



Dispersal effects on a discrete two-patch model for plant–insect interactions

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ABSTRACT

A two-patch discrete time plant–insect model coupled through insect dispersal is studied. The model is based on three different phases: Plant growth is followed by the dispersal of insects followed by insect attacks. Our objective is to understand how different intensities of dispersal impact both local and global population dynamics of the two-patch model. Special attention is paid to two situations: When the single-patch model (i.e., in the absence of dispersal) is permanent and when the single-patch model exhibits Allee-like effects. The existence and stability of synchronous and asynchronous dynamics between two patches is explored. If the single-patch system is permanent, the permanence of the system in two patches is destroyed by extremely large dispersals and large attacking rates of insects, thus creating multiple attractors. If the single-patch model exhibits Allee-like effects, analytical and numerical results indicate that small intensity of dispersals can generate source–sink dynamics between two patches, while intermediate intensity of dispersals promote the extinction of insects in both patches for certain parameter ranges. Our study suggests a possible biology control strategy to stop the invasion of a pest by controlling its migration between patches.

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1. Introduction

The expansion of alien insects as a function of their population dynamics has been extensively studied by ecologists for decades due to the fact that biological invasions are among the most significant threats to the stability of natural and agricultural ecosystems (Liebhold et al., 1995). When alien insects invade a new area, the success of expansion and its rate of spreading are determined by the interplay of dispersal, population growth, interactions with other species and environmental heterogeneity (Kawasaki and Shigesada, 2007). For alien insects that feed on plants (herbivores), studying the population dynamics of the interactions between plants and insects combined with the migration of insects can be crucial for ecologists to understand how alien insects succeed in expanding local established population to nearby new regions. An alien insect is in the establishment stage if its growth phase of the population density is above some threshold for which it is usually assumed that the natural extinction is highly unlikely. An alien insect population is in the expansion stage if the population is established in a local region and starts to spread to nearby new regions. During the expansion stage, the population may expand in space through dispersal without a significant increase in size, resulting in a drop of its

density. This might pose the risk of extinction for species subject to an Allee effect or Allee-like effect. An Allee effect refers to a process that leads to decreasing net population growth with decreasing density, thus inducing the existence of an Allee threshold below which populations are driven toward extinction (Liebhold and Tobin, 2008). The Allee-like effect, first introduced by Amarasekare (1998), refers to a metapopulation-level Allee effect (Amarasekare, 2004; Zhou and Wang, 2004; Zhou et al., 2005), where the colonization rate for new suitable patches is disproportionately reduced when the level of occupancy is low. In this article, we extend the concept of Allee-like effects to processes that involve predator–prey interactions (e.g., plant and alien insect) where fluctuating population of prey cause local extinction of predators when the predator population is low enough. Kang et al. (2008) studied a discrete plant–herbivore model which exhibits an Allee-like effect, i.e., initial population densities of plants and herbivores determine whether the herbivore population exists in the long run for a specific set of parameter values. There are many other studies of discrete two-species systems supporting such Allee-like effects (e.g., Kon, 2006; Kuang and Chesson, 2008). Both Allee effects and dispersal of insects are central to a better understanding of why some alien insects successfully expand into new geographical areas. Recently there has been a growing recognition of the importance of these two components in biological invasions (Drake, 2004; Leung et al., 2004; Taylor and Hastings, 2005; Ackleh et al., 2007; Kang and Lanchier, in press). Understanding the impact that Allee effects and dispersal have on insect demographics is of critical importance to gain insight into

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why some particular alien insects are more invasive than others. From this we may suggest some proper biological control strategies to regulate undesirable populations (Liebhold and Tobin, 2008).

Our study is motivated by invasive forest pests. In general, forest pests have strong seasonal life cycles leading to a discrete time model of their population dynamics. Kang et al. (2008) have studied the dynamics of the interactions between plants and insects by adopting a host–parasite model with density-dependence acting before parasitism. Such density dependencies can either be permanent or exhibit Allee-like effects depending on the range of parameter values. We are interested in studying how implementing insect dispersal into new areas will affect insect populations based on a variety of parameter values. It is of specific importance to investigate whether or not insects can successfully expand to new areas and then maintain a significant population level. Assuming an alien insect has established its population in one area, i.e., either the single-patch plant–insect system is permanent (i.e., plants and insects coexist for any strictly positive initial conditions) or the population densities of plants and insects are above the Allee-like threshold in this area, then the first step of population expansion is to spread its population to a nearby new area where the insects are absent. A natural way to model this situation is to consider a two identical patch model (i.e., two patches have the same values of parameters) with heterogeneous initial conditions such that

1. both patches are coupled through the dispersal of insects, and
2. in the absence of insect dispersal, i.e., when the patches are uncoupled, the initial conditions lead to establishment of the insect population in one patch and extinction of insects in the other patch.

This approach has been used previously by Adler (1993). In this article, we follow this modeling strategy to study the impact of the different intensities of insects' dispersals on the dynamics of the coupled two-patch discrete plant–insect model analytically and numerically. More specifically, we would like to seek answers to the following questions:

1. When the single-patch plant–insect system is permanent, what kind of dispersal can make sure that plant and insect coexist in both patches for all strictly positive initial conditions?
2. When the single-patch plant–insect system exhibits Allee-like effects, then what kind of dispersal can generate source–sink dynamics in the coupled two-patch system and what kind of dispersal combined with Allee-like effects can promote the extinction of insect in both patches, i.e., not only stop the expansion to new areas but also eradicate the insect population in the established ones?

There is a copious amount of literature on patch models (e.g., Maynard Smith and Slatkin, 1973; Allen, 1975; Holt, 1985; Reeve, 1988; Taylor, 1988; Adler, 1993; Gyllenberg et al., 1993; Hastings, 1993; Doebeli, 1997; Yakubu, 2000; Amarasekare, 2000; Yakubu and Castillo-Chavez, 2002; Holt et al. 2004; also see a review paper by Briggs and Hoopes, 2004; and references therein; Selgrade and Roberds, 2005; Kang and Lanchier, in press). Only a few are discrete two-species-interacting models in a patchy environment (e.g., Maynard Smith and Slatkin, 1973; Allen, 1975; Reeve, 1988; Taylor, 1988; Adler, 1993; Doebeli, 1997; Yakubu, 2000; Yakubu and Castillo-Chavez, 2002; Selgrade and Roberds, 2005). Maynard Smith and Slatkin (1973), as well as Allen (1975) and Reeve (1988) show that the unstable equilibrium of a single-patch predator–prey model cannot be stabilized by diffusive coupling with identical patches, since the coupled system behaves

identically to the single-patch system if the patches are synchronized. Taylor (1988) proposed that heterogeneity among patches, low but non-zero migration rates and large numbers of patches are three mechanisms that maintain the asynchrony of populations among patches. Thus, maintenance of asynchrony among populations large enough to avoid extinction determines the persistence of coupled locally unstable systems (Adler, 1993). Adler (1993) numerically showed that two identical patches of deterministic Nicholson–Bailey models coupled by migration can maintain bounded oscillations. Doebeli (1997) showed that genetic variability reduces extinction probabilities and can lead to persistence in the Nicholson–Bailey models. Yakubu (2000) studied a discrete time predator–prey model of Comins and Hassell (1976) that includes dispersion in a patchy habitat. His study showed that in a two-patch system, the prey species with a high average growth rate dominates the system by driving all the prey species with low average growth rates to extinction. Yakubu and Castillo-Chavez (2002) studied the effects of synchronous dispersal on discrete-time metapopulation dynamics with local patch dynamics of the same compensatory, overcompensatory, or mixed types. They showed that dispersal gives rise to multiple attractors with complex basin structures. Selgrade and Roberds (2005) investigated a four-dimensional system of non-linear difference equations tracking allele frequencies and population sizes for a two-patch meta-population model. They studied the meta-population stability, instability and bistability, as well as found that differentially greater migration into a stable patch results in meta-population stability.

