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Establishing a beachhead: A stochastic population model with an Allee effect applied to species invasion

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Abstract

We formulated a spatially explicit stochastic population model with an Allee effect in order to explore how invasive species may become established. In our model, we varied the degree of migration between local populations and used an Allee effect with variable birth and death rates. Because of the stochastic component, population sizes below the Allee effect threshold may still have a positive probability for successful invasion. The larger the network of populations, the greater the probability of an invasion occurring when initial population sizes are close to or above the Allee threshold. Furthermore, if migration rates are low, one or more than one patch may be successfully invaded, while if migration rates are high all patches are invaded.
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1. Introduction

Biotic invasion is one of the greatest threats to the integrity of ecosystems around the world (Drake et al., 1989; Edsall et al., 1995; Fagan et al., 2002). Invasive species, free of whatever normally regulates their growth, spread to fill up their new habitat causing disruptions in the local biological community in the process. Nutria (*Myocastor coypus*) is a prime example. In 1937, about 15–20 individual nutrias were introduced into Louisiana for the purpose of fur farming (Lowery, 1974). The nutria escaped or were released into marshes and readily adapted to their new environment. Within 20 years, the nutria population was estimated at 20 million animals (Lowery, 1974; Carter and Leonard, 2002).

All taxons have proven to have species that in one context or another become invasive (Drake et al., 1989; Lodge, 1993; Mack et al., 2000; Ludsin and Wolfe, 2001). Because biotic invasion is almost a universal phenomenon, several authors have explored the possibility that the process of invasion can be used to understand ecological processes in general (i.e., Hengeveld, 1989). However, the diversity of invading taxons, and the diversity of systems invaded have made it difficult to find general principles that can be broadly applied (Moyle and Light, 1996; Mack et al., 2000).

Not all arrivals succeed, not all species that become established become "invasive", and lag times often exists between the time the future invader arrives and the time it begins to exhibit invasive behavior (Gordon and Thomas, 1997; Mack et al., 2000). Therefore, one could argue that the most important stage in an invasion is not arrival of the invader but the invader's establishment as a viable self-sustaining population, its "beachhead" in the community.

While the specific mechanisms by which invaders arrive vary widely, most are accidental and they often have several factors in common (e.g., Carlton and Geller, 1993; Malecki, 1995; Veit and Lewis, 1996; Higgins and Richardson, 1998; Carter and Leonard, 2002). First, most introductions involve relatively small numbers of individuals. Second, these introductions often occur multiple times and in multiple locations. Third, successful

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introductions depend on the species finding suitable habitat that is often distributed in discrete patches across the landscape.

For any generalization about biotic invasion to be useful it will have to be based on population processes that can be (1) broadly applied to a great diversity of taxonomic groups and (2) be spatially explicit since invasion is a spatially explicit process. We propose the Allee effect (Allee, 1931) as a mechanism that may explain the lag between initial introduction and the establishment of the invasive phase of species behavior.

The Allee effect was first proposed in 1931 for social mammals (Allee, 1931) but the concept has since been extended to a wide variety of organisms. The Allee effect is a density-mediated drop in a population's intrinsic growth rate at low densities. In many cases, this can result in a negative growth rate below a critical population density, also referred to as a "strong" Allee effect (Owen and Lewis, 2001). The mechanism for a density-mediated decline in the intrinsic growth rate is species dependent and variable. In some cases it is due to a density-mediated decrease in reproductive rate, in others it is due to a density-mediated decrease in survivorship (Henle et al., 2004). Alternatively, individual fitness may be highest at intermediate levels of density (Stephens et al., 1999).

The Allee effect was also studied by Petrovskii et al. (2005) as a possible mechanism for the lag between introduction and establishment. However, their model structure is quite different from ours. They included both predator and prey with random diffusion, where the Allee effect is included in the prey dynamics. Our model is applied to a single species with multiple patches. In addition, we include stochastic effects in the birth, death and migration processes.

Variability in births, deaths, and migration can significantly affect species establishment. Stochastic effects often result in species extinction when population densities are low. The Allee effect coupled with stochastic effects can increase the probability of extinction for densities above the threshold but can decrease the probability of extinction for densities below the Allee threshold (Dennis, 2002). We show with multiple introductions in different locations and random migration between these locations that invasion success is higher than for a single patch. Whether the invasion is successful in multiple patches depends on the local population size, the migration rate, and the connectivity. Our goal is to study how stochastic variability coupled with an Allee effect may impact species invasion success in a multi-patch system.

To study the effect of an invasion, we introduce a stochastic model with an Allee effect in the next section. The stochastic model is a continuous-time Markov chain and is based on an underlying deterministic model with an Allee effect and with multiple patches. A brief analysis of the underlying deterministic model is presented. Then specific numerical examples for the stochastic model are studied in regard to the initial phase of invasion. Specifically, the probability of species invasion for one and two patches are compared. Then the effect of the migration rates on the probability of invasion and number of patches occupied is studied for three patches. The last numerical examples compare the probability of invasion for three, four and nine patches with one patch. The effect of connectivity on invasion success is investigated in a nine-patch model. A discussion of our results and their implications for species invasion are presented in the last section.

2. The model

Suppose the deterministic population model with an Allee effect has the form

$$\begin{cases} \dfrac{dN(t)}{dt} = rN(t)\left(\dfrac{N(t)}{E_0} - 1\right)\left(1 - \dfrac{N(t)}{K}\right) \equiv f(N(t)), \\ N(0) = N_0, \end{cases} \tag{2.1}$$

where $N(t)$ is the population size at time t. The equilibrium E_0 represents the Allee threshold below which there is population extinction, and K is the environmental carrying capacity, $0 < E_0 < K$. In addition, $r > 0$ is the intrinsic growth rate. The threshold E_0 represents the minimal population size for population survival, and the carrying capacity K represents the maximal population size if the invasion is successful. For this model it is easy to see that if $N_0 < E_0$, then $\lim_{t\to\infty} N(t) = 0$ and if $N_0 > E_0$, then $\lim_{t\to\infty} N(t) = K$.

We use the model (2.1) as a basis for constructing a stochastic population model with an Allee effect (e.g., Allen, 2003b; Liebhold and Bascompte, 2003). In the stochastic model, we need to define the birth rate $b(N)$ and the death rate $d(N)$ so that $dN/dt = b(N) - d(N) = f(N)$, where $f(N)$ is defined in (2.1). For example, we let

$$b(N) = r_1 N + r\left(\frac{1}{E_0} + \frac{1}{K}\right)N^2 - c_1\frac{r}{E_0 K}N^3 \tag{2.2}$$

and

$$d(N) = r_2 N + c_2\frac{r}{E_0 K}N^3 \tag{2.3}$$

with nonnegative parameters r_i and c_i, $i = 1, 2$, where $r_2 - r_1 = r$ and $c_1 + c_2 = 1$ (Allen, 2003b). Clearly $b(N) - d(N) = f(N)$. Splitting the growth term as in (2) and (3) is not very restrictive because it allows for an infinite number of choices for the form of the birth and death rates (infinite number of parameter values r_i and c_i) that yield the same deterministic population model (1) (Allen and Allen, 2003; Allen, 2003b). The choice of $b(N)$ and $d(N)$ depends on the particular invasive species under investigation and requires fitting the parameters to data. The magnitude of the parameters determine the importance of the density-dependent effects in the birth and death rates.

