

The minimum founding population in dispersing organisms subject to strong Allee effects

Devin W. Goodisman^{1*} and Mark A. Lewis^{1,2}

¹Department of Biological Sciences, University of Alberta, CW 405 Biological Sciences Bldg, Edmonton, AB T6G 2E9, Canada; and ²Mathematical and Statistical Sciences, University of Alberta, 632 CAB, Edmonton, AB T6G 2G1, Canada

Summary

1. Dispersal can push population density below strong Allee thresholds ensuring the demise of small founding populations. As a result, for isolated populations of dispersing organisms, the minimum founding population size that enables establishment can be quite different from the Allee threshold.
2. We derive an expression for the minimum founding population size for a general integrodifference equation model of a dispersing population with a strong Allee effect. We demonstrate the utility of the general model by using it to approximate minimum founding populations for the mountain pine beetle.
3. The minimum founding population of the general model increases linearly with the mean squared displacement of the dispersing organism. Transient dynamics of the general model suggest that population density at the point of introduction will often decrease before increasing, even when the minimum founding population size is exceeded.
4. Calculation of minimum founding population sizes may prove useful for predicting invasion success based on propagule size and for maximizing the success of species reintroductions when strong Allee effects exist.

Key-words: biological control, depensation, dispersal, establishment, insect, integrodifference equation, invasion, mate finding, model, propagule

Introduction

For populations that exhibit positive density dependence, dispersal can have negative consequences because it can spread populations thinly in space (Taylor & Hastings 2005). When population growth or fitness is positively density-dependent, the population is subject to an Allee effect (Allee 1931; Stephens, Sutherland & Freckleton 1999). A strong Allee effect describes the scenario in which population size diminishes below a critical density threshold and increases above it (Stephens, Sutherland & Freckleton 1999). Allee thresholds are typically expressed in terms of population densities per unit area. In organisms that disperse, however, non-spatial Allee thresholds must be interpreted with caution because organisms are typically not uniformly distributed in space.

Allee effects in demographic data are measured in multiple ways (Kramer *et al.* 2009). Component Allee effects (Stephens, Sutherland & Freckleton 1999) are commonly measured by quantifying the positive impact of population density on *per-capita* birth, growth or mortality rates. Demographic Allee effects (Stephens, Sutherland & Freckleton 1999) are usually measured by quantifying the positive effect of population density at some time in the past, on current or future population densities, or on population establishment or survival probability (Kramer *et al.* 2009). More recently, researchers have begun to quantify Allee effects in moving populations by fitting

spatiotemporal models to data using statistical methods (Heavilin & Powell 2008). These spatiotemporal models feature population growth and movement components and thereby account for dispersal. However, like the Allee thresholds computed using non-spatial models, strong Allee thresholds computed using the parameters of the non-spatial component of spatiotemporal models are also misleading when organisms are not uniformly distributed in space.

Dynamic models of moving populations can be continuous in time, such as reaction–diffusion models (Lewis & Kareiva 1993) with concurrent movement and population growth, or discrete in time, such as integrodifference equation models (Kot, Lewis & Van Den Driessche 1996), with sequential dispersal and growth processes. Individual-based models can fall into either category. Regardless of the modelling framework, the population growth component of the model that controls the Allee effect is usually expressed as a function of the current population density and/or the population density at some time in the past. Although a non-spatial Allee threshold can often be computed from the population growth component of spatial population models, it is difficult to interpret biologically.

Early work investigated the impact of movement on population dynamics in the presence of an Allee effect using reaction–diffusion models (Bradford & Philip 1970a,b). The authors investigated steady state solutions on a finite spatial domain and found that to achieve population persistence, the peak of the steady state solution must be larger than the non-spatial Allee threshold. The authors identified critical starting

*Correspondence author. E-mail: goodisman@ualberta.ca

distributions of organisms such that populations would persist. Lewis & Kareiva (1993) extended this work to include an advection term, and also derived critical uniform initial conditions, defined in terms of the radius of the initial uniform population, such that a population subject to a strong Allee effect could establish. Petrovskii & Shigesada (2001) derived what they call the critical aggregation. The critical aggregation is the starting distribution with a specific amplitude and width such that an invasion can occur in a single species reaction–diffusion model that features a strong Allee effect (Petrovskii & Shigesada 2001). Later, Soboleva *et al.* (2003) showed that for a reaction diffusion model in two spatial dimensions, initial conditions that were not radially symmetrical enabled populations (or genes) to establish at lower densities than if they were symmetrically distributed. For integrodifference equation models of biological invasions in which the organism is subject to an Allee effect, Kot, Lewis & Van Den Driessche (1996) also showed that there is a critical radius of the uniform initial population in space such that invasion can occur.

Using simulations of spatially explicit models, researchers have found that one consequence of dispersal in populations with strong Allee effects is that when populations are introduced only at a single point in space, they must be introduced in large numbers to establish (Hopper & Roush 1993; Etienne *et al.* 2002; Robinet *et al.* 2008; Robinet & Liebhold 2009). Analyses of empirical data on the establishment of parasitoids introduced for the biological control of lepidopterans have largely confirmed the existence of critical numbers of introduced individuals which must be surpassed for establishment to occur (Hopper & Roush 1993).

Our research was inspired by the idea of a point introduction as described by Hopper & Roush (1993) or by an introduction via firewood infested with an invasive insect such as the emerald ash borer (Herms & McCullough 2014). This differs from previous theoretical work in that we are not interested in an initial distribution of the invasive organism, but rather in a point source. In addition, we consider the problem on an infinite spatial domain and emphasize transient rather than asymptotic dynamics. In this context, we define the minimum founding population as the minimum number of individuals which, if introduced at a point in space, will persist there indefinitely in spite of dispersal and a strong Allee effect. Mathematically we define the minimum founding population as the founding population such that the maximum population density never drops below the Allee threshold as $t \rightarrow \infty$ where t represents the passage of time since the founding event at $t = 0$. Unlike the Allee threshold, the minimum founding population has a clear biological definition and interpretation in spatial models of dispersing organisms.

We propose an idealized integrodifference model for a dispersing organism subject to a strong Allee effect and produce an analytic solution that we use to derive an expression for the minimum founding population. Our idealized integrodifference equation model with an Allee effect can be perceived as a limiting case of more realistic models of invasion, and thus, we use it to estimate approximate minimum founding populations

for the mountain pine beetle (*Dendroctonus ponderosae* Hopkins).