Although we formulate a discrete plant–insect interaction two-patch model following the approach of Adler (1993), our study is different from others and our results are new. We particularly study how different intensities of the dispersal of insects affect the global and local dynamics of the two-patch model. Our analytical results show that in the case when the single-patch model is permanent, the two-patch model can maintain the permanence in both patches if dispersal is small, while large dispersal and large attacking rate of insects leads to a local extinction of insects in one patch. In the case when the single-patch model exhibits an Allee-like effect, the small intensity of dispersal generates a source–sink dynamic. Our numerical simulations suggest that the intermediate intensity of the dispersal promotes the extinction of insects in both patches for almost all positive initial conditions. This may suggest a control strategy to regulate the population of invasive forest pests and stop their spreading.

The rest of the article is organized as follows. In Section 2, we formulate a discrete two-patch plant–insect interaction model and identify the objectives of the study. In Section 3, we study the impact of the dispersal to the local dynamics, e.g., the number of the equilibrium points and their stabilities. In Section 4, we study the impact of the dispersal on the permanence of the two-patch system. In Section 5, we study the impact of the small intensity of the dispersal combined with Allee-like effects on the two-patch system. In Section 6, we numerically study the impact of the intermediate intensity of the dispersal combined with Allee-like effects on the two-patch system and apply our findings to suggest an explanation why the spread of the gypsy moth population retreats in some years. Finally, Section 7 is the conclusion and future studies. The appendix provides the proofs.

2. Model formulation

The plant–herbivore models studied by Kang et al. (2008) demonstrate plant–herbivore dynamics through their biomass changes by assuming that the herbivore population growth is a non-linear function of herbivore feeding rate, and that the plant

population growth decreases gradually with increasing herbivores. In the absence of the herbivore, they allow for a density-dependent growth rate in the plant since the plant population density is regulated by intraspecific competition. Let P_n represent the plant population biomass after the attacks by the insect (herbivore) but before its seasonal defoliation. Let H_n represent the biomass of the insect (herbivore) before it dies at the end of season n . There are two parameters in the model. Namely r , which is a constant describing the maximum growth rate of plants (leaves, more specifically) and a is a constant that correlates with the total amount of the biomass that the herbivores consume:

$$P_{n+1} = P_n e^{r(1-P_n)-aH_n} \tag{1}$$

$$H_{n+1} = P_n e^{r(1-P_n)} [1 - e^{-aH_n}] \tag{2}$$

Kang et al. (2008) show that the dynamics of model (1) and (2) include permanence of two species, Neimark–Sacker bifurcation and crisis of strange attractors. In particular, this system shows Allee-like effects for certain parameter ranges. For instance, if the system (1)–(2) has a locally stable interior steady state with $2 < r < 2.52$ and $a^2 P_1 P_2 < 1$ (where $P_i, i=1,2$ is a period-2 orbit of Ricker’s map $P_{n+1} = P_n e^{r(1-P_n)}$), then the system (1)–(2) can exhibit Allee-like effects. The Allee-like threshold can be represented as $\theta(P_0, H_0)$ which is a curve in \mathbb{R}_+^2 . Figs. 2 and 3 gives dynamics and the Allee-like threshold when $r=2.45$ and $a=0.98$ (the Allee-like threshold is the boundary separating white and grid-shadowed area in Fig. 3, see Section 6 for more detailed illustrations).

To set up a two-patch model we have the following definitions and assumptions:

- P_n^I and H_n^I represent the density of edible plant biomass and the population density of insects respectively in Patch I at generation n . Similarly, P_n^{II} and H_n^{II} represent the density of plants and insects respectively in Patch II at generation n . Both patches have identical values of the parameters r and a .
- There are three distinct temporal phases: the growth phase of the plant, followed by the dispersal phase of the insect, followed by the feeding phase of the insect. This is a very important assumption as it distinguishes the discrete time model from a similar differential equation model. Any differential equation model that incorporates such well defined temporal phases will have to be non-autonomous. Clearly, any cyclic permutation of the three phases will lead to the same dynamic behavior; however, any interchange of two phases will lead to a different model.
- We assume that the insect is the only species that disperses. Let $l \in (0, 1)$ be the fixed fraction of the insect population leaving its patch. The net effect on a patch is density-dependent since the patch above the mean density always loses insects, whereas those below it receive them. There are lH_n^I insects leaving Patch I during generation n and lH_n^{II} insects entering Patch I at the same time. The net change of the insect population in Patch I is given as

$$H_{n+d}^I = H_n^I - lH_n^I + lH_n^{II} = (1-l)H_n^I + lH_n^{II}$$

l can also be interpreted as a parameter measuring the barrier between two patches. The smaller the l , the more difficult for insects to disperse or the greater the distance between the two patches.

Let H_{n+d}^I, H_{n+d}^{II} be the population of insects in Patch I and II respectively after the dispersal during generation n , i.e.,

$$H_{n+d}^I = (1-l)H_n^I + lH_n^{II} \tag{3}$$

$$H_{n+d}^{II} = (1-l)H_n^{II} + lH_n^I \tag{4}$$

Then the population of plants and insects in Patch I and II at generation $n+1$ can be modeled by

$$P_{n+1}^I = P_n^I e^{r(1-P_n^I)-aH_{n+d}^I} \tag{5}$$

$$H_{n+1}^I = P_n^I e^{r(1-P_n^I)} [1 - e^{-aH_{n+d}^I}] \tag{6}$$

$$P_{n+1}^{II} = P_n^{II} e^{r(1-P_n^{II})-aH_{n+d}^{II}} \tag{7}$$

$$H_{n+1}^{II} = P_n^{II} e^{r(1-P_n^{II})} [1 - e^{-aH_{n+d}^{II}}] \tag{8}$$

where H_{n+d}^I and H_{n+d}^{II} are defined as (3)–(4). Although the system (5)–(8) is symmetric in two patches, *asymmetry* will be introduced by considering different initial conditions in each patch, i.e.,

$$(P_0^I, H_0^I) \neq (P_0^{II}, H_0^{II}).$$

If there are no plants in Patch II, then the system (5)–(8) is reduced to the following one-patch model (9)–(10) with emigration

$$P_{n+1}^I = P_n^I e^{r(1-P_n^I)-a(1-l)H_n^I} \tag{9}$$

$$H_{n+1}^I = P_n^I e^{r(1-P_n^I)} [1 - e^{-a(1-l)H_n^I}] \tag{10}$$

The system (9)–(10) can be a model describing the situation when there is a natural barrier for insects to spread to its adjacent patches. Notice that replacing a with $a(1-l)$ in (1)–(2) gives (9)–(10), thus dispersal just reduces the impact of insect’s attacking rate a . According to the bifurcation diagram on a and r of (1)–(2) in Kang et al. (2008), we can conclude that large enough dispersal stabilizes the system. For instance, in the case that $a=4$, $r=1.9$, without dispersal the system exhibits chaotic behavior, while for $l=0.65$, the system is locally stable at its interior equilibrium (0.37,0.85) (see Fig. 1). Partial results in Theorem 3.2 can also apply to this case.

