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

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ABSTRACT

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 λ_m, λ_n, α_m, α_n, β_m, β_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