Materials and methods

We used integrodifference equation models to represent spatiotemporal dynamics of organisms with distinct dispersal and growth stages (Kot, Lewis & Van Den Driessche 1996). Integrodifference equation models of population dynamics comprise population growth and dispersal components. A prototypical one-species example in two spatial dimensions is as follows:

$$N_{t+1}(\mathbf{x}) = \int_{\mathbf{R}^2} \underbrace{N_t(\mathbf{y})f(N_t(\mathbf{y}))}_{\text{Growth function}} \underbrace{k(\mathbf{x} - \mathbf{y})}_{\text{Dispersal kernel}} d\mathbf{y}, \quad \text{eqn 1}$$

where $N_t(\mathbf{x})$ is the population density at location $\mathbf{x} = (x_1, x_2)$ and time t . The growth function $N_t(\mathbf{y})f(N_t(\mathbf{y}))$ maps the population density at time t and location \mathbf{y} onto the population density at that location after reproduction, and $f(N_t(\mathbf{y}))$ is the *per-capita* growth function. The dispersal kernel ($k(\mathbf{x} - \mathbf{y})$) is a continuous probability density function that describes the probability of moving from location \mathbf{y} to location \mathbf{x} after time t but before time $t + 1$. Note that the integrodifference equation gives the distribution of the organism after the dispersal event.

IDEALIZED MODEL

We used an idealized integrodifference equation model to study how dispersal and the strong Allee threshold interact to produce the minimum founding population in organisms that arrive at a location, then disperse and thereafter grow and disperse repeatedly. We assume that N_0 individuals arrive at a previously uninhabited point location $\mathbf{y} = (0, 0)$. Individuals then disperse according to the Gaussian kernel in two spatial dimensions:

$$k(\mathbf{x} - \mathbf{y}; \sigma^2) = \frac{1}{2\pi\sigma^2} \exp\left(-\frac{|\mathbf{x} - \mathbf{y}|^2}{2\sigma^2}\right), \quad \text{eqn 2}$$

where σ^2 is the variance of the Gaussian distribution, which determines how widely the organism disperses. After this initial dispersal event, the distribution of the organism in space is given by

$$N_1(\mathbf{x}) = N_0 k(\mathbf{x}; \sigma^2) = N_0 \frac{1}{2\pi\sigma^2} \exp\left(-\frac{(|\mathbf{x}|)^2}{2\sigma^2}\right). \quad \text{eqn 3}$$

The spatial distribution of the population over time thereafter is given by (1) with $k(\mathbf{x} - \mathbf{y}) = k(\mathbf{x} - \mathbf{y}; \sigma^2)$.

We model population growth with the following *per-capita* growth function:

$$f(N_t(\mathbf{y})) = R[N_t(\mathbf{y})]^{\gamma-1}, \quad \text{eqn 4}$$

where $\gamma > 1$. This *per-capita* growth function has no mechanistic biological underpinning, but rather produces a succinct growth model, which we call the power growth function, when it is multiplied by $N_t(\mathbf{y})$:

$$g(N_t(\mathbf{y})) = R[N_t(\mathbf{y})]^\gamma. \quad \text{eqn 5}$$

This power growth function has an Allee threshold ϕ :

$$\phi = \left(\frac{1}{R}\right)^{1/(\gamma-1)}, \quad \text{eqn 6}$$

below which the population will decline and above which the population will grow. We derive an analytic solution for the nonlinear

integrodifference equation model (eqns 1, 2 and 4). The analytic solution is

$$N_t(\mathbf{x}) = R^{\frac{\gamma^t-1}{\gamma-1}}(N_0)^{\gamma^{t-1}} k\left(\mathbf{x}; \left(\frac{\gamma^t-1}{(\gamma-1)\gamma^{t-1}}\right)\sigma^2\right)h(t), \quad \text{eqn 7}$$

where

$$h(t) = \prod_{i=2}^t \left(\frac{1}{\gamma(2\pi\sigma^2)^{\frac{\gamma^{i-1}-1}{\gamma-1}}\gamma^{i-1}}\right)^{\gamma^{t-i}}, \quad \text{eqn 8}$$

and $t > 1$ is a positive integer (derivation in Appendix S1). Using this analytic solution, we can derive the approximate minimum founding population N_{MFP} (details and derivation in Appendix S1):

$$N_{MFP_1} \approx 2\pi\sigma^2\phi^{\frac{1}{\gamma-1} + \frac{1}{\gamma M-1}} \exp\left(\sum_{i=2}^M [(\gamma-1)\gamma^{1-i}] \log\left(\frac{\gamma^{i-1}-1}{\gamma^{i-2}}\right)\right), \quad \text{eqn 9}$$

where M controls the accuracy of our approximation of the infinite product in (8) as $t \rightarrow \infty$. Choosing larger values of M (a positive integer) results in a better approximation [see Data S2 for sample code that can be used to compute (9)].

If instead we assume that the organism arrives at a new location and then reproduces before dispersing, the minimum founding population N_{MFP_2} follows from (9) as

$$N_{MFP_2} = [(1/R)N_{MFP_1}]^{1/\gamma}. \quad \text{eqn 10}$$

MINIMUM FOUNDING POPULATION IN OTHER SYSTEMS

The idealized solvable integrodifference equation with a strong Allee effect described in the previous section can be used to approximate the minimum founding population for more general models based on the integrodifference equation framework.

Consider an integrodifference equation model with a growth component that features a non-spatial Allee threshold equal to ψ which can be computed numerically or analytically. We equate ψ to the non-spatial Allee threshold of the power growth function (ϕ) given in (6) to obtain

$$\psi = \left(\frac{1}{R}\right)^{1/(\gamma-1)}. \quad \text{eqn 11}$$

We then obtain the value of R such that the Allee threshold of the power growth function (5) matches that of the nonlinear function in the system we wish to approximate:

$$R = \psi^{1-\gamma}, \quad \text{eqn 12}$$

which contains an unspecified parameter γ . However, in addition to matching the Allee threshold, we also want the approximating power growth function to have the same slope at the Allee threshold as our nonlinear function. We begin by computing the slope of the nonlinear function (η) at the Allee threshold. We then equate this to the derivative of the power function with respect to N_t at its Allee threshold $N_t = \phi = \psi$:

$$R\gamma\psi^{\gamma-1} = \eta. \quad \text{eqn 13}$$

By replacing R in (13) with the right hand side of (12), we see that $\gamma = \eta$. Thus, we can use the power function to approximate more complex nonlinear functions at their Allee thresholds by setting γ equal to the slope of the original nonlinear growth function at its Allee threshold and by setting $R = \psi^{1-\gamma}$. The most important caveat when approximating nonlinear functions using the power function in this way is that the nonlinear function must be concave up at its Allee threshold because the power growth function is always concave up.

The accuracy of minimum founding population estimates for integrodifference equation models with Gaussian dispersal kernels and arbitrary nonlinear functions depends on how well the nonlinear functions are approximated at their Allee threshold by the power growth function. Fortunately, many popular discrete-time difference equation models that feature Allee effects are well approximated at their Allee thresholds by a power growth function when the Allee threshold is small. In Table 1, we list some popular difference equations with Allee effects and their small N approximations. Note that all but one of these reduces to a power function with a power greater than one when N is small.

NUMERICAL SOLUTIONS TO INTEGRODIFFERENCE EQUATIONS

We compared our approximate minimum founding population to minimum founding populations discovered by trial and error simulations of a mountain pine beetle integrodifference model (Heavilin & Powell 2008). The method that we used to simulate our integrodifference equations models is based on a tutorial by Jim Powell (<http://www.math.usu.edu/powell/wauclass/node1.html>) and on the appendix of Andersen (1991).