We study the following two scenarios:

When the system (1)–(2) is permanent (i.e., plant and insect coexist for strictly positive initial conditions in \mathbb{R}_+^2): We say that (5)–(8) is permanent if plant and insect coexist in *both* patches for positive initial conditions

$$\{(P_0^I, H_0^I, P_0^{II}, H_0^{II}) \in \mathbb{R}_+^4 : P_0^i > 0 (i = I \text{ and } II), H_0^j > 0 (j = I \text{ or } II)\}.$$

We are interested in exploring how dispersal l affects the permanence of the coupled system (5)–(8) when $l \in (0, 1)$.

When the system (1)–(2) exhibits Allee-like effects. In this case, we are interested in how Allee-like effects combined with insects’ dispersal affect the dynamics of the coupled system (5)–(8) when one patch is initially below and the other patch above the Allee-like threshold. In this case and in the absence of dispersal, the population of herbivores goes extinct in the first patch, but establishes itself in the second one.

Our analytical results suggest the following picture of the local and global dynamics of the coupled system (5)–(8). The system has no interior equilibrium if the system (1)–(2) has no interior equilibrium, but always has four boundary equilibria (0,0,0,0), (1,0,0,0), (0,0,1,0), (1,0,1,0) where the first three are always unstable and the fourth one, (1,0,1,0), is locally stable when $0 < a < 1$ and $0 < r < 2$ (Theorem 3.1). For large values of l and sufficient values of a such that $a > 1/(1-l)$, the system can have two extra boundary equilibria $(P^0, H^0, 0, 0)$ and $(0, 0, P^0, H^0)$ which can be locally stable for a certain range of parameter values (Theorem 3.2). Thus, large values of a and extremely large intensity of dispersals l (i.e., $l > \frac{1}{2}$) can spoil permanence of the coupled system and generate multiple attractors (Theorem 4.1). If, in the absence of dispersal the system exhibits Allee-like effects, then with dispersal the coupled system also exhibits Allee-like effects (Theorem 5.1). Moreover, our study shows that Allee-like effects combined with small intensity of dispersals may generate source–sink dynamics, i.e., locally stable asymmetric interior periodic orbits (Theorem 5.2).

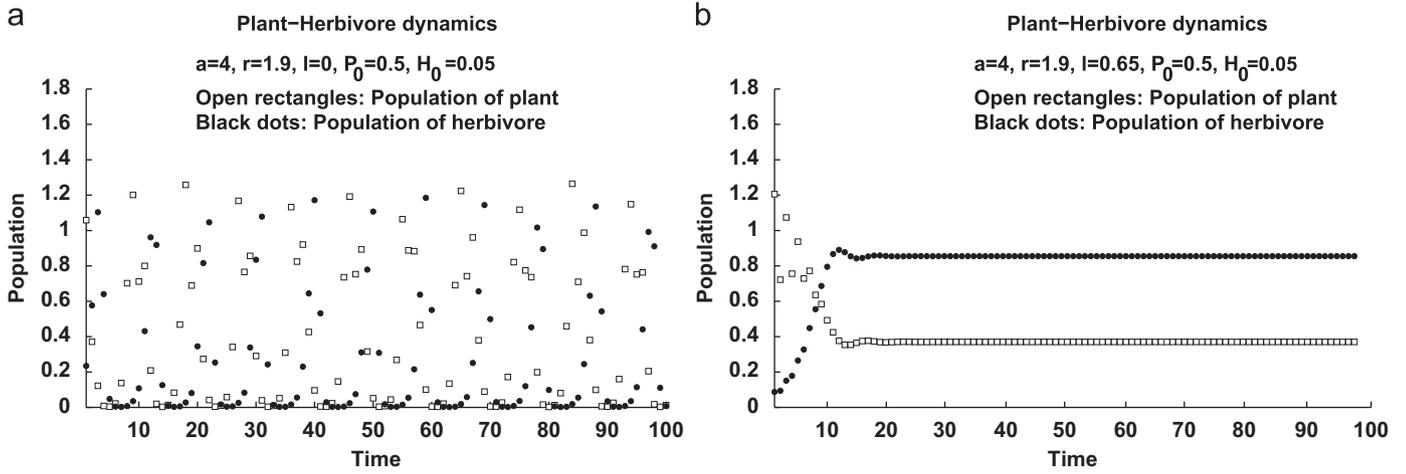


Fig. 1. An example of large dispersals l that can stabilize the system (9)–(10). (a) Chaotic dynamics of the system (9)–(10) when $a=4, r=1.9, l=0$. Open rectangles represent plant populations and black dots represent herbivore populations. (b) Stable interior equilibrium of the system (9)–(10) when $a=4, r=1.9, l=0.65$. Open rectangles represent plant populations and black dots represent herbivore populations.

Numerical simulations in Section 6 suggest that Allee-like effects combined with *intermediate* intensity of dispersals can promote the extinction of insects in both patches, when one patch is initially below and the other patch above the Allee-like threshold. These results are stated rigorously in Sections 3–5. Simulation results are given in Section 6.

3. The impact of dispersal on the local dynamics

Theorem 3.1 (Equilibria and their stability). For any positive value of parameters $a, r,$ and $l,$ the coupled system (5)–(8) always has the following four boundary equilibria:

$$(0,0,0,0), (1,0,0,0), (0,0,1,0), (1,0,1,0). \tag{11}$$

The first three boundary equilibria are always unstable and the fourth one $(1,0,1,0)$ is locally stable when

$$0 < r < 2, \quad 0 < a < 1, \quad 0 < l < 1.$$

Moreover, if the system (1)–(2) has no interior equilibrium, then the coupled system (5)–(8) has no interior equilibrium either and hence the four boundary equilibria (11) are the only equilibria in this case.

The local stability of these four boundary equilibria (11) follows from the eigenvalues of their associated Jacobian matrices at these boundary equilibria, which indicates that $(1,0,1,0)$ is not stable when $r > 2$ or $a > 1$. Let \mathbb{R}_+^n be the interior of \mathbb{R}_+^n . If the system (1)–(2) has no interior equilibrium, i.e., there is no $(P,H) \in \mathring{\mathbb{R}}_+^2$ satisfying the following two equations:

$$0 = r(1-P) - aH, \quad H = P(e^{aH} - 1)$$

excluding a symmetric interior equilibrium (P,H,P,H) .

