficient refuge habitat for N. Fig. 3(b) similarly shows that conditions that lead to N outcompeting M in Model 1 can result in coexistence in Model 2. Fig. 3(d) shows that the conditions that led to unstable coexistence in Model 1 ($1 < v < u$) may yield stable coexistence in Model 2. The amount of refuge habitat is sufficient for species persistence when the population inside the refuge habitat can persist by itself. This is equivalent to

$$(1 - \varphi_m) GS_{m_1} \lambda_m > 1 \tag{74}$$

for species M and

$$(1 - \varphi_n) GS_{n_2} \lambda_n > 1 \tag{75}$$

for species N.

3.4. Numerical validation

To quantify the accuracy of the persistence criteria described in Section 3.1, we ran numerical simulations of Model 1 and compared the outcomes with those predicted by p, q, u, and v, with an unknown predicted outcome (either M or N surviving) when $v > 1$ and $u > v$. We generated 10,000 sets of random parameter values, with each parameter randomly drawn from a distribution that we judged to reflect biologically feasible values (see Table 1). We assumed Gaussian dispersal for both species. Numerical IDEs were then run for 100 time steps, using the randomly generated parameter values. If the mean densities of the resulting populations were at least one-tenth the carrying capacity of the species, then the population was recorded as persisting, and extirpated otherwise. The value of the threshold will inevitably affect model performance, but we believe ten percent is a conservative choice.

We also tested the effects of refuge habitat by running 10,000

Table 1
Parameter values and prior distributions that were used for numerical simulations of Models 1 and 2, assuming Gaussian dispersal. We assumed that $L_m = L_n$.

Growth rate	λ_m, λ_n	Exp(2) + 1
Dispersal distance	σ_m, σ_n	Lognormal(0.5, 0.5)
Intraspecific competition	α_m, α_n	Lognormal(-2, 1)
Interspecific competition	β_m, β_n	Exp($1/\alpha_i$)
Habitat size	L_m, L_n	10 - Exp(1.5)
Overlap (Model 2)	φ_m, φ_n	Uniform(0, 1)
Speed of climate change	c	Exp(1)

simulations with the same sets of parameter values as Model 1, but with an amount of overlap between the two habitats determined by random draw. We then compared the differences in observed outcomes between Models 1 and 2. All numerical simulation and analysis was conducted in R (Core Team, 2015), and our code is provided as supplementary material.

The persistence criteria described in Section 3.1 correctly predicted the outcome of Model 1 in 95.2% of the simulations. Approximately 38% of the models ended with mutual extinction, 29% with M surviving over N, 29% with N surviving over M, and 5% with mutual survival. Of the 593 unknown (M or N) or incorrectly predicted outcomes, 111 had outcomes that matched the predictions of one species outcompeting the other dependent on initial conditions; another 391 may have been attributable to the effects of transient population dynamics, with one or both species going extinct before the populations were able to reach the predicted equilibrium. Model 2 had 341% more instances of mutual survival than Model 1, due to the availability of refuge habitat. Table 2a compares the predicted outcomes with the observed outcomes, and

Table 2
(a) Predicted vs. observed survival outcomes for 10,000 numerical simulations of Model 1. Each simulation was run for 100 time steps with a different set of randomly chosen parameter values. Bold numbers indicate agreement between model predictions and observations. Starred numbers indicate incorrect model predictions in which transient dynamics may have had an effect on the observed outcome. Predictions of "M or N" were excluded from the calculations of performance metrics. (b) Total observed outcomes for Models 1 and 2. Bold numbers indicate agreement between models, and italic numbers indicate cases in which the presence of refuge habitat resulted in mutual survival that would not otherwise occur.

(a) Model 1

Predicted survival	Observed survival			
	None	M	N	Both
None	**3501**	26	13	0
M	140[*]	**2725**	17[*]	18
N	124[*]	16[*]	**2752**	27
Both	5	51[*]	43[*]	**429**
M or N	2	45	66	0
Sensitivity	0.929	0.967	0.974	0.905
Specificity	0.994	0.975	0.976	0.989
Precision	0.989	0.940	0.943	0.812
Prevalence	0.381	0.285	0.286	0.048
Balanced Accuracy	0.961	0.971	0.975	0.947
Overall accuracy		0.952		
Cohen's Kappa		0.930		

(b) Observed survival

Model 2	Model 1			
	None	M	N	Both
None	**3710**	4	0	0
M	24	**2235**	0	0
N	38	13	**2377**	8
Both	0	*611*	*514*	**466**

provides basic summary statistics.