In the stochastic formulation, we assume that N is a discrete random variable, with values in the range

$\{0, 1, 2, \ldots, M\}$, where M is the maximum population size. Let the time step Δt be sufficiently small such that there can be a change in the population size of at most one, $\Delta N(t) = N(t + \Delta t) - N(t) \in \{-1, 0, 1\}$. We formulate a birth and death process by specifying the infinitesimal transition probabilities. Let a denote the change in the population size; a is an integer. Then the transition probabilities equal

$$P\{\Delta N(t) = a|N(t)\} = \begin{cases} b(N(t))\Delta t + o(\Delta t) & \text{if } a = 1, \\ d(N(t))\Delta t + o(\Delta t) & \text{if } a = -1, \\ 1 - [b(N(t)) + d(N(t))]\Delta t + o(\Delta t) & \text{if } a = 0, \\ o(\Delta t) & \text{if } a \neq -1, 0, 1. \end{cases} \tag{2.4}$$

The preceding transition probabilities define a continuous-time Markov chain model for the random variable $N(t)$ (Karlin and Taylor, 1975; Allen, 2003a). The stochasticity in this model arises due to variability in births and deaths (i.e., demographic stochasticity). Therefore, in this model, it is not the environmental conditions that determine invasion success but the species demographic characteristics.

The continuous-time Markov chain model will be used to model population dynamics within one patch. To formulate a stochastic model for spatial spread to other patches, we first formulate a deterministic patch model with an Allee effect. Let $N_j(t)$ be the population size in patch j. Then

$$\frac{dN_j}{dt} = f(N_j) + \sum_{k=1, k\neq j}^{n} (m_{jk}N_k - m_{kj}N_j), \quad j = 1, \ldots, n, \tag{2.5}$$

where m_{jk} is the rate of population movement out of patch k into patch j, $j \neq k$, and n is the total number of patches. We assume random migration between patches, as opposed to density-dependent migration or selective migration (Greene, 2003; Petrovskii and Li, 2003). Let Δt be chosen sufficiently small such that there can be a change in the patch population size by at most one, $\Delta N_j(t) \in \{-1, 0, 1\}$. Let the parameters a and b denote the change in patch population sizes j and k, respectively; a and b are integers. The stochastic patch model assumes the same infinitesimal transition probabilities for the intrapatch dynamics given by (2.4), but for the interpatch dynamics, the transition probabilities equal

$$P\{(\Delta N_j(t + \Delta t), \Delta N_k(t + \Delta t)) = (a, b)|(N_j(t), N_k(t))\} = \begin{cases} m_{jk}N_k(t)\Delta t + o(\Delta t) & \text{if } (a, b) = (1, -1), \\ m_{kj}N_j(t)\Delta t + o(\Delta t) & \text{if } (a, b) = (-1, 1), \\ 1 - [m_{jk}N_k(t) & \\ \quad + m_{kj}N_j(t)]\Delta t + o(\Delta t) & \text{if } (a, b) = (0, 0), \\ o(\Delta t) & \text{if } (a, b) \neq (1, -1), \\ & \quad (-1, 1), (0, 0). \end{cases}$$

The transition probabilities imply that during a small interval of time Δt there is movement from patch k to j with $m_{jk}N_k(t)\Delta t + o(\Delta t)$ probability or from patch j to k with probability $m_{kj}N_j(t)\Delta t + o(\Delta t)$ or there is no movement with probability $1 - [m_{jk}N_k(t) + m_{kj}N_j(t)]\Delta t + o(\Delta t)$. Other types of movement, such as movement from patch j to k and returning to patch j, have a very small probability ($o(\Delta t)$) of occurring during the time interval Δt. The assumptions regarding the explicit intrapatch dynamics given by (2.5) make our stochastic patch model approach different from the patch occupancy models of Hanski and colleagues (Hanski and Ovaskainen, 2003; Ovaskainen and Hanski, 2001, 2004; Hanski and Simberloff, 1997). The patch occupancy models of Hanski and colleagues consider colonization, extinction, and migration of a patch but do not consider specific birth and death processes within a patch.

3. Analytical and numerical results

We theoretically analyze the behavior of the deterministic model and show that the Allee effect determines a sharp threshold for persistence. In the stochastic model, we show, by studying specific numerical examples, that this threshold is not sharp and is dependent on the initial conditions. A probability of invasion is defined for initial conditions near the Allee threshold.

3.1. Analysis of the deterministic model

We now establish the following results for the deterministic n-patch dispersion model, (2.5), with an Allee effect. To this end, we make the following assumption on the dispersal parameters:

(H1) We assume that $\sum_{k=1,k\neq j}^{n} m_{jk} = \sum_{k=1,k\neq j}^{n} m_{kj}$ for $j = 1, \ldots, n$.

It is not difficult to show that if (H1) holds, then $(0, \ldots, 0)$, $(E_0, \ldots, E_0)$, and $(K, \ldots, K)$ are equilibrium points of model (2.5).

Theorem 3.1. *Assume* (H1) *holds. Then* (2.5) *has only one equilibrium point* $(\bar{N}_1, \ldots, \bar{N}_n)$ *with* $\bar{N}_j < E_0$, $j = 1, \ldots, n$, *namely* $(0, \ldots, 0)$. *Furthermore*, (2.5) *has one equilibrium with* $E_0 < \bar{N}_j \leqslant K$ *or* $K < \bar{N}_j$ *for* $j = 1, \ldots, n$, *namely* $(K, \ldots, K)$.

Proof. Suppose there exists an equilibrium with $\bar{N}_j \neq \bar{N}_k$ and $E_0 \geqslant \bar{N}_j > \bar{N}_k \geqslant 0$, $k \neq j$. Then from (2.5) we get

$$0 = f(\bar{N}_j) + \sum_{k\neq j} m_{jk}\bar{N}_k - \sum_{k\neq j} m_{kj}\bar{N}_j,$$

where the summation is over the index k. But using (H1) we obtain

$$0<f(\bar{N}_j)+\sum_{k\neq j}(m_{jk}-m_{kj})\bar{N}_j=f(\bar{N}_j)\leqslant 0,$$

a contradiction.

Now suppose that there exists an equilibrium with $\bar{N}_j\neq\bar{N}_k$, $K\geqslant\bar{N}_k>\bar{N}_j\geqslant E_0$, for all $k\neq j$. Then

$$\begin{aligned}0&=f(\bar{N}_j)+\sum_{k\neq j}m_{jk}\bar{N}_k-\sum_{k\neq j}m_{kj}\bar{N}_j\\&>f(\bar{N}_j)+\sum_{k\neq j}(m_{jk}-m_{kj})\bar{N}_j=f(\bar{N}_j)\geqslant 0,\end{aligned}$$

a contradiction.

For the last case, suppose there exists an equilibrium with $\bar{N}_j\neq\bar{N}_k$, $\bar{N}_j>\bar{N}_k\geqslant K$, for all $k\neq j$. Again it is straightforward to show that a contradiction is obtained.

Thus, the only nonnegative equilibrium with components less than E_0 is the origin and one with all components greater than or equal to K or greater than E_0 but less than or equal to K is $(K,\ldots,K)$. □

Theorem 3.2. *Assume* (H1) *holds and that* $0<N_j(0)<E_0$ *for* $j=1,\ldots,n$, *then* $\lim_{t\to\infty}N_j(t)=0$, $j=1,\ldots,n$.