To exclude the possibility that the coupled system may have asymmetric interior equilibria, i.e.,

$$(P^I, H^I, P^{II}, H^{II}), (P^{II}, H^{II}, P^I, H^I) \in \mathring{\mathbb{R}}_+^4 \tag{12}$$

we argue by contradiction: Assume that the coupled system has such an asymmetric interior equilibrium. Then P^I, H^I, P^{II}, H^{II} have to satisfy Eqs. (22)–(25). We can show that

$$P^I \neq P^{II}, \quad H^I \neq H^{II} \quad \text{and} \quad l \neq 1/2$$

By introducing two new variables $U^I = (1-l)H^I + lH^{II}$ and $U^{II} = (1-l)H^{II} + lH^I,$ the existence of asymmetric interior fixed points is

equivalent to the existence of fixed points of the map $F \cdot F,$ where

$$F(U) = \frac{(1-l)U}{l} + \frac{(2l-1)f(U)}{l} \quad \text{and} \quad f(U) = \left(1 - \frac{aU}{r}\right)[e^{aU} - 1]$$

However, $F \cdot F$ has no fixed point other than $U=0$ from the fact that the system (1)–(2) has no interior equilibrium. Thus, the coupled system has no asymmetric interior equilibria and therefore, the statement holds. The detailed proof is given in Appendix.

Theorem 3.2 (Interior equilibria). If (P,H) is a locally stable interior equilibrium of the system (1)–(2), then (P,H,P,H) is a locally stable interior equilibrium of the coupled system (5)–(8) if

$$2 > 1 + aPe^{aH}(1-2l)(1-rP) > |1 + P(a(1-2l)-r)|. \tag{13}$$

In the case that $a(1-l) > 1,$ the coupled system has two extra boundary equilibria

$$(P^0, H^0, 0, 0), \quad (0, 0, P^0, H^0), \quad P^0 > 0, \quad H^0 > 0$$

where P^0 and H^0 satisfy Eqs. (34) and (35). If, in addition,

$$aH^0 > r \quad \text{and} \quad 2 > 1 + aP^0 e^{a(1-l)H^0}(1-l)(1-rP^0) > |1 + P^0(a(1-l)-r)|, \tag{14}$$

then these two extra boundary equilibria are locally stable.

The condition on the existence of the extra boundary equilibria $(P^0, H^0, 0, 0), (0, 0, P^0, H^0)$ is equivalent to the condition on the existence of the interior equilibrium of the system (1)–(2) when we replace the impact parameter a by its dispersal modified version $a(1-l)$. Their stability and the stability of the symmetric interior equilibrium (P,H,P,H) can be shown from the Jury test (P57, Edelstein-Keshet, 2005). A detailed proof is given in the Appendix.

Theorem 3.2 shows that one necessary condition of the coupled system (5)–(8) to have locally stable boundary equilibria $(P^0, H^0, 0, 0), (0, 0, P^0, H^0)$ is that the inequality

$$aH^0 > r \tag{15}$$

holds, which implies that the intensity of dispersal l cannot be small since

$$H^0 < \frac{r}{a(1-l)} \Rightarrow aH^0 < al \frac{r}{a(1-l)} = \frac{lr}{1-l}$$

Thus, the inequality (15) can be true only if $l > \frac{1}{2}$. In addition, the existence of $(P^0, H^0, 0, 0)$ requires either $a(1-l) > 1$ or $r > 2$ (Kang et al., 2008), which indicates that a also should be large

enough such that (15) can hold. Therefore, extremely large values of the dispersal parameter l and insect's impact rate a promote local extinction of the insect population in one patch.

Theorems 3.1 and 3.2 imply that the existence of the interior equilibrium of the system (1)–(2) determines the existence of the interior equilibrium of the coupled system (5)–(8). In addition, Theorem 3.2 gives a necessary condition on when the coupled system has synchronized population dynamics, e.g., the locally stable symmetric interior equilibria (P, H, P, H) . It is well-known that a small dispersal causes asynchronized dynamics, e.g., source–sink dynamics (Amezcu and Holyoak, 2000; Amarasekare, 2000). Thus, it is interesting to study whether the coupled system (5)–(8) can have locally stable asymmetric interior equilibria (12) when the single-patch system (1)–(2) has an interior equilibrium (P, H) and the intensity of dispersal is small.

If the single-patch system (1)–(2) has an interior equilibrium (P, H) , then the two boundary equilibria $(0, 0)$ and $(1, 0)$ are unstable. For $l = 0$, the coupled system (5)–(8) becomes two independent systems that are identical to the system (1)–(2) and hence the equilibria

$$(0, 0, P, H), (P, H, 0, 0), (P, H, 1, 0), (1, 0, P, H) \quad \text{where } (P, H) \in \mathring{\mathbb{R}}_+^2 \quad (16)$$

are all unstable. If we increase the value of the dispersal parameter l from 0 and keep it small enough, then by perturbation theory (Levin, 1974; Hirsch and Smale, 1974; Guckenheimer and Holmes, 1983; Amarasekare, 2000, 2004), the coupled system can have asymmetric interior equilibria (12) with the same stability as (16). Thus, we have the following remark:

Remark. If dispersal l is small enough, then the coupled system (5)–(8) has no locally stable asymmetric interior equilibria (12).

4. Extremely large dispersals can spoil permanence and promote multiple attractors

In this section, we study the impact of dispersal on the global dynamics of the coupled system (5)–(8). The following theorem gives some insight on how extremely large dispersals l affect the permanence of the coupled system. Here we consider the dispersal l is extremely large if it is greater than $\frac{1}{2}$.

Theorem 4.1 (Permanence and multiple attractors). Assume that $0 < r \leq 2$ and $a(1-l) > 1$. Then

1. the system (9)–(10) is permanent with (P^0, H^0) as its unique interior equilibrium. If, in addition, the inequalities (14) hold, then the coupled system (5)–(8) has at least two attractors:

$$(P^0, H^0, 0, 0) \quad \text{and} \quad (0, 0, P^0, H^0).$$

2. the coupled system (5)–(8) is permanent in both patches if $0 < l < \frac{1}{2}$, i.e., there exists two positive numbers $0 < b < B$, such that for any initial condition $(P_0^I, H_0^I, P_0^{II}, H_0^{II}) \in \mathring{\mathbb{R}}_+^4$, the following inequalities hold:

$$b < \liminf_{n \rightarrow \infty} \min\{P_n^I, H_n^I, P_n^{II}, H_n^{II}\} \leq \limsup_{n \rightarrow \infty} \max\{P_n^I, H_n^I, P_n^{II}, H_n^{II}\} < B$$

The proof of Theorem 4.1 is given in the Appendix. Here, we only illustrate the idea briefly. When $0 < r \leq 2$ and $a(1-l) > 1$, permanence of the system (9)–(10) follows from Salceanu and Smith (2009). In addition, according to Kang et al. (2008), the system (9)–(10) has a unique interior equilibrium (P^0, H^0) if $a(1-l) > 1$, which implies that $(P^0, H^0, 0, 0)$ and $(0, 0, P^0, H^0)$ are two boundary equilibria of the coupled system (5)–(8). From Theorem 3.2, we know that these two boundary equilibria are locally stable if the inequalities (14) hold. Thus, the first

part of Theorem 4.1 is true. In order to show that the coupled system is permanent for both patches if $l < \frac{1}{2}$, we can show that the population of plants in the coupled system (5)–(8) is persistent in Patch I by applying Hutson's (1984) Theorem 2.2 and its Corollary 2.3 with the average Lyapunov function $h(P^I, H^I, P^{II}, H^{II}) = P^I$. Similarly, we can show that the plant population is persistent in Patch II. Then we can restrict the coupled system to the compact space

$$\{(P^I, H^I, P^{II}, H^{II}) \in \mathring{\mathbb{R}}_+^4 : P^I \geq \varepsilon, P^{II} \geq \varepsilon\} \quad \text{for some } \varepsilon > 0$$

and apply Hutson's (1984) Theorem 2.2 again to obtain persistence of the insect population in both patches by using the average Lyapunov functions

$$h(P^I, H^I, P^{II}, H^{II}) = H^I \quad \text{and} \quad h(P^I, H^I, P^{II}, H^{II}) = H^{II}.$$