4. Application to populations of competing trout

We provide an illustration of Model 2 with two hypothetical populations of competing trout species, in a river that is warming due to climate change. We attempted to use realistic parameter values where possible, but we caution the reader against overinterpreting the results; this example is intended to illustrate the dynamics of competitive invasion and the effects of climate change, but should not be construed as a model for real populations (Real and Levin, 1991).

Bull trout (*Salvelinus confluentus*) is a salmonid that thrives in clear, cold mountain streams in the Pacific Northwest. Bull trout tolerate a relatively small range of water temperatures, preferring mean summer temperatures below 13 °C (US Fish and Wildlife Service et al., 2008; Isaak et al., 2015). They are currently recognized as threatened under the Endangered Species Act, due to loss and degradation of spawning habitat, increasing numbers of barriers to migration such as dams, and increasing competition from nonnative species (Nakano et al., 1998; Gunckel et al., 2002). The invasive brook trout (*S. fontinalis*) is one such species – intentionally introduced as a recreational fishing species in the late 1800s (Dunham et al., 2002) – with habitat requirements similar to those of bull trout, but more tolerant of warm water, thriving in temperatures up to 22 °C (Dunham et al., 2002).

The undammed Salmon River in central Idaho provides ideal salmonid habitat, stretching 684 km through sparsely populated mountainous terrain, and spanning the thermal tolerances of both species. We used the NorWeST stream temperature database downscaled to a 200 m resolution to obtain a mean August stream temperature profile for 2011 and a projected future profile based on global climate model ensemble averages that represent the A1B warming trajectory for 2080s (2070–2099) (Isaak et al., 2011).

We used carrying capacities of 5.1 fish/200 m and 15 fish/200 m for bull and brook trout, respectively, which reflect mean population densities observed via snorkeling surveys conducted by the Idaho Department of Fish and Game (Levin et al., 2002; High et al., 2008). Growth rates of $\lambda_m = 1.09$ and $\lambda_n = 1.1$ were similarly estimated (Adams, 1999; High et al., 2008).

We modeled dispersal with Laplace kernels with mean dispersal distances of 1 km for bull trout and 200 m for brook trout (Hutchings and Gerber, 2002), representing populations with relatively high site fidelity. A number of studies have found success at modeling fish dispersal with mixture kernels, a linear combination of two kernels that collectively represent the sedentary and mobile dispersal processes commonly observed in stream networks (Skalski and Gilliam, 2000; Rodríguez, 2009). There is evidence of long-distance dispersal ability in both bull and brook trout (Dunham et al., 2002; US Fish and Wildlife Service et al., 2008), but we opted not to use mixture kernels here, as this would have introduced several new parameters to the model, with no population data to support their estimation.

Competition coefficients are notoriously hard to quantify from observational field studies (Pfister, 1995); Gunckel et al. (2002) noted that bull trout appear to demonstrate a competitive advantage over the invasive brook trout when interacting directly, but Nakano et al. (1998) found no significant difference between the two. Thus, we explored model outcomes for a variety of scenarios, using 1681 ordered pairs of β_m and β_n, with values ranging between 0 and 1.

We initialized the population density $M_0(x)$ of bull trout at carrying capacity at any 200 m segment of the Salmon River that was below its thermal limit of 13 °C, and the initial population density $N_0(x)$ of brook trout at carrying capacity downstream of the primary section of bull trout habitat to simulate potential upstream invasion (see Fig. 5a). We then allowed the populations to grow, disperse, and interact according to the dynamics specified in (48) and (49) for 70 years with speed of climate change $c = 0.0377$ °C/yr, reflecting the predicted mean annual increase in temperature between 2011–2080 (Isaak et al., 2011). This
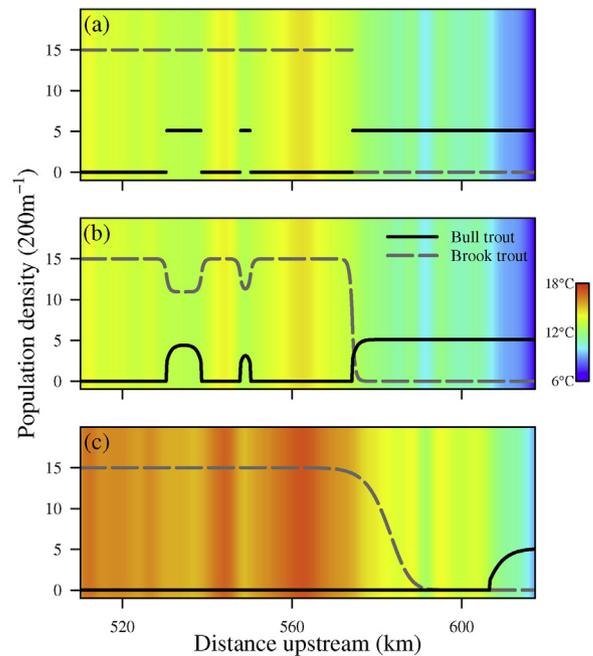
Fig. 5. Population distributions of bull (solid) and brook (dashed) trout for competition coefficients $\beta_m = 0.08$, $\beta_n = 0.01$. (a) shows the initial densities $M_0(x)$ and $N_0(x)$, with bull trout at carrying capacity $K_m = 5.1$ in waters below 13 °C and brook trout at carrying capacity $K_n = 15$ downstream of the primary section of bull trout habitat; (b) shows the densities $M_{2011}(x)$ and $N_{2011}(x)$ after one time step, with lower brook trout density in locations overlapping with bull trout due to competition; (c) shows $M_{2080}(x)$ and $N_{2080}(x)$ after 70 time steps, with an average warming of $c = 0.0377$ °C/yr, with significant loss of bull trout habitat due to warming, and expansion of brook trout habitat in the absence of competition.