Proof. Let $S(t)=\sum_{j=1}^{n}N_j(t)$. Clearly $dS/dt|_{t=0}=\sum_{j=1}^{n}f(N_j(0))<0$ which follows directly from assumption (H1),

$$\sum_{j=1}^{n}\sum_{k=1,k\neq j}^{n}(m_{jk}N_k-m_{kj}N_k)=0,$$

and the assumptions regarding the initial conditions. We claim that $N_j(t)\leqslant E_0$ for $j=1,\ldots,n$. Suppose not, then there exists a minimum t_0 such that $dN_j(t_0)/dt>0$, $N_j(t_0)=E_0$ for some j and $N_k(t_0)\leqslant E_0$, $k\neq j$. Hence,

$$\begin{aligned}0<\frac{dN_j(t_0)}{dt}&=\sum_{k\neq j}m_{jk}N_k(t_0)-\sum_{k\neq j}m_{kj}N_j(t_0)\\&\leqslant\sum_{k\neq j}(m_{jk}-m_{kj})E_0=0,\end{aligned}$$

a contradiction. Thus $N_j(t)\leqslant E_0$ for all $t\geqslant 0$ which implies $dS/dt\leqslant 0$ for all $t\geqslant 0$. Thus $\lim_{t\to\infty}S(t)$ exists. But $dS/dt=\sum_{j=1}^{n}f(N_j)$. If the limit is positive, then $dS/dt<0$ at the limit which is impossible. Hence, $\sum_{j=1}^{n}f(N_j)=0$. From Theorem 3.1 it follows that $\lim_{t\to\infty}N_j(t)=0$. □

Theorem 3.3. *Assume* (H1) *holds and that the initial conditions satisfy either* (i) $E_0<N_j(0)<K$ *or* (ii) $K<N_j(0)$ *for all* $j=1,\ldots,n$, *then* $\lim_{t\to\infty}N_j(t)=K$ *for* $j=1,\ldots,n$.

Proof. By applying arguments similar to the preceding theorem one can show that depending on the two sets of initial conditions either (i) $E_0\leqslant N_j(t)\leqslant K$ or (ii) $K\leqslant N_j(t)$ for all j. In case (i), $dS/dt=\sum_{j=1}^{n}f(N_j)\geqslant 0$ for $t\geqslant 0$ implying $S(t)$ has a limit. Since there are only two equilibria in this region, $(E_0,\ldots,E_0)$ and $(K,\ldots,K)$, and since $S(t)$ is increasing, it follows that $\lim_{t\to\infty}N_j(t)=K$. Case (ii) follows in a similar manner. □

For the deterministic model (2.5) satisfying assumption (H1), we have shown that there are three invariant regions in $\mathbf{R}_+^n=\{(x_1,\ldots,x_n):0\leqslant x_i,i=1,\ldots,n\}$ for the n-patch model: $\Omega_1=\{(x_1,\ldots,x_n):0\leqslant x_i\leqslant E_0,i=1,\ldots,n\}$, $\Omega_2=\{(x_1,\ldots,x_n):E_0\leqslant x_i\leqslant K,i=1,\ldots,n\}$, and $\Omega_3=\{(x_1,\ldots,x_n):K\leqslant x_i,i=1,\ldots,n\}$. In the interior of these three regions, solutions either converge to $(0,\ldots,0)$ or to $(K,\ldots,K)$. This behavior is similar to the behavior for the deterministic model in one patch. The Allee threshold has a clearly defined boundary given by the boundary for the basin of attraction of the origin. There may exist additional equilibria outside of these three regions. But because we are primarily interested in invasion, the behavior of the model close to E_0 is of primary interest. In addition, choices for our initial conditions in the numerical examples are such that solutions to the underlying deterministic model are either in the basin of attraction for the origin or $(K,\ldots,K)$. For example, for initial conditions $N_j(0)=i_0$ for $j=1,\ldots,n$, if $0<i_0<E_0$, then $\lim_{t\to\infty}N_j(t)=0$ and if $E_0<i_0$, then $\lim_{t\to\infty}N_j(t)=K$ for all j. For these initial conditions, E_0 is a sharp Allee threshold.

As an illustration, consider the case $n=2$, where the parameter values in model (2.5) are equal to $E_0=20$, $K=500$, $m_{12}=m_{21}=0.2$, and $r=0.1$. In this case, there are only the three equilibria: $(0,0)$, $(20,20)$, and $(500,500)$. The origin and $(500,500)$ are stable nodes and $(20,20)$ is an unstable node. One can see clearly the basins of attraction for $(0,0)$ and $(500,500)$ in Fig. 1 (separatrices are identified by the green (solid) curves and nullclines by yellow and orange (dashed) curves). However, if r is increased to $r=0.5$, then two more equilibria exist: $(12.637,24.974)$ and $(24.974,12.637)$. These latter equilibria are saddle points and except for the two orbits approaching each of these saddle points, solutions either approach $(0,0)$ or $(500,500)$.

In the stochastic models, we study one, two, three, four and nine patches, where the underlying deterministic models satisfy assumption (H1). In addition to these models, we study a stochastic nine-patch model, where the underlying deterministic model does not satisfy assumption (H1). However, the dispersal structure of the nine-patch model is chosen so that it can be easily compared to the other models. In the nine-patch model not satisfying assumption (H1), the equilibrium values for different patches are not the same but there exist two equilibria, one close to $(E_0,\ldots,E_0)$ and another close to $(K,\ldots,K)$. For the stochastic models, the Allee threshold boundaries are not sharp. For initial values less than E_0, there is a positive probability of invasion and for initial values greater than E_0, there is a positive probability of no invasion. Because of the inherent demographic stochasticity for small population sizes, it is important to study invasion using the stochastic models.