Boundary conditions on all four sides of the spatial domain for our simulations were reflecting, but all simulations were performed on large spatial domains such that interaction with the boundaries was minimal.

Table 1. Some univariate difference equations for organisms with non-overlapping generations that experience strong Allee effects. We computed the small population (N) approximation for each difference equation to illustrate why power growth models approximate them well when populations are small. For brevity, the parameters in the original models are replaced with r_1, r_2, r_3 , etc. We refer the interested reader to the original work for parameter definitions and units. Note that all but the modified Ricker difference equation have small population approximations that are power functions with powers > 1

Model	Name	Small N
$N_{t+1} = \frac{r_1 N_t^2}{r_3 + N_t^2}, r_2 > 1$	Sigmoid Beverton-Holt*	$N_{t+1} \approx \frac{r_1 N_t^2}{r_3}$
$N_{t+1} = \frac{r_4 N_t^2}{r_5 + 2N_t + N_t^2/r_6}$	Beverton-Holt with mate-finding Allee effect†	$N_{t+1} \approx \frac{r_4 N_t^2}{r_5}$
$N_{t+1} = N_t \exp(r_7(1 - \frac{N_t}{r_8}) \frac{N_t - r_9}{r_8})$	Modified Ricker‡	$N_{t+1} \approx \exp(-\frac{r_7 r_9}{r_8}) N_t$
$N_{t+1} = r_{10} N_t (1 - \exp(-r_{11} N_t))$	Mate-finding Allee effect§	$N_{t+1} \approx r_{10} r_{11} N_t^2$

*Thomson (1993).

†Veit & Lewis (1996).

‡Liebhold & Bascompte (2003).

§Dennis (1989).

As our objective was to investigate when populations go extinct due to spatial Allee effects, we chose reflecting rather than absorbing boundary conditions to prevent populations from going extinct due to dispersal out of the domain.

Our simulations are coded in open source R software (R Core Team 2015) and the Rcpp package (Eddelbuettel & Romain 2011; Eddelbuettel 2013) in R to speed up computation by interfacing with C++. We also used the rootSolve (Soetaert 2009; Soetaert & Herman 2009) R package to compute the roots of nonlinear difference equations. Example code for simulations is supplied in the Data S1.

Results

IDEALIZED MODEL

By inspecting (9), it is clear that for our idealized model, the minimum founding population increases linearly with mean squared displacement of dispersers in two spatial dimensions ($2\sigma^2$) and with the variance of the two-dimensional Gaussian kernel σ^2 (Fig. 1a). For example, when $\gamma = 2$, (9) reduces to

$$N_{MFP1} \approx \underbrace{C}_{\text{Constant}} \times \underbrace{(2\sigma^2)}_{\text{Mean squared displacement}} \times \underbrace{(1/R)}_{\text{Allee threshold}}, \quad \text{eqn 14}$$

where the constant C represents all of the terms in (9) that contain $\gamma = 2$. The R parameter dictates how distant the Allee threshold is from $N_t = 0$ (see eqn 6). From (14), we can see that the minimum founding population varies inversely with R (Fig. 1b). We can plot level sets of (13) (Fig. 1c). It is clear from the level sets of (14) that to maintain a constant minimum founding population with increasing variance of the Gaussian kernel in two dimensions, the R parameter must increase as a linear function of variance (Fig. 1c), which results in an Allee threshold that quickly approaches zero.

When organisms reproduce before they disperse from their initial location, the minimum founding population increases nonlinearly with mean squared displacement (or the variance of the Gaussian kernel). This is evident from (10), which simplifies to

$$N_{MFP2} \approx (1/R)[C(2\sigma^2)]^{1/2}, \quad \text{eqn 15}$$

when $\gamma = 2$. When $\gamma = 2$, the minimum founding population increases linearly with the standard deviation, but this will not be generally true if $\gamma \neq 2$.

Our idealized integrodifference equation model exhibits three transient behaviours after the initial colonists arrive and disperse that depend on the initial population density. If the initial population density is below the minimum founding population, the peak of the distribution of individuals over space will fall after every generation (Fig. 2a), even if part of the density distribution of individuals remained above the Allee threshold for several dispersal events.

Transient behaviour when the initial population is above the minimum founding population depends on how much the minimum founding population is exceeded. If the initial population size is slightly above the minimum founding population, the peak of the distribution will fall initially but will later rise as

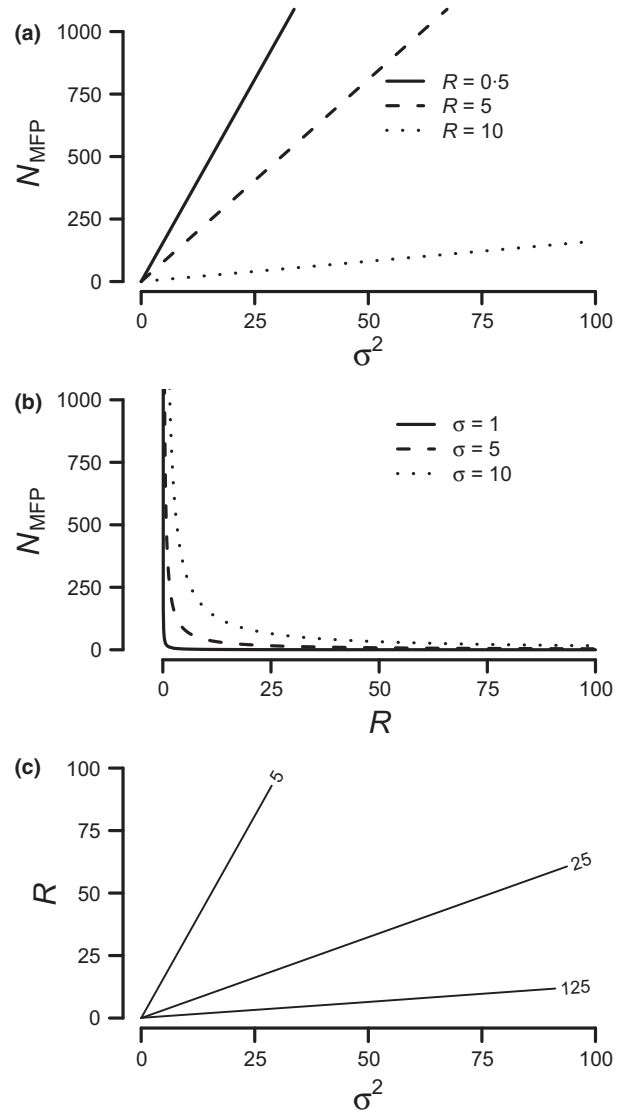


Fig. 1. Solutions of (9) or equivalently (14) for the idealized integrodifference equation model with $\gamma = 2$, and varying R and σ parameters. The (a) minimum founding population varies linearly with the variance of the two-dimensional Gaussian dispersal kernel and (b) varies inversely with the R parameter of the power growth function. The (c) level sets of (14) for each possible minimum founding population are linear functions of the variance of the Gaussian dispersal kernel in two dimensions.