Theorem 4.1 indicates the following: Assume that $0 < r \leq 2, a(1-l) > 1$. If there is no plant population in one of the two patches, the other patch shows emigration (i.e., (9)–(10)), which is permanent. If plants in both patches are edible for insects (i.e., $P_0^i > 0, i = I, II$), then the population of insects will have successful expansion and persist in both patches if one of the two patches has insects (i.e., $H_0^I > 0$ or $H_0^{II} > 0$) and $0 < l < \frac{1}{2}$. However, in the presence of plants in both patches, extremely large dispersal (e.g., $l > \frac{1}{2}$), and large herbivore attacking rate a , permanence of the coupled system (5)–(8) is spoiled, and the boundary equilibria $(P^0, H^0, 0, 0), (0, 0, P^0, H^0)$ become locally stable. Thus, generating multiple attractors in the coupled system. The biological explanation of this result is that extremely large dispersal l moves a large number of insects having a large attacking rate a , from one patch to the other in a very short time. Hence plants in the second patch are severely damaged and eventually all plants in this patch are killed if the initial population of plant in this patch is too small. On the other hand, the damage to the plants in the original patch is less due to the large dispersal of insects. As a result insect and plant populations coexist in the original patch. Therefore, we can conclude that large values of dispersal l and insect's attacking rate a can promote the local extinction of insects in one patch.

5. Allee-like effects combined with small dispersals generate source–sink dynamics

The objective of this section is to explore whether an Allee-like effect could create source–sink dynamics among homogeneous patches of habitat. Two-patch two-competing-species models with interpatch migrations (Levin, 1974; Nishimura and Kishida, 2001; Amarasekare, 2004) have a similar model structure as our two-patch plant–insect model. In two-patch competition models, stable coexistence of the competing species is accomplished partly by refuge patch effects via certain migration rates between patches when a destabilizing competition effect is embedded in either or both patches. Our two-patch plant–herbivore model is similar to these competition models in that refuge effects lead to stable coexistence for sufficiently low migration rates of insects. Thus, a complete source–sink structure of our model (wherein one patch is the source and the other patch is only a sink) provides the mechanism for stable coexistence. Therefore, the small dispersal combined with Allee-like effects may not be able to prevent the expansion of insects. We first show that the coupled two-patch model (5)–(8) is transversally stable when $a < 1$:

Theorem 5.1 (Transversal stability). If $a < 1$, then all the periodic orbits in the invariant manifold $P^{II} = H^I = H^{II} = 0$ of the coupled system (5)–(8) are unstable and all the periodic orbits in the invariant manifold $\{(P^I, 0, P^{II}, 0) \in \mathring{\mathbb{R}}_+^4 : P^I > 0, i = I, II\}$ are transversally stable.

If, in addition, $2 < r < 2.52$, then the coupled system (5)–(8) has a locally stable period-2 orbit $\{(P_i, 0, P_i, 0) \in \mathbb{R}_+^4 : P_i > 0, i = 1, 2\}$ that attracts all initial conditions in $\{(P^I, 0, P^{II}, 0) \in \mathbb{R}_+^4 : P^i > 0, i = I, II\}$ except a Lebesgue measure zero set.

The detailed proof is given in the Appendix. Briefly, we study eigenvalues and their associated eigenvectors of the Jacobian matrices at these periodic orbits. Then the period-2 orbit $\{(P_1, 0, P_1, 0), (P_2, 0, P_2, 0)\}$ restricted to the invariant manifold $\{(P^I, 0, P^{II}, 0) \in \mathbb{R}_+^4 : P^i > 0, i = I, II\}$, gives a period-2 orbit of two independent Ricker maps

$$P_{n+1}^I = P_n^I e^{r(1-P_n^I)} \quad \text{and} \quad P_{n+1}^{II} = P_n^{II} e^{r(1-P_n^{II})}.$$

If $2 < r < 2.52$, then the period-2 orbit is locally stable and attracts all initial conditions in $\{(P^I, 0, P^{II}, 0) \in \mathbb{R}_+^4 : P^i > 0, i = I, II\}$ except a Lebesgue measure zero set according to Theorem 4.2 (Elaydi and Sacker, 2004). This combined with the transversal stability ensures that the period-2 orbit is locally stable in \mathbb{R}_+^4 .

In the case that $2 < r < 2.52$ and $a < 1$, the single-patch model can have a locally stable interior equilibrium (P, H) and a locally stable period-2 orbit $(P_1, 0), (P_2, 0)$, which indicates that the single-patch model exhibits Allee-like effects (e.g., $r = 2.45, a = 0.98$, Fig. 2). Thus, according to perturbation theory, if dispersal l is small enough, then the coupled system can also exhibit Allee-like effects. Moreover, the coupled system can have locally stable asymmetric interior period-2 orbits, i.e.,

$$E_i = (P_i^I, H_i^I, P_i^{II}, H_i^{II}), E_i^s = (P_i^{II}, H_i^{II}, P_i^I, H_i^I) \quad \text{with} \quad P_i^I \neq P_i^{II}, H_i^I \neq H_i^{II}, i = 1, 2 \quad (17)$$

Theorem 5.2 (Stable asymmetric positive interior period-2 orbits). Assume that (P, H) is a stable interior equilibrium of the system (1)–(2) such that the inequality (13) holds. If $0 < a < 1$ and $2 < r < 2.52$, then the coupled system (5)–(8) has bistability between the boundary attractor $\{(P_1, 0, P_1, 0), (P_2, 0, P_2, 0)\}$ and the interior attractor (P, H, P, H) , i.e., exhibits an Allee-like effect. If l is small enough, then the coupled system has locally stable asymmetric interior period-2 orbits (17)

$$P_i^I = P + \odot(l), \quad H_i^I = H + \odot(l), \quad P_i^{II} = P_i + \odot(l), \quad H_i^{II} = \odot(l), \quad i = 1, 2, \quad (18)$$

where $\{P_1, P_2\}$ is a period-2 orbit of the Ricker map $P_{n+1} = P_n e^{r(1-P_n)}$.

Proof. For $0 < a < 1, 2 < r < 2.52$, the single-patch model (1)–(2) has a locally stable interior equilibrium (P, H) . Hence without dispersal, i.e., $l = 0$, the system (5)–(8) becomes two independent single-patch models with the following two locally stable attractors: One is the boundary attractor, i.e., a period-2 orbit $(P_1, 0, P_1, 0), (P_2, 0, P_2, 0)$ and the other one is the symmetric interior attractor (P, H, P, H) . Therefore, the stable asymmetric period-2 orbits are

$$(P_1, 0, P, H), \quad (P_2, 0, P, H), \quad (P, H, P_1, 0), \quad (P, H, P_2, 0).$$

When we increase the dispersal l from 0 and keep it small enough, then according to the perturbation theory (Levin, 1974; Hirsch and Smale, 1974; Guckenheimer and Holmes, 1983; Amarasekare, 2000), the coupled system (5)–(8) should have locally stable asymmetric interior period-2 orbits of the form (18). \square

Theorem 5.2 demonstrates that source–sink dynamics can emerge between habitat patches of identical quality when an Allee-like threshold is present. The coupled system has at least four alternate attractors. The first, when both populations are above the Allee threshold, is referred to as a source–source dynamic. The second is when both populations go extinct after dropping below the Allee threshold. The third and fourth attractors, when one population is above the Allee-like threshold and the other is below, results in source–sink dynamics. Source populations are at densities above the Allee threshold and sink populations are

below the Allee-like threshold. Initial population sizes are important in determining the attractor.