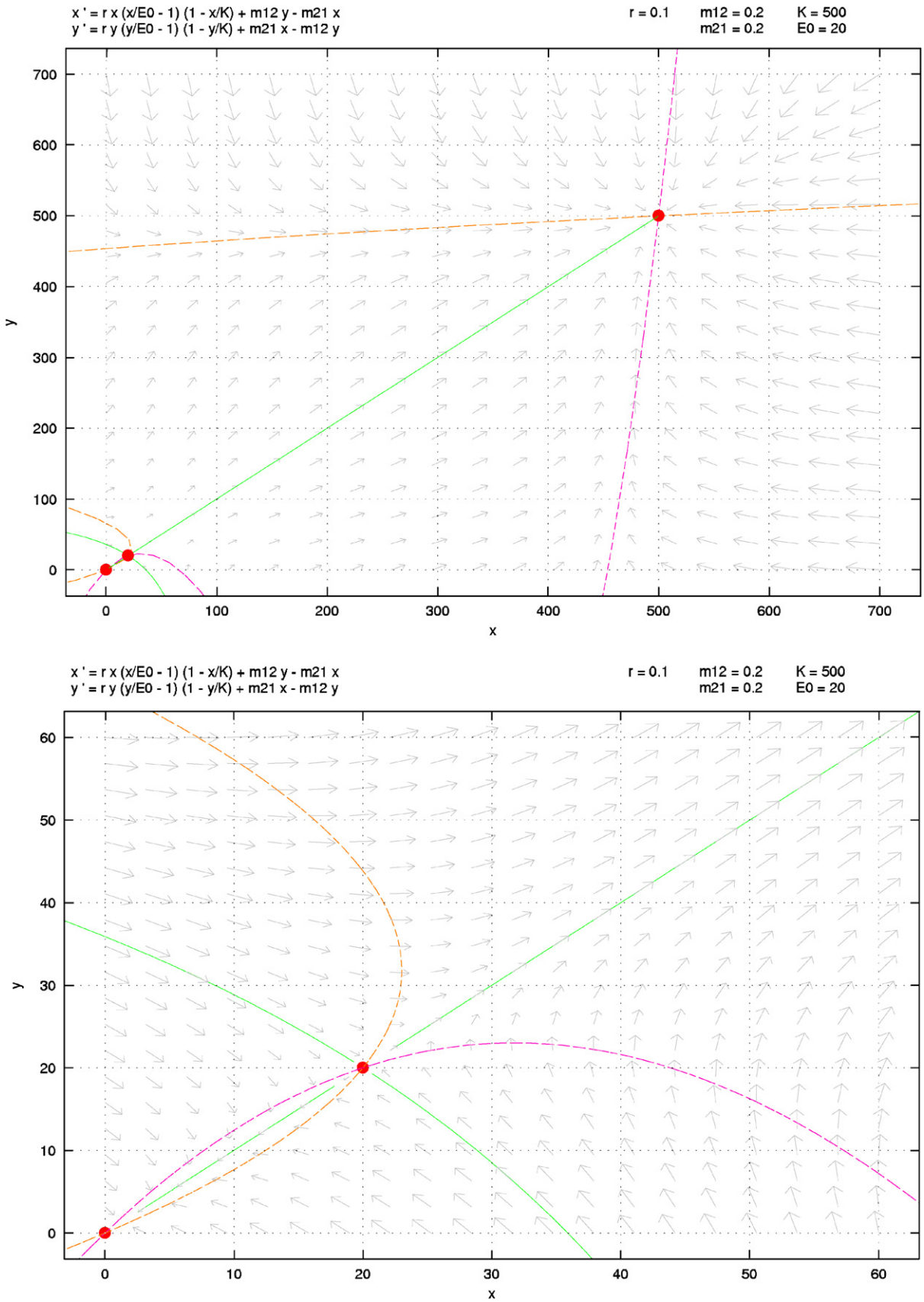

Fig. 1. Phase plane graphs for (2.5) with $n = 2$ and parameters values $E_0 = 20$, $K = 500$, $m_{12} = m_{21} = 0.2$, and $r = 0.1$. The figure on the left illustrates the dynamics in the region $[0, 700] \times [0, 700]$, whereas the figure on the right zooms in to show the Allee threshold, region $[0, 60] \times [0, 60]$. The green (solid) curves are the separatrices and the purple and orange (dashed) curves are the nullclines. The phase planes were generated with J. K. Polking's *pplane7*.

3.2. Analysis of the stochastic model via numerical simulations

In all stochastic simulations, the probability of invasion is calculated based on 500 individual sample paths. We define the probability of invasion as the probability that at least one patch is invaded (with population size $>K/2$). In the numerical simulations, either a failure to invade or a successful invasion occur for each sample path in the multi-patch system if there exists a time T such that either $N_i(T)=0$ for $i=1,\ldots,n$ (failure to invade) or $N_i(T)>K/2$ for some i (successful invasion) whichever occurs first. Therefore, an estimate for the probability of invasion is obtained from the proportion of sample paths (out of 500) with a successful invasion.

With the nutria population in mind, an Allee threshold is chosen as $E_0=20$ and an environmental carrying capacity as $K=500$, $E_0/K=0.04$. A large value is chosen for K because invasive species, such as nutria, generally reach very high local densities. The form of the birth and death rates satisfy (2.2) and (2.3), where $r=0.1$, $c_1=\frac{49}{50}$, $c_2=\frac{1}{50}$, $r_1=0$, and $r_2=r$. The choice of these parameter values is not necessarily related to nutria but rather for illustrative purposes. Graphs of the birth and death rates, $b(N)$ and $d(N)$, are given in Fig. 2.

3.2.1. One and two patches

The dynamics of the stochastic patch model are studied in one and two patches. For a single patch, the underlying deterministic model satisfies (2.1). Solutions to the deterministic single patch model approach zero if $0<N(0)<E_0$ and approach K if $N(0)>E_0$. The variability in the corresponding stochastic model is illustrated in Fig. 3. Ten sample paths are numerically simulated for the stochastic Allee population model for three different initial conditions, $N(0)=10$, 15, and 20. These figures illustrate the variability in a stochastic sample path and the dynamics near the Allee boundary. Applying our definition of probability of invasion for this example with only 10 sample paths, an estimate for the probability of invasion for population sizes $N(0)=10, 15$, and 20 yields 0, 0.1, and 0.5, respectively. We obtain a better estimate based on 500 sample paths. But note as $N(0)$ increases, so does the probability of invasion. At the threshold level, $N(0)=E_0=20$, the probability of invasion is $\frac{1}{2}$ because the probabilities of a birth or a death are equal:

$$\frac{b(20)}{b(20)+d(20)}=\frac{1}{2}=\frac{d(20)}{b(20)+d(20)}.$$

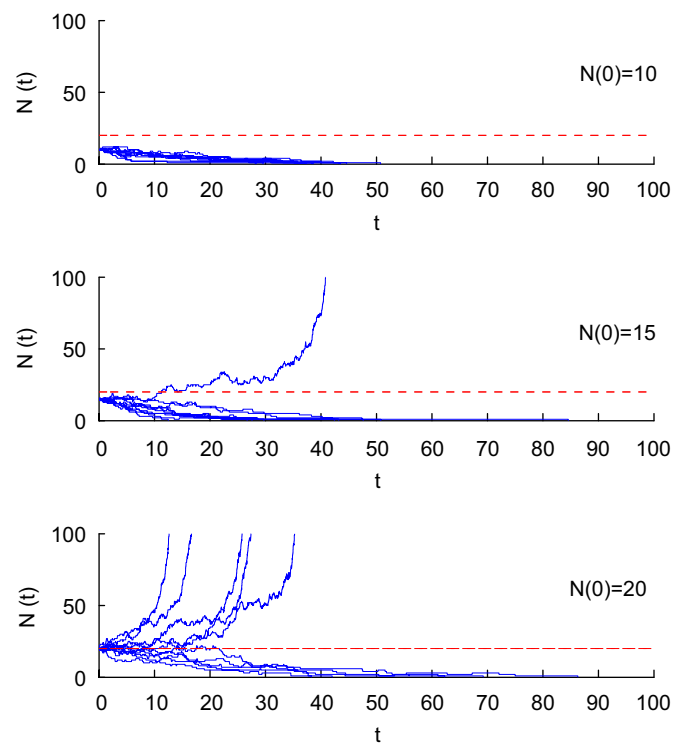

Fig. 3. Ten sample paths for a single patch stochastic Allee model with initial population sizes $N(0)=10$, 15, and 20. The dashed line represents the Allee effect threshold.

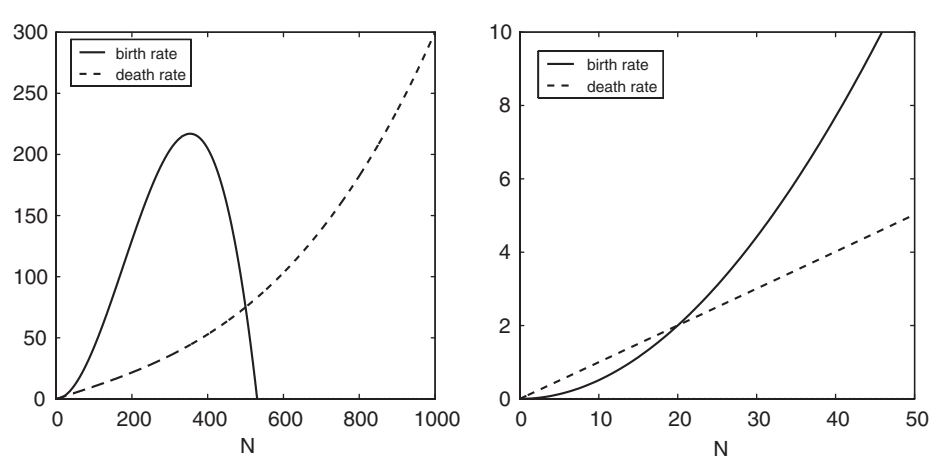

Fig. 2. Graphs (on two different x and y scales) of the birth and death rates, $b(N)$ and $d(N)$, when $E_0=20$, $K=500$, and $M=530$. Note that $b(N)<d(N)$ for $N<E_0$ and $N>K$ and $b(N)>d(N)$ for $E_0<N<K$. In addition, $b(N)>0$ for $0<N<M$.