the effect of population growth overpowers the negative effect of dispersal (Fig. 2b). If the initial population size is considerably above the minimum founding population size, the peak of the distribution will rise continuously (Fig. 2c). All of these dynamics can be conveniently compared using the analytic solution (7) solved for the location of introduction ($\mathbf{x} = (0, 0)$) (Fig. 2d). Minute deviations from the minimum founding population size have dramatic consequences for population dynamics (Fig. 2d) leading to either extinction or population explosion. When populations are introduced at well-defined points in space below their minimum founding population sizes, the population can appear to expand initially before

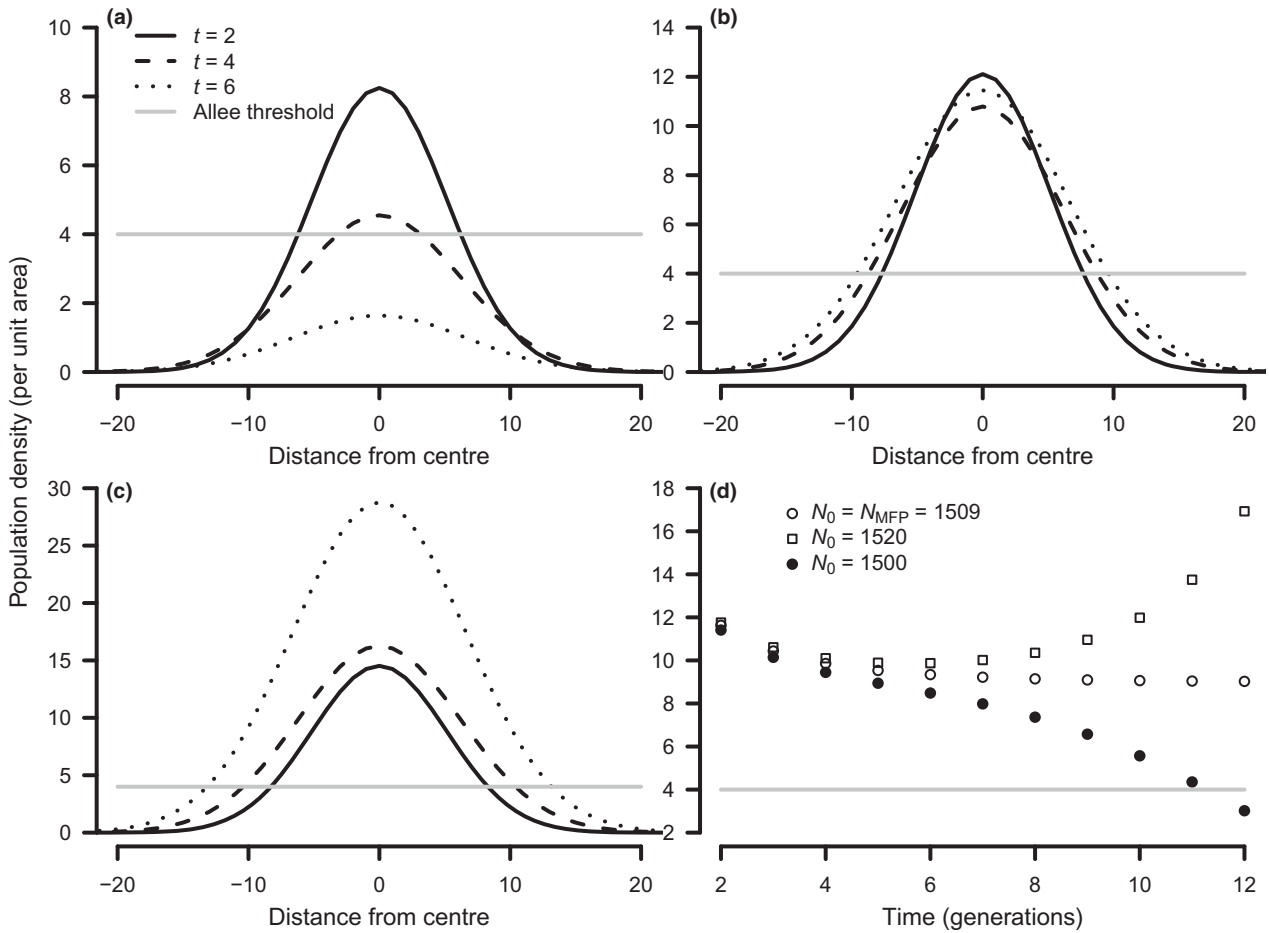


Fig. 2. Transient dynamics when a population initially lands at $\mathbf{x} = (0, 0)$ in a two-dimensional spatial domain and then disperses according to (2) with parameter $\sigma = 4$. Subsequently, the dynamics are iterated with (1) with the power growth function (5) and parameters $R = 0.5$ and $\gamma = 1.5$. The minimum founding population (N_{MFP}) computed using (9) for these parameters is 1509 individuals. One-dimensional slices through the centre of two-dimensional population density distributions after the second, fourth and sixth dispersal events are shown with (a) a founding population of 1200 individuals (less than the N_{MFP}), (b) a founding population of 1550 individuals (slightly higher than the N_{MFP}) and (c) a founding population of 1750 individuals (much higher than the N_{MFP}). Alternatively, (d) transient dynamics of the peak population density can be visualized by plotting solutions of (7) for $\mathbf{x} = (0, 0)$ as a function of t .

imploding (Fig. 3). This can result in ephemeral local invasions that expand in space before collapsing on their own.

MINIMUM FOUNDING POPULATION FOR THE MOUNTAIN PINE BEETLE

In North America, the mountain pine beetle (*D. ponderosae* Hopkins) causes widespread mortality in most native species of pine tree and sometimes causes outbreaks in which continuous expanses of pine are affected (Safranyik & Carroll 2006). To overcome a potential host tree’s resistance, the mountain pine beetle must mass-attack, which leads to an Allee effect because mountain pine beetles are unable to colonize high-quality trees when their densities are too low (Raffa & Berryman 1983). The mountain pine beetle life cycle completes in 1 year in most locations in North America, and trees typically die after being colonized by mountain pine beetle (Safranyik & Carroll 2006). Thus, the local dynamics of the mountain pine beetle can be represented using a difference equation, and

dispersal can be incorporated using integrodifference equation models (Heavilin & Powell 2008). We approximated the minimum founding population for the mountain pine beetle based on a model proposed by Heavilin & Powell (2008):

$$I_{t+1}(\mathbf{x}) = \int_{\mathbf{R}^2} \underbrace{m(I_t(\mathbf{y}))}_{\text{Beetle growth function}} \underbrace{S_t(\mathbf{y})}_{\text{Susceptible host trees}} \underbrace{k(\mathbf{x} - \mathbf{y}; \sigma^2)}_{\text{Gaussian dispersal kernel}} d\mathbf{y}, \quad \text{eqn 16a}$$

$$S_{t+1}(\mathbf{x}) = \underbrace{S_t(\mathbf{x})}_{\text{Susceptible host trees}} - \underbrace{I_{t+1}(\mathbf{x})}_{\text{Recently infested trees}}, \quad \text{eqn 16b}$$

in which $I_t(\mathbf{x})$ is the density of mountain pine beetle-infested pine trees and $S_t(\mathbf{x})$ is the density of susceptible host trees at location \mathbf{x} at time t . The isotropic Gaussian kernel ($k(\mathbf{x} - \mathbf{y}; \sigma^2)$) is the same as in (2), and $m(I_t(\mathbf{y}))$ is a nonlinear function that describes the proportion of susceptible trees that are successfully attacked by mountain pine beetles as a function of mountain pine beetle-infested tree density at time t :