resulted in population densities $M_t(x)$ and $N_t(x)$ for each year t (see Fig. 5b and c).

In all cases, bull trout were heavily impacted by warming river temperature, displaced upstream by more than 30 km. In cases where β_n was approximately less than $\frac{1}{3}\beta_m$, bull trout displayed a significant initial competitive advantage over brook trout, and brook trout were prevented from populating the river where bull trout were present. Despite this advantage, brook trout were able to maintain a population due to the downstream warmer water refuge that the bull trout could not occupy. As the river warmed and bull trout were displaced to higher elevations, the brook trout slowly replaced them at a pace determined by their dispersal ability. When β_n was approximately greater than $\frac{1}{3}\beta_m$, brook trout were able to outcompete bull trout, and the bull trout were displaced from the river by the end of the burn-in period. Our model suggests that bull trout will likely be extirpated from the Salmon River by the beginning of the 22nd century if temperature increases continue on a similar trajectory as the 2080 projections.

5. Discussion

The speed of climate change plays a critical role in the long-term stability of the two-species system. Beginning with conditions otherwise amenable to mutual persistence, different speeds of climate change can either support persistence or result in either species outcompeting the other. In all but the simplest cases, an analytic formula for the critical speed at which a species is no longer able to persist does not exist (Zhou and Kot, 2011). Rinnan (2018) demonstrated how to approximate characteristics of a single-species model using the generalized average dispersal success, and we demonstrated that this same method can likewise be used to gain insight into multiple-species systems.

Although our model explicitly accounts for growth, dispersal, and

competition, we emphasize that this model provides a very simple representation of population, habitat, and climate, and does not account for many ecological processes and biological traits that may in fact help bull trout to persist. Among other things, a more detailed understanding of life history, adaptive capacity, and habitat heterogeneity would undoubtedly be needed to predict extirpation with any confidence. In this respect, a number of caveats to our results are worth mentioning.

At the continental scale, population distributions are largely determined by climate processes (Pearson and Dawson, 2003). At the scale of the individual, however, habitat selection can be strongly influenced by other processes such as spatial heterogeneity, resource availability, and environmental stochasticity. Our model delineates suitable habitat by thermal tolerances alone, but this is no doubt overly simplistic from the perspective of an individual organism. Kareiva (1982) found that habitat heterogeneity led to different rates and patterns of dispersal in flea beetles, and there is good reason to believe that the same behavior could be found in trout species, due to their preferential selection of areas with vegetative cover or deep pools.

Similarly, our model assumes thoroughly homogeneous populations. In reality, demographic stochasticity will create different tolerances and reactions to changes in climate (Selong et al., 2001). Indeed, adaptation can be a very effective response to climate change, and adaptive processes such as evolutionary rescue and phenotypic plasticity likely play an equally important role as dispersal (Bell and Gonzalez, 2009). Accounting for adaptation in this context is difficult, in large part due to its unpredictability.