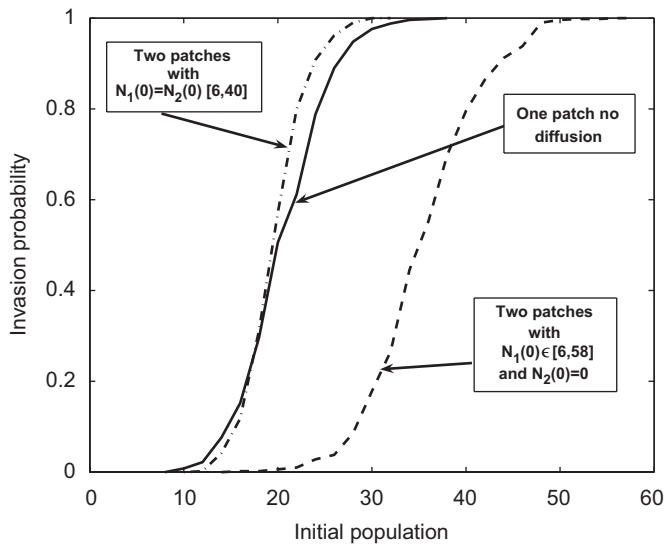

Fig. 4. A comparison of invasion probabilities for the one-patch, two-patches with equal population sizes in both patches, and two-patches with patch 2 empty.

In Fig. 4, the probability of invasion for one patch is graphed as a function of the initial population size. The graph changes concavity as the population size increases. Below the Allee threshold the graph for the probability of invasion is concave upward but as the initial population size increases beyond this value, the concavity changes. This change in concavity has already been demonstrated by Dennis (1989, 2002) for a single patch. Below the Allee threshold, the probability of invasion is still positive (unlike the deterministic model), but is much smaller than without an Allee threshold (where the graph would be concave downward).

Next, we investigate the probability of invasion with two patches. Suppose each patch has the same carrying capacity, $K = 500$, and the same extinction threshold, $E_0 = 20$ and let $m_{12} = m_{21} = 0.2$. To illustrate how invasion success depends on the initial population sizes in two patches, we estimated the probability of invasion in two patches with two sets of initial conditions. In the first set of initial conditions, the initial population sizes in the two patches are equal, $N_1(0) = N_2(0)$ in the range $[6, 40]$ and in the second set, the initial population size in patch 2 is fixed at zero but the initial population size in patch 1 is in the range $[6, 58]$. It is worth pointing out that from Fig. 1 one can see that for the first set of initial conditions, the initial population sizes $N_1(0) = N_2(0) < 20$ are in the basin of attraction of $(0, 0)$ and $N_1(0) = N_2(0) > 20$ are in the basin of attraction of (K, K) for the deterministic model (2.5). As for the second set of initial conditions, the phase-plane diagram (Fig. 1) shows that initial population sizes $N_1(0) < 37$ and $N_2(0) = 0$ are in the basin of attraction of $(0, 0)$ and the initial population sizes $N_1(0) > 37$ and $N_2(0) = 0$ are in the basin of attraction of (K, K) for the deterministic model (2.5). These invasion curves are plotted against those for the single patch model in Fig. 4. Note that when $N_1(0) = 20 = N_2(0)$ this figure shows a probability of invasion around 0.6 while when $N_1(0) = 40$ and $N_2(0) = 0$ this figure shows a probability of invasion around 0.8. When a species invasion is successful in one patch, it is successful in the second patch (for the migration rate $m_{jk} = 0.2$). Therefore, two patches with equal number in each patch have a greater chance of a successful invasion than one patch when their numbers are close to or above the Allee threshold. However, when one patch is empty (in the two patch case) it acts as a sink and unless the number in the occupied patch is much larger than the Allee threshold, the chance of a successful invasion in one of the two patches is very small.

The probability of a successful invasion depends on the dispersal rates m_{kj} but does not depend on K provided $K \gg E_0$. Invasive species are generally very good at dispersing to new regions. If the dispersal rates are sufficiently small relative to the other parameters, then if the initial population sizes are small in all patches with the exception of one patch, the results concerning invasion are similar to the single patch model. On the other hand, if the dispersal rates are sufficiently large, then if the initial population sizes are small in all patches with the exception of one patch, the patches with small initial population sizes act as a sink.

In the next set of examples, we study the effect of migration rates in a three-patch model.

3.2.2. Three patches with different migration rates

In this section, we are interested in understanding how migration rates affect the number of invaded patches during a large time interval. In a three-patch network, the dispersal rates were set equal between all patches, either $m_{kj} = 0.001$ or $m_{kj} = 0.01$, $k \neq j$. Let $T = 100$ (a sufficiently large time), a sample path is stopped in this simulation if one of the following three conditions is met: (1) $N_i(t) = 0$ for $t \in (0, T]$ and $i = 1, 2, 3$ (i.e., extinction for all three populations), (2) $N_i(t) > K/2$ for $t \in (0, T]$ and $i = 1, 2, 3$ (invasion for all three populations), and (3) $t \geqslant T$ (stopping time reached). Four different initial conditions were chosen near the Allee threshold, $N_i(0) = 14, 16, 18, 20$ for $i = 1, 2, 3$. Let $P_i =$ probability of invasion of i patches, $i = 0, 1, 2, 3$. Then for low migration rates, $m_{kj} = 0.001$, we found that if invasion is successful, one or more than one patch can be invaded, $P_i > 0$ for $i = 0, 1, 2, 3$ (Fig. 5). However, for larger migration rates, $m_{kj} = 0.01$, either there was no successful invasion or all patches were invaded, $P_0 > 0$, $P_3 > 0$, and $P_i = 0$, $i = 1, 2$ (Fig. 6). For larger migration rates, $m_{kj} > 0.01$, the results are similar to Fig. 6.

Thus, for very low migration rates, a patchy distribution of invasion may be observed, where only some of the patches are occupied. However, for intermediate to high migration rates, a successful invasion means all patches will eventually be invaded.