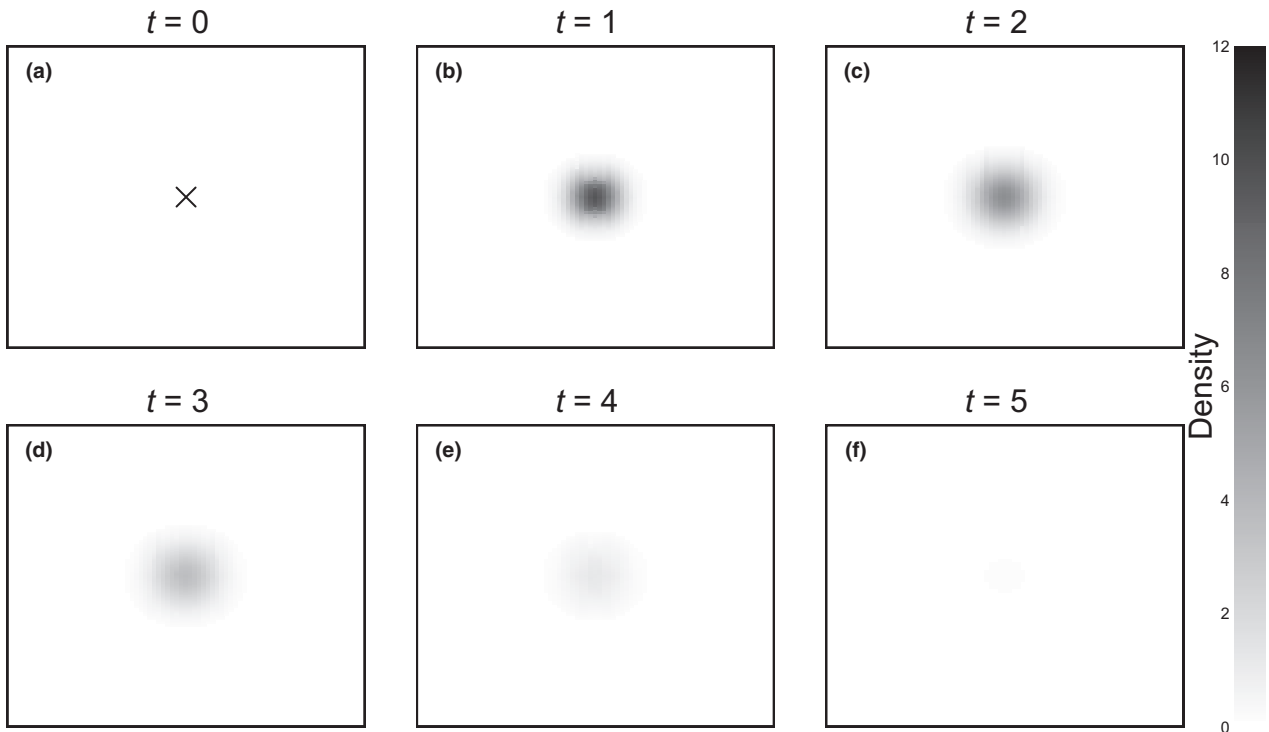


Fig. 3. The dynamics of a failed invasion modelled using the idealized integrodifference eqn (1) featuring the power growth function (5). Parameters were set to $\sigma = 4$ m, $R = 0.2$, and $\gamma = 2$. We (a) introduced 1000 individuals at the spot marked with an X knowing that the minimum founding population (N_{MFP}) was 1294.214 individuals. At first, the population expanded (b), but the density diminished at the location of introduction (c) even while the population expanded in space. Eventually, the population contracted (d–f) and the maximum population density fell below the non-spatial Allee threshold (5 individuals m^{-2}) leading to population collapse. Such ephemeral population expansions may be common when populations start out with an insufficient number of individuals.

$$m(I_t(\mathbf{y})) = \frac{[I_t(\mathbf{y})]^2}{\alpha^2 + [I_t(\mathbf{y})]^2}, \tag{eqn 17}$$

wherein α represents the half saturation constant or the density of infested trees at time t such that half of the susceptible pine trees will become infested by time $t + 1$. Note that when $I_t(\mathbf{y}) \ll 1$, $m(I_t(\mathbf{y})) \approx (1/\alpha^2)[I_t(\mathbf{y})]^2$. In other words, when $I_t(\mathbf{y})$ is near zero, (15) behaves approximately like a power function with a power of two. The α and σ parameters were estimated by Heavilin & Powell (2008) by fitting (16) to data from the Sawtooth National Recreation Area in central Idaho (Table 2).

For the purposes of our analysis, we will ignore negative density dependence in the mountain pine beetle population as a result of host depletion and set the number of susceptible trees to a constant (S) resulting in the following simplified integrodifference equation model for the distribution of mountain pine beetle-infested trees over time:

$$I_{t+1}(\mathbf{x}) = \int_{\mathbf{R}^2} \underbrace{m(I_t(\mathbf{y}))(S)}_{\text{Simplified beetle growth function}} \underbrace{k(\mathbf{x} - \mathbf{y}; \sigma^2)}_{\text{Gaussian dispersal kernel}} d\mathbf{y}. \tag{eqn 18}$$

Using the parameter estimates from Heavilin & Powell (2008), we were able to compute R and γ for two power growth functions that approximated $m(I_t(\mathbf{y}))(S)$ near the Allee threshold (Table 2). Note we fixed $S = 0.0257$ stems m^{-2}

Table 2. Parameter estimates for (16) after it was fitted to two spatiotemporal data sets (separate time series) by Heavilin & Powell (2008). Parameter estimates for the power growth function approximation of the simplified mountain pine beetle growth function in (18) with a constant number of susceptible host trees ($S = 0.0257$ stems m^{-2}) are also given. The parameters of the power growth function approximation were obtained as described in the methods section using (12) and (13)

Time series	Parameter type	Parameter	Estimate	Units
1990–1993	Dispersal	σ	12.251	m
	Growth function	α	3.096e-03	Stems m^{-2}
	Power growth function	R	2091.873	Stems $m^{-\gamma}$
	Power growth function	γ	1.971	Unitless
1995–2001	Dispersal	σ	11.221	m
	Growth function	α	1.167e-03	Stems m^{-2}
	Power growth function	R	18.077	Stems $m^{-\gamma}$
	Power growth function	γ	1.996	Unitless

which is the average density of lodgepole pine stems estimated by Heavilin & Powell (2008). The power growth function (5) matched the simplified mountain pine beetle growth function featured in (18) very well near the Allee threshold (Fig. 4).

