Temporally variable dispersal and demography can accelerate the spread of invading species

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ABSTRACT

We analyze how temporal variability in local demography and dispersal combine to affect the rate of spread of an invading species. Our model combines state-structured local demography (specified by an integral or matrix projection model) with general dispersal distributions that may depend on the state of the individual or its parent. It allows very general patterns of stationary temporal variation in both local demography and in the frequency and distribution of dispersal distances. We show that expressions for the asymptotic spread rate and its sensitivity to parameters, which have been derived previously for less general models, continue to hold. Using these results we show that random temporal variability in dispersal can accelerate population spread. Demographic variability can further accelerate spread if it is positively correlated with dispersal variability, for example if high-fecundity years are also years in which juveniles tend to settle further away from their parents. A simple model for the growth and spread of patches of an invasive plant (perennial pepperweed, *Lepidium latifolium*) illustrates these effects and shows that they can have substantial impacts on the predicted speed of an invasion wave. Temporal variability in dispersal has received very little attention in both the theoretical and empirical literature on invasive species spread. Our results suggest that this needs to change.

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1. Introduction

Invasive organisms are "altering the world's natural communities and their ecological character at an unprecedented rate" (Mack et al., 2000, p. 706), and often have substantial impacts on the structure and function of the ecosystem (Simberloff, 2011). Troublesome invasives in our current home states include zebra mussels, emerald ash borer, giant hogweed, avocado thrips, and smooth cordgrass (*Spartina*).

Spatial models of population spread have a potentially important role in evaluating and designing strategies for preventing or slowing the spread of invasive species (e.g., Taylor and Hastings, 2004; Grevstad, 2005; Jongejans et al., 2008; Bogich et al., 2008; Epanchin-Niell and Hastings, 2010). For well-studied species, simulation models allow detailed demographic modeling and accurate representations of landscape structure (e.g., Higgins et al., 2000; Jongejans et al., 2008; Andrew and Ustin, 2010; Minor and Gardner, 2011). But simple "strategic" models (such as deterministic or stochastic matrix models) have often been useful for identifying

the life stages or demographic processes that are the best targets of opportunity for management efforts to preserve a native species or control an invasive (e.g., Shea and Kelly, 1998; Heppell et al., 2000; Morris and Doak, 2002; Lande et al., 2003; Shea and Kelly, 2004; Shea et al., 2010). Sensitivity analysis of the long-term population growth rate λ, or of the long-term population spread rate c^*, has often been a key tool in these applications.

In a seminal paper Kot et al. (1996) showed how integrodifference equations could be used to model realistic patterns of organism redistribution (e.g., long-tailed distributions rather than the Gaussian spread that results from classical reaction–diffusion models), and gave a simple expression for the asymptotic rate of population spread. They found that long-tailed dispersal distributions can give faster rates of spread than a Gaussian distribution with the same mean square displacement. This has been proposed as a resolution of "Reid's Paradox", the rapid northward advance of tree species after the last glacial retreat (Clark, 1998). The analysis by Kot et al. (1996) was quickly extended to include temporal variability in local population growth (Neubert et al., 2000), demographic stochasticity (Lewis, 2000), discrete stage structure (Neubert and Caswell, 2000), and two-dimensional spread (Lewis et al., 2006). Two recent extensions are models with continuous population structure (Jongejans et al., 2011) and models that combine

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discrete stage structure and demographic variability (Schreiber and Ryan, 2011; Caswell et al., 2011). Caswell et al. (2011) also provide formulas for sensitivity analysis of the long-term population spread rate for periodic or stochastic environmental variation.

Here we take two additional steps. The first is the natural step of combining demographic variability with continuous population structure, using the formalism of integral projection models. The second is to analyze the effects of an ecologically important aspect of population spread that has received surprisingly little attention in previous work: temporal variability in dispersal. Empirical evidence is very limited, but suggests that the frequency and range of long-distance dispersal can vary greatly from one year to the next (Andrew and Ustin, 2010). The general formulas for population spread rate and its sensitivity in models with temporal variability (Neubert et al., 2000; Schreiber and Ryan, 2011; Caswell et al., 2011) allow for temporal variability in both local demography and dispersal, but previous to this paper there has not been (to our knowledge) a mathematical analysis of how dispersal variability can affect the rate of population spread. However, a recent numerical study by Seo and Lutscher (2011) did examine periodic fluctuations in dispersal rates for populations with sedentary and randomly diffusing individuals. They found that fluctuations in dispersal rates could increase or decrease rates of spatial spread depending on temporal correlations between dispersal and demography. To better understand these and other interactions between demography and dispersal on population spread, we analyze three forms of variability, separately and in combination: temporal variation in local demographic parameters (e.g. survivorship and fertility), a single mode of dispersal whose parameters (e.g., mean dispersal distance) vary over time, and multiple modes of dispersal (e.g., local wind dispersal and long-range animal dispersal) whose frequencies vary over time.