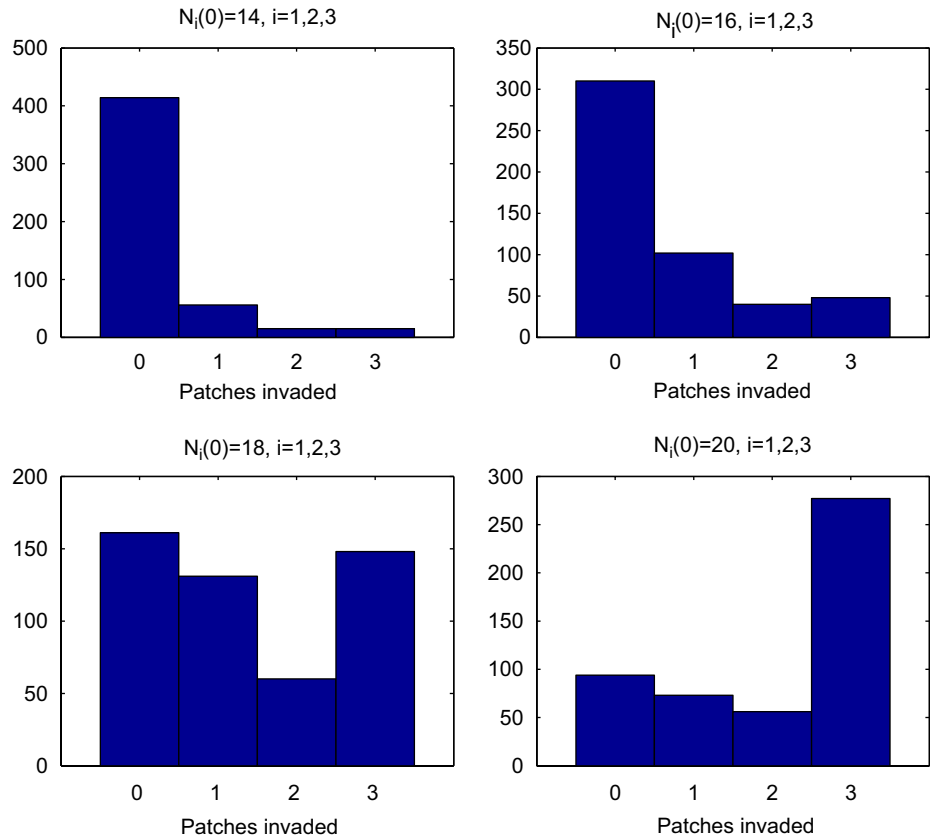

Fig. 5. Frequency histogram of invasion of i patches $i = 1, 2, 3$ based on 500 simulations when $m_{kj} = 0.001$, $k \neq j$.

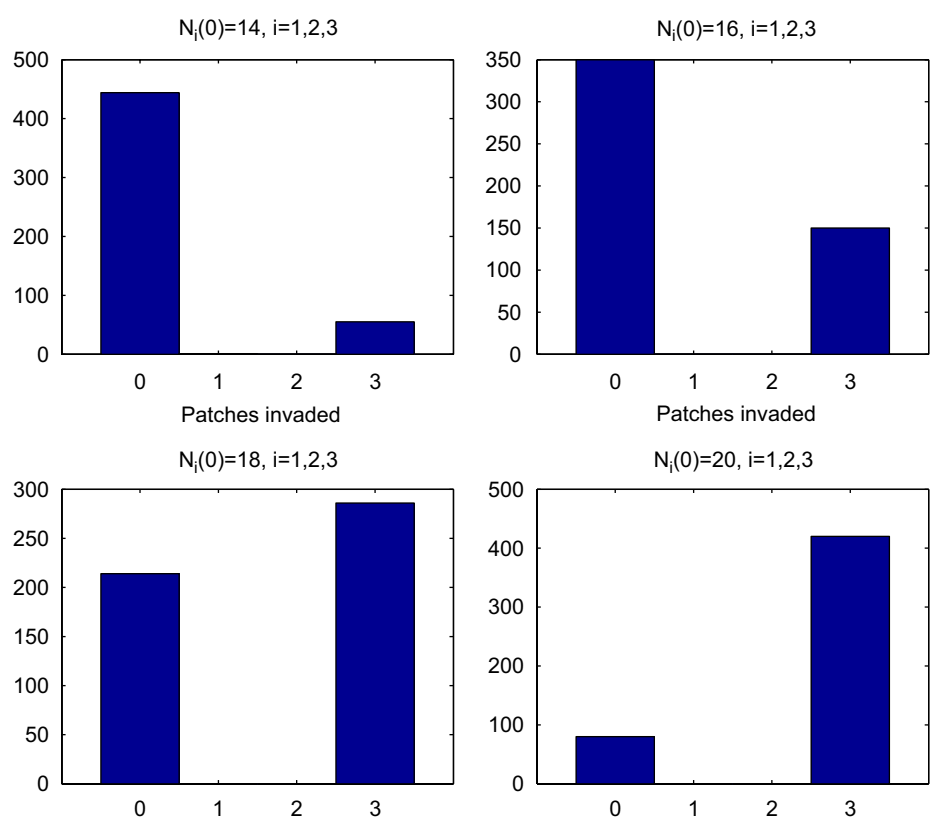

Fig. 6. Frequency histogram of invasion of i patches $i = 1, 2, 3$ based on 500 simulations when $m_{kj} = 0.01$, $k \neq j$.

In the remaining examples, we examine more closely the probability of invasion in the stochastic Allee patch model when the spatial structure is more complex.

3.2.3. Three, four and nine patches

Introductions often occur in multiple places creating discrete patches or networks across the landscape. We tested invasion success in three, four and nine-patch models. For $n = 3, 4, 9$ patches we assumed that all patches are connected and that $m_{kj} = 0.2/(n-1)$ $k \neq j$. Thus the total rate of movement out of each patch $\sum_{k \neq j} m_{kj} = 0.2$. Based on the previous simulations for the three-patch model, a successful invasion for migration rates $m_{kj} = 0.1$ means all patches are invaded. All patches were initialized at the start of the simulation with the same number of individuals in each patch, with numbers ranging from 6 to 40. Our objective is to compare how the number of introductions (number of patches) affect invasion success when the total size of the introduced population varies (but is equal in all patches).

Fig. 7 shows the probability of invasion (at least one patch is invaded) as a function of the initial population size. A one-patch network is included for comparison. Once again we point out that based on previous simulations (Fig. 6) invasion of one patch for such values of migration rates means all patches are eventually invaded. All curves in Fig. 7 exhibit a sigmoid shape, similar to those in Fig. 4. Note that as the number of patches increases in any given network, the probability of an invasion increases as well, provided the initial population size is not significantly below the Allee threshold. This was also shown for the two-patch model in Fig. 4. Therefore, the greater the number of donor patches with sufficient initial population size, the greater the probability that at least one patch will be invaded.

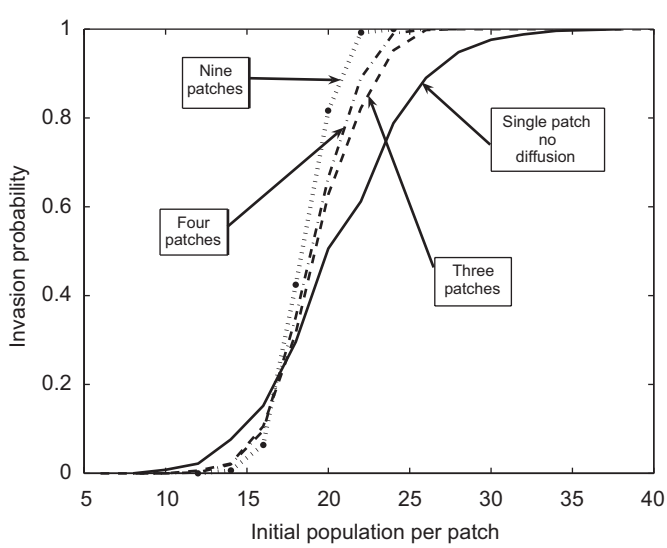

Fig. 7. A comparison of invasion probabilities for the one-patch, three-patch, four-patch and nine-patch models given that each patch has the same initial population size. Assumption (H1) is satisfied for all models.