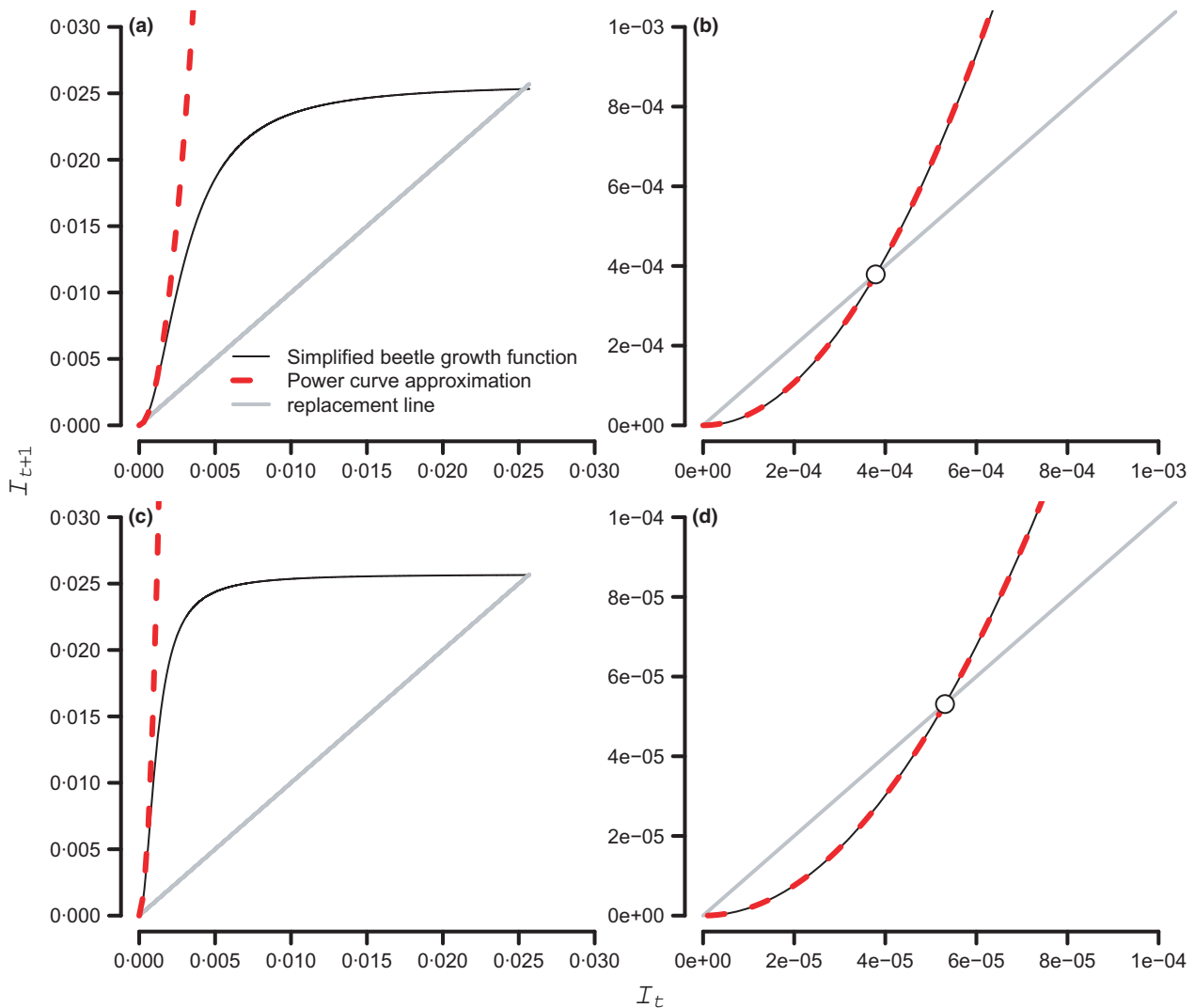


Fig. 4. Mountain pine beetle growth functions assuming a constant number of susceptible host trees ($S = 0.0257$ stems m^{-2}) and no depletion over time (simplified growth function) with parameters estimated from two spatiotemporal data sets by Heavilin & Powell (2008). The growth curve resulting from (a) $\alpha = 3.098e-03$ stems m^{-2} estimated from the first data set shows an inflection point and when magnified (b) the strong Allee threshold can be seen (open circle). The growth curve resulting from (c) $\alpha = 1.167e-03$ stems m^{-2} , estimated from the second data set results in (d) an even smaller Allee threshold (open circle). The power curve approximation with R and γ parameters given in Table 2 approximates both mountain pine beetle growth functions very well near the strong Allee threshold.

Using (9) with $M = 100$ and the R and γ parameters given in Table 2, we computed the approximate minimum founding population for the mountain pine beetle system. For the 1990–1993 time series, the non-spatial Allee threshold was $3.789e-04$ mountain pine beetle-infested stems m^{-2} , while the approximate minimum founding population was 0.933 beetle-infested trees or the equivalent number of beetles. For the 1995–2001 time series, the non-spatial Allee threshold was $5.311e-05$ mountain pine beetle-infested stems m^{-2} and the approximate minimum founding population was 0.108 beetle-infested trees or the equivalent number of beetles.

To test the accuracy of our approximations of the minimum founding populations for the mountain pine beetle system, we compared them to numerical simulations of (16) with different starting densities of mountain pine beetle-infested trees. The

approximate minimum founding populations computed using (9) were slightly biased relative to the numerically computed minimum founding populations. For example, for the 1990–1993 time series, our minimum founding population approximated using (9) was 0.933 beetle-infested trees or the equivalent number of beetles, but the minimum founding population obtained by simulating (16) was 1.012 beetle-infested trees or the equivalent number of beetles (8% higher than the approximate minimum founding population). When the Allee threshold was low as in the 1995–2001 time series, however, the approximate minimum founding population was 0.1084 beetle-infested trees or the equivalent number of beetles compared to the simulated 0.1094 beetle-infested trees or the equivalent number of beetles (1% higher than the approximate minimum founding population).

Discussion

Although it is related to the strong Allee threshold, the minimum founding population is not directly comparable to it. The strong Allee threshold has units of individuals per unit area, whereas the minimum founding population has units of individuals. In the context of point introductions of dispersive species, the minimum founding population statistic is easier to understand and apply than the strong Allee threshold because an initial point density has no singular interpretation in terms of individuals per unit area. For example, an introduction of 10 individuals at a point in space may consider a density of 10 individuals m^{-2} or 10 individuals ha^{-1} (which is equivalent to $1\text{e-}3$ individuals m^{-2}), depending on how the researcher defines a unit of area. It is, therefore, difficult to determine whether or not a point introduction of an invasive species exceeds a critical density required for establishment in the absence of the minimum founding population concept.