Species interactions are complex and varied, and are often not simply a matter of competitive exclusion. The impacts of brook trout on bull trout populations, for example, are not just limited to resource pressures; hybridization between the two species has negatively impacted bull trout as well. Moreover, interactions are often not limited to just two competing species. Bull and brook trout are both sympatric with cutthroat trout, *Oncorhynchus clarkii,* and there is considerable evidence that brook trout have caused significant declines in cutthroat trout populations (Nakano et al., 1998; Dunham et al., 2002). The model can be generalized to accommodate hybridization or a greater number of species, but this will likely become unwieldy for even the simplest of cases. Nor are interactions constant through time and space. The consequences of climate change are sometimes described as an example of a collective risk social dilemma, in which cooperation is vital for mutual survival (Chen et al., 2012). In this context, climate change may actually introduce incentive for cooperation, thereby changing the nature of interaction between competing populations. A more realistic model might describe competition as $\beta_m(y)$ and $\beta_n(y)$, with competition strength varying spatially as a function of habitat quality, amount of climate change, or other extrinsic factors.

Finally, climate change is represented in our model as a simple linear increase in temperature. In reality, there is considerable variation in climate patterns year to year, and decade to decade. In mountain streams, the quality of habitat is influenced by drought, snowpack, and forest fires (Isaak et al., 2010). Some amount of temperature variability could be introduced to the model by drawing values of the speed of climate change c at each time step from a specified distribution.

Although our analysis involved several approximations and simplifications, our delineation of parameter space nonetheless provides relatively accurate predictions of the long-term outcome of the underlying IDE model. It is important to recognize, however, that this approach only predicts model *outcome*, and fails to capture many of the interesting spatial characteristics of the IDE model. There is undoubtedly a great deal more to study regarding the size and spatial distributions of the populations themselves, as we glimpsed in our example of competing species of trout, and such a study will require an approach that preserves these properties. Fortunately, it is quite straightforward to simulate the IDE competition model explicitly, which provides useful reference and validation for any analysis.

Our model demonstrates how simple growth, dispersal, and competition processes can give rise to a variety of outcomes commonly observed in the ecologies of competition and climate change. The fundamental model structure described in Section 2.2.1 and Section 2.2.2 does not only apply to the case of competition, but can be generalized to model different types of interactions such as mutualism or predator-prey by the appropriate selection of growth functions f and g. We believe our approach provides a useful framework for exploring complex ecological systems and processes, and deserves further exploration.

Acknowledgements

Appendix A. Asymptotic stability of (M^*, N^*)

The stability of the nontrivial coexistence equilibrium

$$L_B = \left(\frac{\alpha_n(\lambda_m - 1) - \beta_m(\lambda_n - 1)}{\alpha_m \alpha_n - \beta_m \beta_n}, \frac{\alpha_m(\lambda_n - 1) - \beta_n(\lambda_m - 1)}{\alpha_m \alpha_n - \beta_m \beta_n} \right) \tag{A.1}$$

has long been established (Leslie and Gower, 1958), but we have not yet demonstrated the stability of our estimate of the mean population density at equilibrium. We provide a proof here.

Represent the approximated average populations by

$$f(M, N) = \frac{GS_m \lambda_m M}{1 + \alpha_m M + \beta_m N}, \tag{A.2}$$

$$g(M, N) = \frac{GS_n \lambda_n N}{1 + \alpha_n N + \beta_n M}, \tag{A.3}$$

with nontrivial fixed point $P_B = (M^*, N^*)$, where

$$M^* = \frac{\alpha_n(GS_m \lambda_m - 1) - \beta_m(GS_n \lambda_n - 1)}{\alpha_m \alpha_n - \beta_m \beta_n}, \tag{A.4}$$

$$N^* = \frac{\alpha_m(GS_n \lambda_n - 1) - \beta_n(GS_m \lambda_m - 1)}{\alpha_m \alpha_n - \beta_m \beta_n}. \tag{A.5}$$

Defining

$$p = \frac{GS_m \lambda_m - 1}{\alpha_m}, \tag{A.6}$$

$$q = \frac{GS_n \lambda_n - 1}{\alpha_n}, \tag{A.7}$$

and noting that

$$\alpha_m M^* + \beta_m N^* = \alpha_m p, \tag{A.8}$$

$$\alpha_n N^* + \beta_n M^* = \alpha_n q, \tag{A.9}$$

we write the Jacobian matrix J as

$$J = \begin{pmatrix} \frac{\partial f}{\partial M} & \frac{\partial f}{\partial N} \\ \frac{\partial g}{\partial M} & \frac{\partial g}{\partial N} \end{pmatrix} \tag{A.10}$$

$$= \begin{pmatrix} \frac{1 + \beta_m N}{1 + \alpha_m p} & -\frac{\beta_m M}{1 + \alpha_m p} \\ -\frac{\beta_n N}{1 + \alpha_n q} & \frac{1 + \beta_n M}{1 + \alpha_n q} \end{pmatrix}. \tag{A.11}$$