In addition, we simulated a stochastic nine-patch model, where the underlying deterministic model did not satisfy assumption (H1). However, we assume the same total rate of movement out of each patch $\sum_{k \neq j} m_{kj} = 0.2$, which agrees with the previous models. We also assume that migration takes place only between neighboring patches, where the total rate of movement out of a patch is divided equally between all the neighboring patches. We arrange the nine patches as an array of three rows and three columns. For this arrangement a patch may have two, three or four neighbors. Thus, if a patch j has three neighbors i, h and l then $m_{ij} = m_{hj} = m_{lj} = 0.2/3$ and $m_{kj} = 0$ for $k \neq i, h, l$.

The probability of invasion for the two nine-patch models are compared in Fig. 8. The nine-patch model satisfying assumption (H1) is a fully connected network, whereas each patch in the nine-patch model that does not satisfy assumption (H1) is connected only to two, three or four neighbors. Notice that with fewer connections, the probability of invasion is greater (even though the total migration rate out of each patch is the same).

4. Discussion

There have been many models of invasion or extinction that have incorporated an Allee effect (e.g., Dennis, 1989, 2002; Veit and Lewis, 1996; McCarthy, 1997; Shigesada and Kawasaki, 1997; Amarasekare, 1998, 2004; Gyllenberg et al., 1999; Berec et al., 2001; Greene and Stamps, 2001; Petrovskii et al., 2002; Wang et al., 2002; Greene, 2003; Hui and Li, 2003; Liebhold and Bascompte, 2003; Petrovskii and Li, 2003; Schreiber, 2003; Zhou et al., 2004). What distinguishes our model from the others is that we focus on the combined effects of stochasticity, the Allee threshold

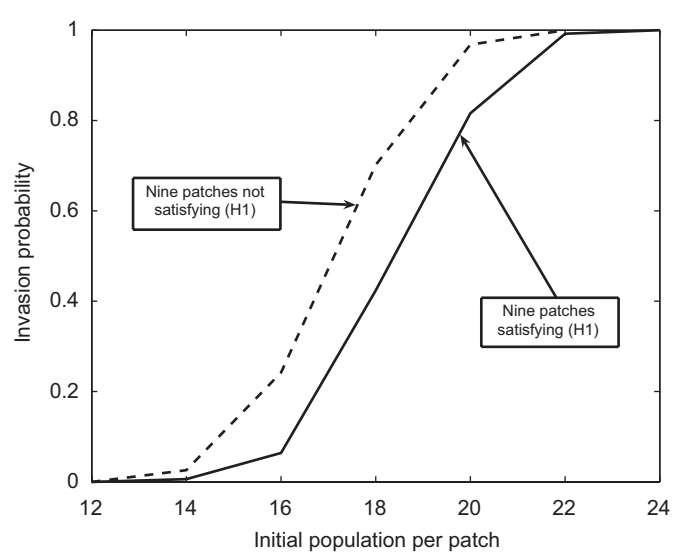

Fig. 8. A comparison of invasion probabilities for the nine-patch models given that each patch has the same initial population size. The nine-patch model satisfying assumption (H1) is a fully connected network with eight neighbors per patch but for the nine-patch model not satisfying assumption (H1) each patch has only two, three or four neighbors.

and multiple patches. We concentrate on the initial phase of the invasion and how the Allee effect may affect establishment, rather than how the Allee effect affects the propagation of an already established invasive population.

Our model demonstrates that populations with initial population sizes below their Allee effect threshold can still become established and invasive if stochastic processes affect life history parameters. The closer the population is to its Allee effect threshold, the greater the probability of invasion. Populations at the threshold in a single patch have a 50:50 chance of becoming established. As populations grow larger than the threshold the probability of extinction rapidly approaches zero (see Fig. 4). The larger the network of patches, where all patches start out occupied but below the Allee effect threshold, the greater the probability of establishing an invasion. This is true even though dispersal from an under-populated patch increases the probability of that patch going extinct. When initial population sizes are far below the Allee effect threshold, the probability of invasion for a network of patches is less than for a single patch (Fig. 7), but these values are small, and their differences are slight.

Probability of invasion in one or more than one patch depends on the size of the local population and the rate of migration. In our model, with high migration rates all patches are invaded, whereas with low migration rates only a few patches may be invaded. The distribution of occupied patches is spatially homogeneous for high migration rates but heterogeneous for low migration rates (Figs. 5 and 6). Migration rates and local population size were also shown to be important in population persistence and spatial heterogeneity in the models of Amarasekare (1998), Gyllenberg et al. (1999) and Greene (2003). In the spatially implicit metapopulation model of Amarasekare (1998), the availability of suitable habitat and the number of occupied patches are important for persistence. Gyllenberg et al. (1999) showed that a combination of the Allee effect, migration intensity, and nonlocal competition can lead to spatial heterogeneous patches. In the model of Greene (2003), habitats are selected according to their suitability reducing the possibility of extinction in a metapopulation.

Local population size has been known to be very important in the invasion process since the work of Kierstead and Slobodkin (1953). The "critical patch size" was first described by Kierstead and Slobodkin (1953) in a reaction–diffusion model. The patch size must be sufficiently large for the population to survive and overcome the diffusive effects of random diffusion (see e.g., Cantrell and Cosner, 2003; Okubo and Levin, 2001; Petrovskii and Li, 2006). In our models, an introduction into one patch in a multi-patch system has a much smaller probability of invasion than multiple introductions or than an introduction into a one-patch system (Fig. 4). But as the local population sizes increase so does the probability of invasion. The distribution of occupied patches becomes skewed as the migration rate increases so that a large proportion of patches are occupied.

Connectivity also affects invasion success as shown in Fig. 8. The nine-patch model with fewer connections but with the same migration rate out of a patch as a fully connected nine-patch model has a higher probability of invasion success. With multiple introductions, the probability of invasion increases with the number of suitable habitats but it increases even more with fewer connections among these habitats. The Allee effect acts as a "sink" resulting in more extinctions when there are more connections.

Because of the stochastic nature of population dynamics and because most invasive populations are introduced at low numbers in multiple locations, it might be expected that species subject to an Allee effect would never become established unless the initial introduction provided sufficient numbers to place the species above the Allee effect threshold; however, populations can overcome this Allee effect threshold if their birth and death rate dynamics have stochastic properties. Thus a "good" year could push a small population that would otherwise eventually go extinct, above the Allee effect threshold resulting in a successful invasion. The oft-noted unpredictable lag time from the initial introduction to an establishment as an invasive species may simply be caused by the combination of an Allee effect and stochastic population processes (Figs. 4 and 7).

Finally, we point out that although the focus of our paper is on invasion, from a conservation biology viewpoint our results also show that multiple introductions and stochasticity increase the probability of establishment of a population with initial number below but near the Allee effect. This result is in contrast to a deterministic model, where the population would go extinct for such initial population numbers.

In this investigation, we have examined the effects of initial conditions, migration rates, and number of suitable patches. We did not extensively examine the model's sensitivity to functions such as birth and death rates (Eqs. (2.2) and (2.3)). In a future report we plan to examine the model's sensitivity to those functions as well as the effect of network re-inoculation. A limitation of this model is that it treats invasions as simultaneous and homogeneous throughout the patch network. Real introductions are more likely to be patchy both in time and space. We plan to explore the implications of multiple introductions in time and space in the future.

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References

Allee, W.C., 1931. Animal Aggregations, a Study in General Sociology. University of Chicago Press, Chicago, IL.

Allen, L.J.S., 2003a. An Introduction to Stochastic Processes with Applications to Biology. Prentice-Hall, Upper Saddle River, NJ.