When organisms disperse after they arrive at a new location and then reproduce, the minimum founding population in our idealized model increased linearly with the mean squared displacement or, alternatively, with the variance of the Gaussian dispersal kernel in two dimensions. In addition, the minimum founding population was inversely proportional to the R parameter of the power growth function. An argument for the generality of these findings can be made based on their similarity to relationships between minimum founding populations and mean squared displacement and net reproductive rates numerically computed for a reaction diffusion equation model featuring a strong Allee effect generated by mating failure [compare Fig. 1A,B to Fig. 6A and Fig. 6C in Hopper & Roush (1993)]. When organisms reproduce immediately after arriving at new location and then disperse, the minimum founding population increases linearly with the mean squared displacement raised to a power <1 . Thus, reproducing before dispersing drastically reduces the minimum founding population required for persistence.

The accuracy of the minimum founding population estimate obtained using our idealized integrodifference equation model depends on how well its growth and dispersal components approximate reality or, alternatively, how well they approximate a less idealized model. Many difference equations that describe population growth in the presence of an Allee effect are well approximated by the power growth function when the population density is much smaller than one. For these, the accuracy of the minimum founding population estimate obtained using the idealized integrodifference equation model will increase as the Allee threshold decreases. This is evident in the mountain pine beetle case study that we present here. In the first time series (1990–1993), the non-spatial Allee threshold was $3.789\text{e-}04$ infested stems m^{-2} and the approximate minimum founding population was 8% below what it should have been. In the second time series (1995–2001), the non-spatial Allee threshold was $5.311\text{e-}05$ infested stems m^{-2} and the approximate minimum founding population was only 1% below what it should have been.

A second potential source of error in the idealized integrodifference equation model arises due to its reliance on the Gaussian dispersal kernel. Dispersal in many species is better described by Leptokurtic kernels, such as the Laplace kernel (Kot, Lewis & Van Den Driessche 1996). To address this issue, the Gaussian dispersal kernel in (1) can be replaced with a Laplace kernel (Powell & Zimmermann 2004; Heavilin & Powell 2008):

$$k(\mathbf{x} - \mathbf{y}; b) = \frac{1}{2\pi b^2} \exp\left(\frac{-1}{b} |\mathbf{x} - \mathbf{y}|\right), \quad \text{eqn 19}$$

where $|\mathbf{x} - \mathbf{y}|$ represents the Euclidean distance between \mathbf{x} and \mathbf{y} . The variance of (19) is $2b^2$. As the minimum founding population for our idealized integrodifference equation model increases linearly with the variance of the Gaussian kernel (14), we make the following conjecture: the minimum founding population for the analogous integrodifference equation model with the power growth function and the Laplace kernel should increase linearly with b^2 . Trial and error simulations with a varying b parameter support this contention (Fig. 5). Therefore, minimum founding population estimates based on the Gaussian kernel will be accurate when extrapolated to organisms that disperse according to the Laplace kernel provided the variance of the Gaussian kernel in the idealized model matches the variance of the Laplace kernel (Fig. 5). Although they are well supported by simulations, these arguments are not mathematically rigorous and would benefit from a mathematical proof or a derivation of the appropriate minimum founding population expression.

When individuals are introduced at a single point in space at numbers just above the minimum founding population, dispersing organisms that are subject to strong Allee effects exhibit a transient behaviour that is not predicted by non-spatial Allee effect models: at that point, the population density initially decreases before rebounding and increasing. The initial decrease in population density at the point of introduction in populations that disperse may lead managers to falsely believe that the population is below the Allee threshold and will therefore go extinct. Dynamics such as these, in which there is a

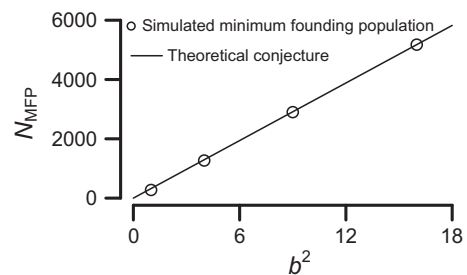


Fig. 5. Minimum founding populations obtained by trial and error simulations of the idealized integrodifference equation model (1) with the Laplace kernel (19) with a varying b parameter ($b = \{1, 2, 3, 4\}$). Population growth for the idealized model with a Laplace kernel was simulated using the power growth function (5) with $R = 0.1$ and $\gamma = 2$. The line representing our conjecture is (14) with $\sigma^2 = 2b^2$. These simulations support the conjecture that the idealized model with a Gaussian kernel can be used to obtain estimates of the minimum founding population with a Laplace kernel by moment matching (matching the variance).

time-lag before invasion becomes evident, have been frequently observed in introductions of invasive species (Crooks 2005). While some authors have attributed this lag phenomenon to a period of genetic adaptation, others argue, as we do, that it is simply a consequence of dispersal from well-defined points of introduction (Hopper & Roush 1993; Shigesada & Kawasaki 1997).

One difficulty associated with applying the minimum founding population concept to real populations is that the underlying model is deterministic and demographic stochasticity may explain the high probability of extinction when populations are small (Dennis 1989; Jerde & Lewis 2007; Jerde, Bampfylde & Lewis 2009). Demographic stochasticity, however, does not preclude the importance of Allee effects. Jerde, Bampfylde & Lewis (2009) found evidence for Allee effects even in populations with high demographic stochasticity. Aside from demographic stochasticity, our idealized integrodifference model also ignores aggregation. Aggregation diminishes the negative impacts of Allee effects and can lower Allee thresholds themselves (Padron & Trevisan 2000; Kanarek *et al.* 2013). In fact, aggregation may explain why Allee thresholds that are quantified using demographic data are consistently low (Boukal & Berec 2002; Heavilin & Powell 2008). Including aggregation in the dispersal component of integrodifference equation models makes analytic calculation of the minimum founding population difficult. However, minimum founding populations can be computed numerically by trial and error simulation for more realistic models. Even when minimum founding populations are computed numerically, the approximate minimum founding population size computed using our idealized integrodifference model will provide a good starting estimate that will prevent searching for the minimum founding population at values far above it.

In this paper, we have defined the minimum founding population for organisms with strong Allee effects as the minimum population size which will eventually grow and expand after a point introduction. If the minimum founding population is not surpassed at the point of introduction, the population will eventually go extinct. While the minimum founding population is driven by the strong Allee effect, it is distinct from the Allee threshold in that it has a clear interpretation for point introductions. The idea of a minimum founding population is closely related to the concept of propagule size, which is defined as the number of individuals in a group that initially arrive at a location (Simberloff 2009). Propagule size is one of the most generally important determinants of invasion success (Von Holle & Simberloff 2005; Colautti, Grigorovich & MacIsaac 2006; Simberloff 2009). Thus, we expect that calculation of minimum founding populations using models may prove useful for the control of invasive species that may be accidentally introduced and desirable species that may be intentionally introduced.