(M^*, N^*) is stable when

$$|\mathrm{Tr}(J)| - 1 < \mathrm{Det}(J) < 1. \tag{A.12}$$

We first show that $\mathrm{Det}(J) < 1$. Assuming $p > 0$, $q > 0$, it follows that

$$\mathrm{Det}(J) = \frac{1 + \beta_m N + \beta_n M}{(\alpha_m p + 1)(\alpha_n q + 1)} \tag{A.13}$$

$$< \frac{1 + \alpha_m M + \beta_m N + \alpha_n N + \beta_n M}{(\alpha_m p + 1)(\alpha_n q + 1)} \tag{A.14}$$

$$= \frac{1 + \alpha_m p + \alpha_n q}{(\alpha_m p + 1)(\alpha_n q + 1)} \tag{A.15}$$

$$= \frac{1 + \alpha_m p + \alpha_n q}{1 + \alpha_m p + \alpha_n q + \alpha_m \alpha_n pq} \tag{A.16}$$

$$< 1. \tag{A.17}$$

Next we show that $\mathrm{Tr}(J) - 1 < \mathrm{Det}(J)$. Defining u, v as

$$u = \frac{\beta_m \beta_n}{\alpha_m \alpha_n}, \quad v = \frac{\beta_m(GS_n \lambda_n - 1)}{\alpha_n(GS_m \lambda_m - 1)}, \tag{A.18}$$

and assuming that $u < v < 1$, then

$$\mathrm{Tr}(J) - 1 = \frac{1 + \beta_m N}{1 + \alpha_m p} + \frac{1 + \beta_n M}{1 + \alpha_n q} - 1 \tag{A.19}$$

$$= \frac{(1 + \beta_m N)(1 + \alpha_n q) + (1 + \beta_n M)(1 + \alpha_m p)}{(1 + \alpha_m p)(1 + \alpha_n q)} - 1 \tag{A.20}$$

$$= \frac{1 + \beta_m N + \beta_n M}{(1 + \alpha_m p)(1 + \alpha_n q)} + \frac{1 + \alpha_n q + \alpha_m p + \alpha_n \beta_m qN + \alpha_m \beta_n pM}{(1 + \alpha_m p)(1 + \alpha_n q)} - 1 \tag{A.21}$$

$$= \mathrm{Det}(J) + \frac{\alpha_n \beta_m qN + \alpha_m \beta_n pM - \alpha_m \alpha_n pq}{(1 + \alpha_m p)(1 + \alpha_n q)}. \tag{A.22}$$

Since $u < v < 1$ implies that $\beta_n p < \alpha_n q$ and $\beta_m q < \alpha_m p$, (A.24) implies that

$$\mathrm{Tr}(J) - 1 < \mathrm{Det}(J) + \frac{\alpha_n \alpha_m pN + \alpha_m \alpha_n qM - \alpha_m \alpha_n pq}{(1 + \alpha_m p)(1 + \alpha_n q)}. \tag{A.23}$$

In order to show that $\mathrm{Tr}(J) - 1 < \mathrm{Det}(J)$, we must have

$$\alpha_m \alpha_n pN + \alpha_m \alpha_n qM < \alpha_m \alpha_n pq \tag{A.24}$$

$$pN + qM < pq \tag{A.25}$$

$$pq\frac{1 - u/v}{1 - u} + qp\frac{1 - v}{1 - u} < pq \tag{A.26}$$

$$1 - u/v + 1 - v > 1 - u \tag{A.27}$$

$$u - u/v > v - 1 \tag{A.28}$$

$$u(v - 1) > v(v - 1) \tag{A.29}$$

$$u < v\frac{(v - 1)}{(v - 1)} \tag{A.30}$$

$$u < v. \tag{A.31}$$

Thus, if $u < v < 1$ and $p > 0$, $q > 0$, the fixed point $P_B = (M^*, N^*)$ is asymptotically stable.