6. Simulations: intermediate dispersals promote the extinction of the insect population

Theorems 5.1 and 5.2 imply that Allee-like effects in the single-patch model (1)–(2) lead to Allee-like effects in the coupled two-patch model (5)–(8), creating source–sink dynamics in the two-patch model for small dispersal. An interesting question is what happens to the population of insects and their dispersal for larger l . Since we are interested in the expansion of the insect population from Patch I into the non-infected Patch II, we choose initial conditions in Patch II at zero for insects, i.e., $H_0^{II} = 0$. For a given dispersal l and an initial condition $(P_0^I, 0)$ in Patch II, the Allee-like threshold can be represented as $\theta(l, P_0^I)$ and divides initial conditions $(P_0^I, H_0^I) \in \mathbb{R}_+^2$ in Patch I into the following two regions:

$$B_0(l, P_0^I) = \left\{ (P_0^I, H_0^I, P_0^{II}, 0) \in \mathbb{R}_+^3 \times \{0\} : \lim_{n \rightarrow \infty} \min\{H_n^I, H_n^{II}\} = 0 \right\}$$

$$B_1(l, P_0^I) = \left\{ (P_0^I, H_0^I, P_0^{II}, 0) \in \mathbb{R}_+^3 \times \{0\} : \lim_{n \rightarrow \infty} \min\{H_n^I, H_n^{II}\} > \varepsilon > 0 \right\}$$

Here $B_0(l, P_0^I)$ and $B_1(l, P_0^I)$ are sets of initial conditions in Patch I of the coupled system (5)–(8) that lead to the extinction of insects in one or both patches and lead to the coexistence of plants and insects in both patches respectively, given a value of the dispersal parameter l and an initial condition $(P_0^I, 0) \in \mathbb{R}_+ \times \{0\}$ in Patch II.

We fix parameters a and r such that the coupled system (5)–(8) exhibits Allee-like effects, then choose a dispersal parameter l and choose initial conditions $(P_0^I, 0) \in \mathbb{R}_+ \times \{0\}$ in Patch II. We study the following questions numerically:

- For which values of dispersal l can the insect population establish itself in the uninfected patch, i.e., Patch II?
- Which values of dispersal l can lead to the extinction of the insect population in both patches?
- How does dispersal l affect the sizes and locations of $B_0(l, P_0^I)$ and $B_1(l, P_0^I)$?

Figs. 2 and 3 illustrate the dynamics of the system (5)–(8) when $a = 0.98$ and $r = 2.45$ in the absence of the dispersal, i.e., $l = 0$, when both patches become uncoupled and behave independently. The uncoupled system either has a stable steady state (Fig. 2(a)) or has a stable period-2 orbit for the boundary dynamics of plant (Fig. 2(b)). Since the two patches are uncoupled, the insect population does not get established in Patch II with initial conditions $H_0^{II} = 0$. Thus, for all initial conditions $(P_0^I, H_0^I) \in \mathbb{R}_+^2$, Patch II only exhibits the dynamics of plant, which is a period-2 orbit (see Figs. 2(a) and 3(b)). Fig. 3(a) shows the basins of attractions for the interior stable steady state and the boundary attractor (a period-2 orbit of plant). The white area is the set of initial conditions for which the system in Patch I converges to a stable steady state and the grid-shadowed area is the set of initial conditions for which the system in Patch I decays to the boundary dynamics of a period-2 orbit for the plant evolution.

With $l > 0$, we vary the initial conditions of Patch I and keep the initial conditions of Patch II unchanged. In practice we choose $P_0^I = 1, H_0^I = 0$ as an initial condition in Patch II. Fig. 4 represents the sizes and locations of $B_0(l, 1)$ (the grid-shadowed area) and $B_1(l, 1)$ (the white area) for $l = 0.01, 0.1, 0.2, 0.4$. We choose a rectangular region $[0 \leq P_0^I \leq 5.5], [0 \leq H_0^I \leq 5]$ where we vary initial conditions of Patch I. This rectangular area is large enough such that it contains $B_1(l, 1)$ for $l = 0.01, 0.1, 0.2, 0.4$. The most interesting finding is that

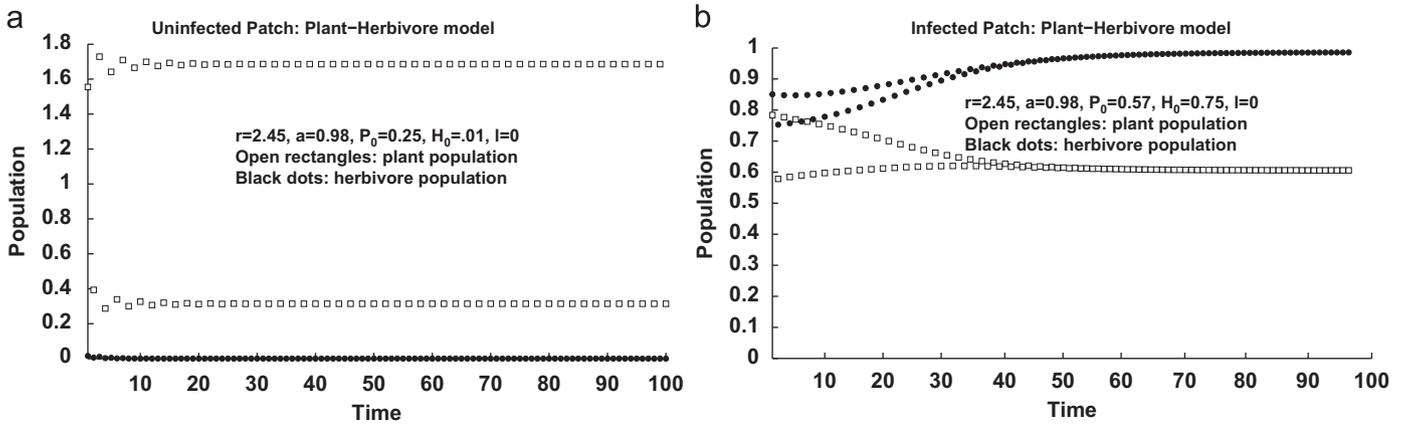


Fig. 2. Time series of plant-herbivore population when $a=0.98, r=2.45, l=0$ for both patches. Open rectangles represent plant populations and black dots represent herbivore populations. (a) Time series of plant-herbivore population in the non-infected patch (Patch II), when $a=0.98, r=2.45, l=0$ with $P_0=0.25, H_0=0.01$ as its initial condition. (b) Time series of plant-herbivore population in the infected patch (Patch I), when $a=0.98, r=2.45, l=0$ with $P_0=0.57, H_0=0.75$ as its initial condition.