Acknowledgements

We thank three anonymous reviewers for insightful comments that greatly improved this work. This research was supported by a grant to M.A.L. from the

Natural Science and Engineering Research Council of Canada (grant no. NET GP 434810-12) to the TRIA Network, with contributions from Alberta Agriculture and Forestry, Foothills Research Institute, Manitoba Conservation and Water Stewardship, Natural Resources Canada-Canadian Forest Service, Northwest Territories Environment and Natural Resources, Ontario Ministry of Natural Resources and Forestry, Saskatchewan Ministry of Environment, West Fraser and Weyerhaeuser. M.A.L. is also grateful for the support through NSERC Discovery and the Canada Research Chair Program.

Data accessibility

No data were used in this work. Parameter estimates that were used in the simulations and calculations have been provided in the tables embedded in the manuscript.

References

- Allee, W.C. (1931) *Animal Aggregations. A Study in General Sociology*. University of Chicago Press, Chicago, Illinois.
- Andersen, M. (1991) Properties of some density-dependent integrodifference equation population models. *Mathematical Biosciences*, **104**, 135–157.
- Boukal, D. & Berec, L. (2002) Single-species models of the Allee effect: extinction boundaries, sex ratios and mate encounters. *Journal of Theoretical Biology*, **218**, 375–394.
- Bradford, E. & Philip, J.R. (1970a) A note on asocial populations dispersing in 2 dimensions. *Journal of Theoretical Biology*, **29**, 27–33.
- Bradford, E. & Philip, J.R. (1970b) Stability of steady distributions of asocial populations dispersing in one dimension. *Journal of Theoretical Biology*, **29**, 13–26.
- Colautti, R.I., Grigorovich, I.A. & MacIsaac, H.J. (2006) Propagule pressure: a null model for biological invasions. *Biological Invasions*, **8**, 1023–1037.
- Crooks, J.A. (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. *Ecoscience*, **12**, 316–329.
- Dennis, B. (1989) Allee effects: population growth, critical density, and the chance of extinction. *Natural Resource Modeling*, **3**, 481–538.
- Eddelbuettel, D. (2013) *Seamless R and C++ Integration with Rcpp*. Springer, New York, New York.
- Eddelbuettel, D. & Romain, F. (2011) Rcpp: seamless R and C++ integration. *Journal of Statistical Software*, **40**, 1–18.
- Etienne, R., Wertheim, B., Hemerik, L., Schneider, P. & Powell, J. (2002) The interaction between dispersal, the Allee effect and scramble competition affects population dynamics. *Ecological Modelling*, **148**, 153–168.
- Heavilin, J. & Powell, J. (2008) A novel method of fitting spatio-temporal models to data, with applications to the dynamics of mountain pine beetles. *Natural Resource Modeling*, **21**, 489–524.
- Hermes, D.A. & McCullough, D.G. (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annual Review of Entomology*, **59**, 13–30.
- Hopper, K.R. & Roush, R.T. (1993) Mate finding, dispersal, number released, and the success of biological control introductions. *Ecological Entomology*, **18**, 321–331.
- Jerde, C.L. & Lewis, M.A. (2007) Waiting for invasions: a framework for the arrival of nonindigenous species. *The American Naturalist*, **170**, 1–9.
- Jerde, C.L., Bampfylde, C.L. & Lewis, M.A. (2009) Chance establishment for sexual, semelparous species: overcoming the Allee effect. *The American Naturalist*, **173**, 734–746.
- Kanarek, A.R., Webb, C.T., Barfield, M. & Holt, R.D. (2013) Allee effects, aggregation, and invasion success. *Theoretical Ecology*, **6**, 153–164.
- Kot, M., Lewis, M.A. & Van Den Driessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology*, **77**, 2027–2042.
- Kramer, A.M., Dennis, B., Liebhold, A.M. & Drake, J.M. (2009) The evidence for Allee effects. *Population Ecology*, **51**, 341–354.
- Lewis, M. & Kareiva, P. (1993) Allee dynamics and the spread of invading organisms. *Theoretical Population Biology*, **43**, 141–158.
- Liebhold, A. & Bascompte, J. (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters*, **6**, 133–140.
- Padron, V. & Trevisan, M. (2000) Effect of aggregating behavior on population recovery on a set of habitat islands. *Mathematical Biosciences*, **165**, 63–78.
- Petrovskii, S. & Shigesada, N. (2001) Some exact solutions of the generalized Fisher equation related to the problem of biological invasion. *Mathematical Biosciences*, **172**, 73–94.
- Powell, J. & Zimmermann, N. (2004) Multiscale analysis of active seed dispersal contributes to resolving Reid's paradox. *Ecology*, **85**, 490–506.
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Raffa, K.F. & Berryman, A.A. (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs*, **53**, 27–49.
- Robinet, C. & Liebhold, A.M. (2009) Dispersal polymorphism in an invasive forest pest affects its ability to establish. *Ecological Applications*, **19**, 1935–1943.
- Robinet, C., Lance, D.R., Thorpe, K.W., Onufrieva, K.S., Tobin, P.C. & Liebhold, A.M. (2008) Dispersion in time and space affect mating success and Allee effects in invading gypsy moth populations. *The Journal of Animal Ecology*, **77**, 966–973.
- Safranyik, L. & Carroll, A. (2006) The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *The Mountain Pine Beetle: A Synthesis of Its Biology, Management and Impacts in Lodgepole Pine* (eds L. Safranyik & B. Wilson), pp. 3–66. Canadian Forest Service, Victoria, BC, Canada.
- Shigesada, N. & Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford, UK.
- Simberloff, D. (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 81–102.
- Soboleva, T.K., Shorten, P.R., Pleasants, A.B. & Rae, A.L. (2003) Qualitative theory of the spread of a new gene into a resident population. *Ecological Modelling*, **163**, 33–44.
- Soetaert, K. (2009) rootSolve: nonlinear root finding, equilibrium and steady-state analysis of ordinary differential equations. R package version 1.6.
- Soetaert, K. & Herman, P.M.J. (2009) *A Practical Guide to Ecological Modelling Using R as a Simulation Platform*. Springer, Berlin.
- Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999) What is the Allee effect? *Oikos*, **87**, 185–190.
- Taylor, C.M. & Hastings, A. (2005) Allee effects in biological invasions. *Ecology Letters*, **8**, 895–908.
- Thomson, G.G. (1993) A proposal for a threshold stock size and maximum fishing mortality rate. Canadian Special Publication of Fisheries and Aquatic Sciences, pp. 303–320. NRC Research Press.
- Veit, R. & Lewis, M. (1996) Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. *The American Naturalist*, **148**, 255–274.
- Von Holle, B. & Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, **86**, 3212–3218.

Received 22 December 2015; accepted 24 March 2016

Handling Editor: Oscar Gaggiotti

Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Data S1. Computer code.

Data S2. Computing MFP

Appendix S1. Mathematical details.