Appendix B. Approximation of $(\overline{M}_{t+1}, \overline{N}_{t+1})$

We wish to approximate the average population densities $\overline{M}_{t+1}$ and $\overline{N}_{t+1}$ at equilibrium for

$$M_{t+1}(x) = \int_{L_{m_1}}^{L_{n_1}} \frac{k_m(x + c - y)\lambda_m M_t(y)}{1 + \alpha_m M_t(y)} dy + \int_{L_{n_1}}^{L_{m_2}} \frac{k_m(x + c - y)\lambda_m M_t(y)}{1 + \alpha_m M_t(y) + \beta_m N_t(y)} dy \tag{B.1}$$

$$N_{t+1}(x) = \int_{L_{n_1}}^{L_{m_2}} \frac{k_n(x + c - y)\lambda_n N_t(y)}{1 + \alpha_n N_t(y) + \beta_n M_t(y)} dy + \int_{L_{m_2}}^{L_{n_2}} \frac{k_n(x + c - y)\lambda_n N_t(y)}{1 + \alpha_n N_t(y)} dy, \tag{B.2}$$

We will make use of a basic property of integrals to rewrite GS_m, GS_n as disjoint sums as well. For an integrable function $f(x, y)$, define

$$F = \frac{1}{L}\int_0^L \int_0^L f\left(x, y\right) dx dy, \tag{B.3}$$

$$F_1 = \frac{1}{a}\int_0^a \int_0^L f\left(x, y\right) dx dy, \tag{B.4}$$

$$F_2 = \frac{1}{(L - a)}\int_a^L \int_0^L f\left(x, y\right) dx\, dy. \tag{B.5}$$

It follows that

$$F = \frac{a}{aL}\int_0^a \int_0^L f\left(x, y\right) dx\, dy + \frac{(L - a)}{(L - a)L}\int_a^L \int_0^L f\left(x, y\right) dx\, dy \tag{B.6}$$

$$= \frac{a}{L}F_1 + \frac{(L - a)}{L}F_2. \tag{B.7}$$

Applying (B.4) and (B.5) to $k_m(x, y)$, $k_n(x, y)$ yields

$$GS_{m_1} = \frac{1}{(L_{n_1} - L_{m_1})}\int_{L_{m_1}}^{L_{n_1}} \int_{L_{m_1}}^{L_{m_2}} f_m(x, y)\, dx\, dy, \tag{B.8}$$

$$GS_{m_2} = \frac{1}{(L_{m_2} - L_{n_1})}\int_{L_{n_1}}^{L_{m_2}} \int_{L_{m_1}}^{L_{m_2}} f_m(x, y)\, dx\, dy, \tag{B.9}$$

$$GS_{n_1} = \frac{1}{(L_{m_2} - L_{n_1})}\int_{L_{n_1}}^{L_{m_2}} \int_{L_{n_1}}^{L_{n_2}} f_n(x, y)\, dx\, dy, \tag{B.10}$$

$$GS_{n_2} = \frac{1}{(L_{n_2} - L_{m_2})}\int_{L_{m_2}}^{L_{n_2}} \int_{L_{n_1}}^{L_{n_2}} f_n(x, y)\, dx\, dy, \tag{B.11}$$

where $f_m(x, y) = \sqrt{k_m(x + c - y)k_m(y + c - x)}$ and $f_n(x, y) = \sqrt{k_n(x + c - y)k_n(y + c - x)}$. As before, denoting the proportions φ_m, φ_n of L_m and L_n in which interaction between the two species is possible as

$$\varphi_m = \frac{L_{m_2} - L_{n_1}}{L_m}, \tag{B.12}$$

$$\varphi_n = \frac{L_{m_2} - L_{n_1}}{L_n}, \tag{B.13}$$

we may now write GS_m, GS_n as

$$GS_m = (1 - \varphi_m)GS_{m_1} + \varphi_m GS_{m_2}, \tag{B.14}$$

$$GS_n = \varphi_n GS_{n_1} + (1 - \varphi_n)GS_{n_2}. \tag{B.15}$$

Applying the same approximation methods as Model 1 then yields

$$\overline{M}_{t+1} = \frac{1}{L_m}\int_{L_{m_1}}^{L_{m_2}} \int_{L_{m_1}}^{L_{n_1}} \frac{k_m(x + c - y)\lambda_m M_t(y)}{1 + \alpha_m M_t(y)} dy + \frac{1}{L_m}\int_{L_{n_1}}^{L_{m_2}} \int_{L_{n_1}}^{L_{m_2}} \frac{k_m(x + c - y)\lambda_m M_t(y)}{1 + \alpha_m M_t(y) + \beta_m N_t(y)} dy \tag{B.16}$$

$$\approx (1 - \varphi_m)\frac{GS_{m_1}\lambda_m \overline{M}_t}{1 + \alpha_m \overline{M}_t} + \varphi_m \frac{GS_{m_2}\lambda_m \overline{M}_t}{1 + \alpha_m \overline{M}_t + \beta_m \overline{N}_t}, \tag{B.17}$$

and similarly,

$$\overline{N}_{t+1} \approx \varphi_n \frac{\mathrm{GS}_{n_1} \lambda_n \overline{N}_t}{1 + \alpha_n \overline{N}_t + \beta_n \overline{M}_t} + (1 - \varphi_n) \frac{\mathrm{GS}_{n_2} \lambda_n \overline{N}_t}{1 + \alpha_n \overline{N}_t}.$$

$$(B.18)$$

Appendix C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolmodel.2018.07.004.