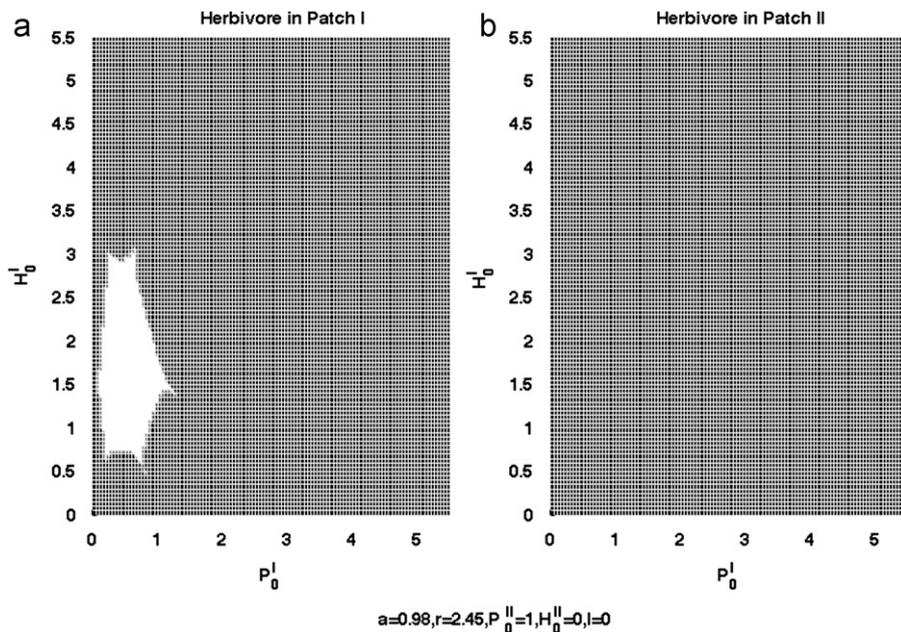


Fig. 3. When $a=0.98, r=2.45, l=0$ and $H_0^{II}=0$, the two patches are uncoupled. (a) shows the basins of attractions of the interior stable steady state and the boundary attractor (a period-2 orbit of plant), where the white area is the set of initial conditions for which the system in infected patch converges to a stable steady state and the grid-shadowed area is the set of initial conditions for which the system decays to the boundary dynamics of a period-2 orbit for the plant evolution. (b) shows that insect population does not get established in uninfected patch due to its initial condition of insect population being zero.

the insect population in both patches become extinct for the intermediate values of the dispersal parameters l . Based on our simulations (see Fig. 4), we have the following findings:

Small intensity of dispersals: When $l=0.01$ (Fig. 4(a)), the coupled system exhibits source-sink dynamics, i.e., the omega limit set of $B_1(0.01,1)$ (the white area) is an interior period-2 orbit

$$\{(P_1^I, H_1^I, P_1^{II}, H_1^{II}), (P_2^I, H_2^I, P_2^{II}, H_2^{II}), i=1,2\}$$

which satisfies (18) and the omega limit set of $B_0(0.01,1)$ (the grid-shadowed area) is a boundary period-2 orbit

$$\{(P_1, 0, P_1, 0), (P_2, 0, P_2, 0)\}$$

Intermediate intensity of dispersals: When $l=0.1$ (Fig. 4(b)), both patches converge to their boundary dynamics for all initial conditions in Patch I, i.e., the omega limit set of $B_0(0.01,1)$ (the grid-shadowed area) is a boundary period-2 orbit

$$\{(P_1, 0, P_1, 0), (P_2, 0, P_2, 0)\}$$

The insect population not only does not expand but dies out even in Patch I where the population of insects was well established before. The mechanisms behind this phenomenon come from Allee-like effects and the separation of time scales: Originally, the population of plants and insects in Patch I lies in $B_1(0,1)$. However, dispersal of insect into Patch II reduces the population of insects in both patches below the threshold for bistability and hence the trajectory converges to the boundary dynamics in both patches.

Strong intensity of dispersal: When $l=0.2, 0.4$ (Fig. 4(c) and (d)), the insect establishes itself permanently in both patches. The dynamic synchronizes and the trajectory converges to the same fixed point in both patches, i.e., the omega limit set of $B_1(l,1)$, $l=0.2,0.4$ (the white area) is the stable interior fixed point. The size of $B(l,1)$ depends on the value of l , which may be smaller or larger than $B_1(0,1)$ (the white area of Fig. 3(a)). However, the minimal initial population of insect that leads to infestation in the case $l=0.2, 0.4$ is significantly higher than the minimal initial population in the case $l=0$.

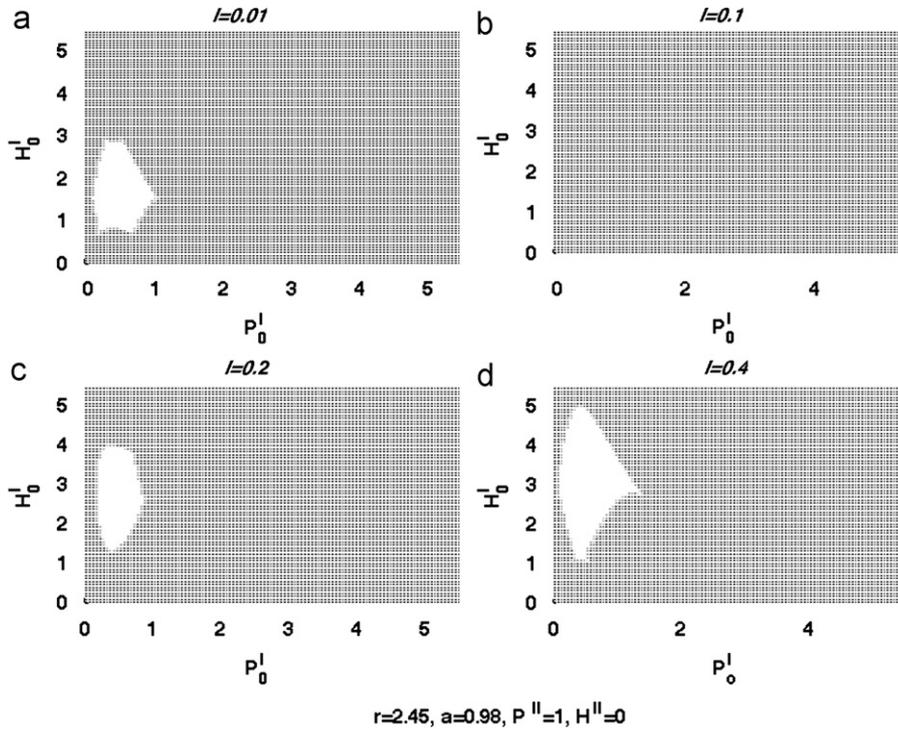


Fig. 4. The sizes and locations of $B_0(l, 1)$ (the grid-shadowed area) and $B_1(l, 1)$ (the white area) when $a=0.98, r=2.45, l=(a) 0.01, (b) 0.1, (c) 0.2$ and $(d) 0.4$. The omega limit set of $B_0(l, 1), l=0.01, 0.1, 0.2, 0.4$ (the grid-shadowed areas) is a boundary period-2 orbit $\{(P_1, 0, P_1, 0), (P_2, 0, P_2, 0)\}$. The omega limit set of $B_1(0.01, 1)$ (the white area) is an interior period-2 orbit that satisfies (18); the omega limit set of $B_1(l, 1), l=0.2, 0.4$ (the white area) is an interior stable fixed point.