Our analysis reveals that the effects of dispersal variability can be very different from those of demographic variability. A classical (Lewontin and Cohen, 1969) and very general result (Tuljapurkar, 1990; Ellner and Rees, 2009) is that temporally uncorrelated demographic variability reduces population growth and spread rates (Lewis, 2000; Clark et al., 2001; Schreiber and Ryan, 2011; Caswell et al., 2011). In contrast, we find that temporally uncorrelated dispersal variability can increase the rate of population spread. Moreover, when dispersal is variable rather than constant, the effect of demographic variability can be reversed: demographic variability that by itself would decrease population growth and spread rate can instead increase those rates, if it is correlated with dispersal variability. These general results are all derived by perturbation analysis for small fluctuations, but we also provide a simple geometric explanation for the effect of dispersal variability. We then use an empirically-based model for the spread of an invasive plant (perennial pepperweed) to show that our results continue to hold at very high levels of variability and that dispersal variability and dispersal–demography covariance can have appreciable effects on population spread rate.

2. Model and assumptions

We consider a continuously structured population in which the state z of an individual (e.g. size or age) lies in a compact set of all possible individual states $\mathbf{Z}$ (Ellner and Rees, 2006). These individuals disperse along a one dimensional transect of their environment (however, rates of spread in a two dimensional region can be computed by "marginalizing" a two-dimensional dispersal kernel along the direction of interest Lewis et al., 2006). Consequently, the location x of an individual can be identified with a point on the line $\mathbf{X} = (-\infty, \infty)$. Let $n_t(x, z)$ denote the population density at location x, state z, and time t. In the absence

of density dependence (which we will consider in Section 4), the most general form of the model is

$$n_{t+1}(x, z) = \iint K_t(x, z, x_0, z_0) n_t(x_0, z_0) dx_0 dz_0 \qquad (1)$$

where x is location, z is individual state, $n_t(x, z)$ is the population distribution in space and state at time t, K_t is the kernel for year t, and the integral runs over the spatial domain $\mathbf{X} = (-\infty, \infty)$ and the (compact) set of possible individual states $\mathbf{Z}$. The kernel $K_t(x, z, x_0, z_0)$ represents the rate at which individuals in state z_0 and location x_0 at time t produce individuals in state z and location x at time t. It includes changes in individual state, changes in location, and production of new offspring which may vary in state and location. We will often write $n_{t+1} = K_t n_t$ as a shorthand for Eq. (1), and similarly for other kernels.

Consistent with prior studies (Kot et al., 1996; Neubert and Caswell, 2000; Neubert et al., 2000; Jongejans et al., 2011; Caswell et al., 2011; Schreiber and Ryan, 2011), we assume spatial homogeneity. In particular, state transition rates are the same at all locations, so our model incorporates temporal variability in environmental conditions but not spatiotemporal variability, and movement probability is a function of the distance between the starting and ending locations. That is,

$$K_t(x, z, x_0, z_0) = K_t(x - x_0, z, z_0), \quad \text{with}$$
$$K_t(v, z, z_0) = K_t(-v, z, z_0). \qquad (2)$$

Within that constraint, however, the dispersal pattern can depend on individual state in any way, in principle. Any constraints on movement dictated by the species' life history is reflected in the structure of the kernel. For example, if new offspring undergo natal dispersal (e.g., seeds or larvae) but then settle for the rest of their life (e.g., trees, corals), the kernel has the form

$$K_t(v, z, z_0) = \delta_0(v) P_t(z, z_0) + k_{d,t}(v) F_t(z, z_0) \qquad (3)$$

where δ_0 is the Dirac delta-function (a unit mass at $v = 0$), F and P are the fecundity and survival/growth kernels respectively, and $k_{d,t}$ is the juvenile dispersal kernel that describes the displacements of offspring from their parent. Without loss of generality we assume that $k_{d,t}$ is a probability distribution, i.e., that any offspring mortality prior to establishment is absorbed into F.

To ensure that invasion speeds are well-defined, we need several additional assumptions. First, we assume that dispersal events have exponentially bounded tails. More precisely, we assume that the transformed kernels

$$H_{s,t}(z, z_0) = \int K_t(v, z, z_0) e^{sv} dv \qquad (4)$$

are finite with probability 1 for all s in some interval $(-s_1, s_1)$; the interval is symmetric because of our spatial homogeneity assumption. In the case of juvenile dispersal, Eq. (3), the transformed kernels are

$$H_{s,t} = P_t + M_t(s) F_t \qquad (5)$$

where M_t is the moment-generating function of $k_{d,t}$. In Eqs. (4) and (5), s characterizes the shape of the invasion wave, and the kernels $H_{s,t}$ determine the spread rate for an invasion wave where total population density decreases exponentially at rate s as a function of distance from the population center (Appendix A). Without an exponentially bounded tail, the rate of spatial spread may constantly accelerate, so there is no asymptotic invasion speed (Kot et al., 1996).

Second, we assume that for all s in $(-s_1, s_1)$, the temporal sequence of transformed kernels $\{\ldots H_{s,-1}, H_{s,0}, H_{s,1}, \ldots\}$ are stationary, ergodic and satisfy the assumptions of Ellner and Rees (2007) for stochastic integral projection models. Stationarity means that the pattern of temporal variability in the environment