References

Adams, S.B., 1999. Mechanisms limiting a vertebrate invasion: Brook trout in mountain streams of the Northwestern United States of America. The University of Montana.

Adler, P.B., HilleRisLambers, J., Levine, J.M., 2007. A niche for neutrality. Ecol. Lett. 10 (2), 95–104.

AlSharawi, Z., Rhouma, M., 2009. Coexistence and extinction in a competitive exclusion Leslie/Gower model with harvesting and stocking. J. Differ. Equ. Appl. 15 (11–12), 1031–1053.

Araújo, M.B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. Glob. Ecol. Biogeogr. 16 (6), 743–753.

Bell, G., Gonzalez, A., 2009. Evolutionary rescue can prevent extinction following environmental change. Ecol. Lett. 12 (9), 942–948.

Bouhours, J., Lewis, M.A., 2016. Climate change and integrodifference equations in a stochastic environment. Bull. Math. Biol. 78 (9), 1866–1903.

Broitman, B., Szathmary, P., Mislan, K., Blanchette, C., Helmuth, B., 2009. Predator-prey interactions under climate change: the importance of habitat vs body temperature. Oikos 118 (2), 219–224.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333 (6045), 1024–1026.

Chen, X., Szolnoki, A., Perc, M., 2012. Risk-driven migration and the collective-risk social dilemma. Phys. Rev. E 86 (3), 036101.

Cosner, C., Lazer, A.C., 1984. Stable coexistence states in the Volterra-Lotka competition model with diffusion. SIAM J. Appl. Math. 44 (6), 1112–1132.

Cushing, J., Levarge, S., Chitnis, N., Henson, S.M., 2004. Some discrete competition models and the competitive exclusion principle. J. Differ. Equ. Appl. 10 (13–15), 1139–1151.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., Wood, S., 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391 (6669), 783–786.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond predictions: biodiversity conservation in a changing climate. Science 332 (6025), 53–58.

Dunham, J.B., Adams, S.B., Schroeter, R.E., Novinger, D.C., 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. Rev. Fish Biol. Fish. 12 (4), 373–391.

Dunson, W.A., Travis, J., 1991. The role of abiotic factors in community organization. Am. Nat. 1067–1091.

Field, C.B., Barros, V.R., Mach, K., Mastrandrea, M., 2014. Climate change 2014: impacts, adaptation, and vulnerability. Contribution of Working Group II to the IPCC 5th Assessment Report of the Intergovernmental Panel on Climate Change.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. Trends Ecol. Evol. 25 (6), 325–331.

Gunckel, S.L., Hemmingsen, A.R., Li, J.L., 2002. Effect of bull trout and brook trout interactions on foraging habitat, feeding behavior, and growth. Trans. Am. Fish. Soc. 131 (6), 1119–1130.

Harris, D.J., 2015. Generating realistic assemblages with a joint species distribution model. Methods Ecol. Evol. 6 (4), 465–473.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Glob. Change Biol. 12 (3), 450–455.

High, B., Meyer, K.A., Schill, D.J., Mamer, E.R., 2008. Distribution, abundance, and population trends of bull trout in Idaho. North Am. J. Fish. Manag. 28 (6), 1687–1701.

Hutchings, J.A., Gerber, L., 2002. Sex-biased dispersal in a salmonid fish. Proc. R. Soc. Lond. Ser. B: Biol. Sci. 269 (1508), 2487–2493.

Isaak, D., Wenger, S., Peterson, E., Ver Hoef, J., Hostetler, S., Luce, C., Dunham, J., Kershner, J., Roper, B., Nagel, D., et al., 2011. NorWeST: an interagency stream temperature database and model for the Northwest United States. US Fish and Wildlife Service. Great Northern Landscape Conservation Cooperative Grant. . Project website: http://www.fs.fed.us/rm/boise/AWAE/projects/NorWeST.html.

Isaak, D.J., Luce, C.H., Rieman, B.E., Nagel, D.E., Peterson, E.E., Horan, D.L., Parkes, S., Chandler, G.L., 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. Ecol. Appl. 20 (5), 1350–1371.

Isaak, D.J., Young, M.K., Nagel, D.E., Horan, D.L., Groce, M.C., 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. Glob. Change Biol.