Allen, L.J.S., 2003b. Risk of population extinction due to demographic stochasticity in population models. Comments Theor. Biol. 8, 433–454.

Allen, L.J.S., Allen, E.J., 2003. A comparison of three different stochastic population models with regard to persistence time. Theor. Popul. Biol. 64, 439–449.

Amarasekare, P., 1998. Interactions between local dynamics and dispersal: insights from single species models. Theor. Popul. Biol. 53, 44–59.

Amarasekare, P., 2004. Spatial dynamics of mutualistic interactions. J. Anim. Ecol. 73, 128–142.

Berec, L., Boukal, D.S., Berec, M., 2001. Linking the Allee effect sexual reproduction, and temperature-dependent sex determination via spatial dynamics. Am. Nat. 157, 217–230.

Cantrell, R.S., Cosner, C., 2003. Spatial Ecology via Reaction–Diffusion Equations. Wiley, Chichester, England.

Carlton, J.T., Geller, J.B., 1993. Ecological Roulette: the global transport of non-indigenous marine organisms. Science 261, 78–82.

Carter, J., Leonard, B.P., 2002. A review of the distribution, spread, of, and efforts to eradicate the coypu worldwide (*Myocastor coypus*). Wildlife Soc. Bull. 30, 162–175.

Dennis, B., 1989. Allee effects, population growth critical density and the chance of extinction. Nat. Resour. Modeling 3, 481–538.

Dennis, B., 2002. Allee effects in stochastic populations. Oikos 96, 389–401.

Drake, J.A., Mooney, H.A., di Castri, F., Groves, H., Kruger, F.J., Rejmanek, M., Williams, M. (Eds.), 1989. Biological Invasions: A Global Perspective. Wiley, New York.

Edsall, T.A., Mills, E.L., Leach, J.H., 1995. Exotic species in the Great Lakes. In: LaRoe, E.T., Farris, G.S., Puckett, C.E., Doran, P.D., Mac, M.J. (Eds.), Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. U.S. Department of the Interior, National Biological Service, Washington, DC, pp. 442–444.

Fagan, W.F., Lewis, M.A., Neubert, M.G., van den Driessche, P., 2002. Invasion theory and biological control. Ecol. Lett. 5, 148–157.

Gordon, D.R., Thomas, K.P., 1997. Florida's invasion by nonindigenous plants: history, screening, and regulation. In: Simberloff, D., Schmitz, D.C., Brown, T.C. (Eds.), Strangers in Paradise. Island Press, Washington, DC, pp. 21–37.

Greene, C., Stamps, J.A., 2001. Habitat selection at low population densities. Ecology 82 (8), 2091–2100.

Greene, C.M., 2003. Habitat selection reduces extinction of populations subject to Allee effect. Theor. Popul. Biol. 64, 1–10.

Gyllenberg, M, Hemminki, J., Tammaru, T., 1999. Allee effects can both conserve and create spatial heterogeneity in population densities. Theor. Popul. Biol. 56, 231–242.

Hanski, I., Ovaskainen, O., 2003. Metapopulation theory for heterogeneous fragmented landscapes. Theor. Popul. Biol. 64, 119–127.

Hanski, I.A., Simberloff, D., 1997. The metapopulation approach, its history, conceptual domain and application to conservation. In: Hanski, I.A., Gilpin, M.E. (Eds.), Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, New York, pp. 5–26.

Hengeveld, R., 1989. Dynamics of Biological Invasions. Chapman & Hall, London.

Henle, K., Sarre, S., Wiegand, K., 2004. The role of density regulation in extinction processes and population viability analysis. Biodiversity Conserv. 13, 9–52.

Higgins, S.I., Richardson, D.M., 1998. Pine invasions in the southern hemisphere: modeling interaction between organism, environment and disturbance. Plant Ecol. 135, 79–93.

Hui, C., Li, Z., 2003. Dynamical complexity and metapopulation persistence. Ecol. Modelling 164, 201–209.

Karlin, S., Taylor, H.M., 1975. A First Course in Stochastic Processes, second ed. Academic Press, New York.

Kierstead, H., Slobodkin, L.B., 1953. The size of water masses containing plankton bloom. J. Mar. Res. 12, 141–147.

Liebhold, A., Bascompte, J., 2003. The Allee effect, stochastic dynamics and the eradication of alien species. Ecol. Lett. 6, 133–140.

Lodge, D.M., 1993. Biological invasions: lessons for ecology. Trends Ecol. Evol. 8, 133–137.

Lowery Jr., G.H., 1974. The Mammals of Louisiana and its Adjacent Waters. Louisiana State University Press.

Ludsin, S.A., Wolfe, A.D., 2001. Biological invasion theory: Darwin's contributions from The Origin of Species. Bioscience 51, 780–789.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. 10, 689–710.

Malecki, R., 1995. Purple loosestrife. In: LaRoe, E.T., Farris, G.S., Puckett, C.E., Doran, P.D., Mac, M.J. (Eds.), Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems. U.S. Department of the Interior, National Biological Service, Washington, DC, pp. 458–459.

McCarthy, M.A., 1997. The Allee effect, finding mates and theoretical models. Ecol. Modelling 103, 99–102.

Moyle, P.B., Light, T., 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biol. Conservation 78, 149–161.

Okubo, A., Levin, S.A., 2001. Diffusion and Ecological Problems Modern Perspectives. Springer, New York.

Ovaskainen, O., Hanski, I., 2001. Spatially structured metapopulation models: global and local assessment of metapopulation capacity. Theor. Popul. Biol. 60, 281–302.

Ovaskainen, O., Hanski, I., 2004. From individual behavior to metapopulation dynamics: unifying the patchy population and classic metapopulation models. Am. Nat. 164, 364–377.

Owen, M.R., Lewis, M.A., 2001. How predation can slow, stop or reverse a prey invasion. Bull. Math. Biol. 63, 655–684.

Petrovskii, S., Li, B., 2003. An exactly solvable model of population dynamics with density-dependent migrations and the Allee effect. Math. Biosci. 186, 79–91.

Petrovskii, S., Li, B.-L., 2006. Exactly Solvable Models of Biological Invasion. In: Mathematical Biology and Medicine Series. Chapman & Hall/CRC, Boca Raton, London.

Petrovskii, S., Morozov, A., Li, B.-L., 2005. Regimes of biological invasion in a predator–prey system with the Allee effect. Bull. Math. Biol. 67, 637–661.

Petrovskii, S.V., Morozov, A.Y., Venturino, E., 2002. Allee effect makes possible patchy invasion in a predator–prey system. Ecol. Lett. 5, 345–352.

Schreiber, S.J., 2003. Allee effects, extinctions, and chaotic transients in simple population models. Theor. Popul. Biol. 64, 201–209.

Shigesada, N., Kawasaki, K., 1997. Introduction. In: Shigesada, N., Kawasaki, K. (Eds.), Biological Invasions: Theory and Practice. Oxford University Press, New York, USA, pp. 1–5.

Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What is the Allee effect? Oikos 87, 185–190.

Veit, R.R., Lewis, M.A., 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern north America. Am. Nat. 48, 255–274.

Wang, M.H., Kot, M., Neubert, M.G., 2002. Integrodifference equations, Allee effects, and invasions. J. Math. Biol. 44, 150–168.

Zhou, S.R., Liu, C.Z., Wang, G., 2004. The competitive dynamics of metapopulation subject to the Allee-like effect. Theor. Popul. Biol. 65, 29–37.