Jesse, K.J., 1999. Modelling of a diffusive Lotka-Volterra-System: the climate-induced shifting of tundra and forest realms in North-America. Ecol. Model. 123 (2), 53–64.

Kan-On, Y., 1997. Fisher wave fronts for the Lotka-Volterra competition model with diffusion. Nonlinear Anal.: Theory Methods Appl. 28 (1), 145–164.

Kareiva, P., 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. Ecol. Monogr. 261–282.

Kot, M., Phillips, A., 2015. Bounds for the critical speed of climate-driven moving-habitat models. Math. Biosci. 262, 65–72.

Leslie, P., Gower, J., 1958. The properties of a stochastic model for two competing species. Biometrika 316–330.

Levin, P.S., Achord, S., Feist, B.E., Zabel, R.W., 2002. Non-indigenous brook trout and the demise of pacific salmon: a forgotten threat? Proc. R. Soc. Lond. B: Biol. Sci. 269 (1501), 1663–1670.

Levine, J.M., Rees, M., 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. Am. Nat. 160 (4), 452–467.

Nakano, S., Kitano, S., Nakai, K., Fausch, K.D., 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, *S. confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. Environ. Biol. Fish. 52 (1–3), 345–355.

Park, T., 1948. Experimental studies of interspecies competition. I. Competition between populations of the flour beetles. *Tribolium confusum Duval* and *Tribolium castaneum Herbst.* Ecol. Monogr. 18, 265–308.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., et al., 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399 (6736), 579–583.

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeogr. 12 (5), 361–371.

Pfister, C.A., 1995. Estimating competition coefficients from census data: a test with field manipulations of tidepool fishes. Am. Nat. 271–291.

Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., Vesk, P.A., McCarthy, M.A., 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods Ecol. Evol. 5 (5), 397–406.

Core Team, R., 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Real, L.A., Levin, S.A., 1991. Theoretical advances: the role of theory in the rise of modern ecology. Foundations of Ecology: Classic Papers with Commentaries. pp. 177–191.

Reimer, J.R., Bonsall, M.B., Maini, P.K., 2015. Approximating the critical domain size of integrodifference equations. Bull. Math. Biol. 1–38.

Rinnan, D.S., 2018. The dispersal success and persistence of populations with asymmetric dispersal. Theor. Ecol. 11 (1), 55–69.

Rodríguez, M.A., 2009. A modeling framework for assessing long-distance dispersal and loss of connectivity in stream fish. American Fisheries Society Symposium, vol. 73.

Selong, J.H., McMahon, T.E., Zale, A.V., Barrows, F.T., 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. Trans. Am. Fish. Soc. 130 (6), 1026–1037.

Skalski, G.T., Gilliam, J.F., 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. Ecology 81 (6), 1685–1700.

Sorte, F.A.L., Thompson III, F.R., 2007. Poleward shifts in winter ranges of North American birds. Ecology 88 (7), 1803–1812.

Svirezhev, Y., 2000. Lotka-volterra models and the global vegetation pattern. Ecol. Model. 135 (2), 135–146.

Thomas, C.D., Hill, J.K., Anderson, B.J., Bailey, S., Beale, C.M., Bradbury, R.B., Bulman, C.R., Crick, H.Q., Eigenbrod, F., Griffiths, H.M., et al., 2011. A framework for assessing threats and benefits to species responding to climate change. Methods Ecol. Evol. 2 (2), 125–142.

Thorson, J.T., Scheuerell, M.D., Shelton, A.O., See, K.E., Skaug, H.J., Kristensen, K., 2015. Spatial factor analysis: a new tool for estimating joint species distributions and correlations in species range. Methods Ecol. Evol. 6 (6), 627–637.

Urban, M.C., Tewksbury, J.J., Sheldon, K.S., 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proc. R. Soc. Lond. B: Biol. Sci. 279 (1735), 2072–2080.

US Fish and Wildlife Service, et al., 2008. Bull Trout Recovery: Monitoring and Evaluation Guidance.

Van der Putten, W.H., Macel, M., Visser, M.E., 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philos. Trans. R. Soc. B: Biol. Sci. 365 (1549), 2025–2034.

Van Kirk, R.W., Lewis, M.A., 1997. Integrodifference models for persistence in fragmented habitats. Bull. Math. Biol. 59 (1), 107–137.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R., Monserrat, V.J., 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecol. Lett. 8 (11), 1138–1146.

Zhou, Y., Kot, M., 2011. Discrete-time growth-dispersal models with shifting species ranges. Theor. Ecol. 4 (1), 13–25.