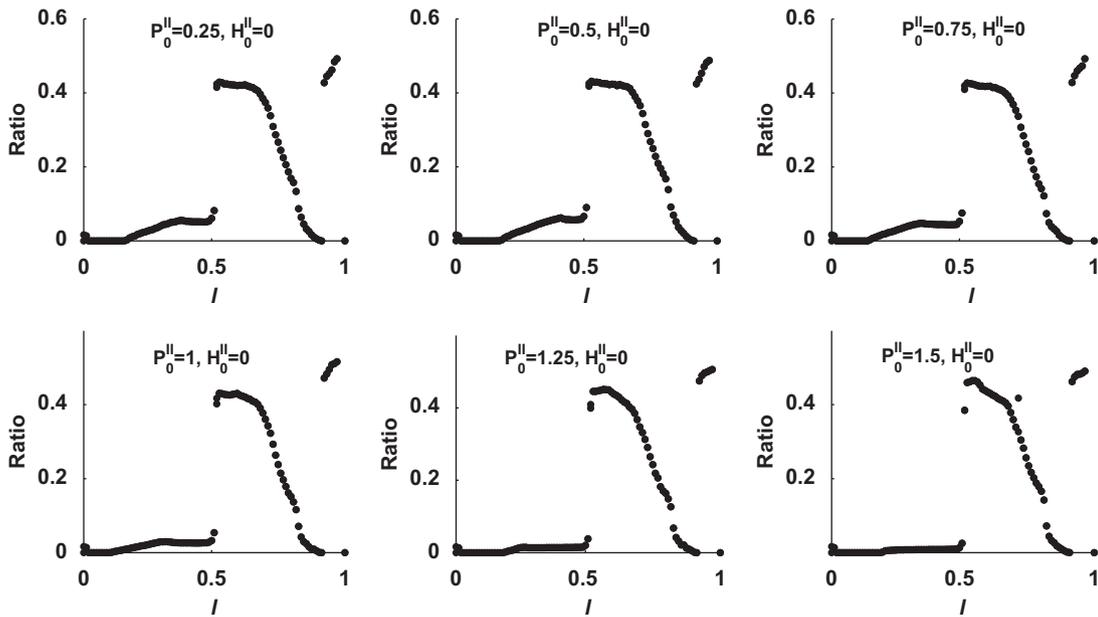


Fig. 5. The percentage of initial conditions in Patch I that lead to the interior attractor in both patches when $a = 0.98, r = 2.45, P_0^{II} = 0.25, 0.5, 0.75, 1, 1.25, 1.5, H_0^{II} = 0, 0 \leq l \leq 1$.

To systematically investigate the relationship between l and the size of $B_1(l, P_0^{II})$, we choose a rectangular region $[0 \leq P_0^I \leq 10], [0 \leq H_0^I \leq 10]$ where we vary initial conditions of Patch I. This rectangular area is large enough so that it contains $B_1(l, 1), 0 \leq l \leq 1$. We determine the percentage of the initial conditions whose omega limit set is the interior attractor by varying l from 0 to 1 numerically. To check the impact of the initial conditions of Patch II, we set $P_0^{II} = 0.25, 0.5,$

$0.75, 1, 1.25, 1.5$ and $H_0^{II} = 0$. Our simulations (Figs. 5 and 6) indicate:

1. At $l=0$, the two patches are uncoupled. About 16% (the red dot in Fig. 6) of the initial conditions in Patch I are attracted to the interior fixed point for all $a=0.98, r=2.45, P_0^{II}=0.25, 0.5, 0.75, 1, 1.25, 1.5, H_0^{II}=0$.

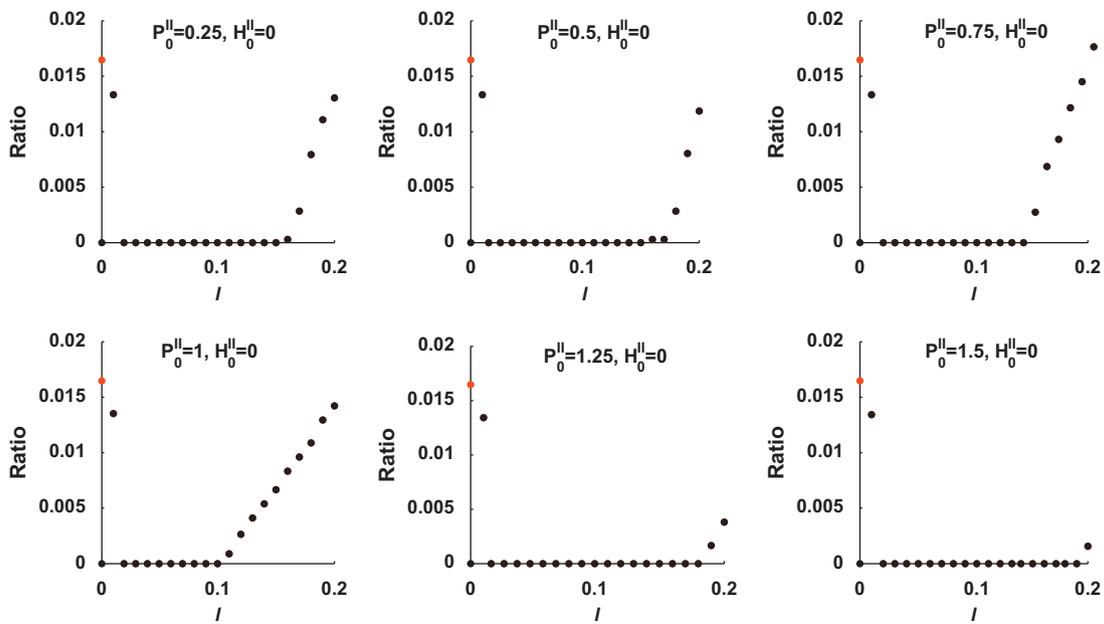


Fig. 6. The percentage of initial conditions in Patch I that lead to the interior attractor in both patches when $a = 0.98, r = 2.45, P_0^{II} = 0.25, 0.5, 0.75, 1, 1.25, 1.5, H_0^{II} = 0, 0 \leq l \leq 0.2$. At $l=0$, the plots have two data points: The first black dot is for the uninfected patch (the percentage of initial conditions is zero), the red dot is for the infected patch (the percentage of initial conditions is about 16%). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
The range of l that lead to the extinction of insects in both patches when $a = 0.98, r = 2.45, P_0^{II} = 0.25, 0.5, 0.75, 1, 1.25, 1.5, H_0^{II} = 0$.

	$P_0^{II} = 0.25$	$P_0^{II} = 0.5$	$P_0^{II} = 0.75$	$P_0^{II} = 1$	$P_0^{II} = 1.25$	$P_0^{II} = 1.5$
The range of l	[0.02, 0.15]	[0.02, 0.15]	[0.02, 0.14]	[0.02, 0.10]	[0.02, 0.18]	[0.02, 0.19]

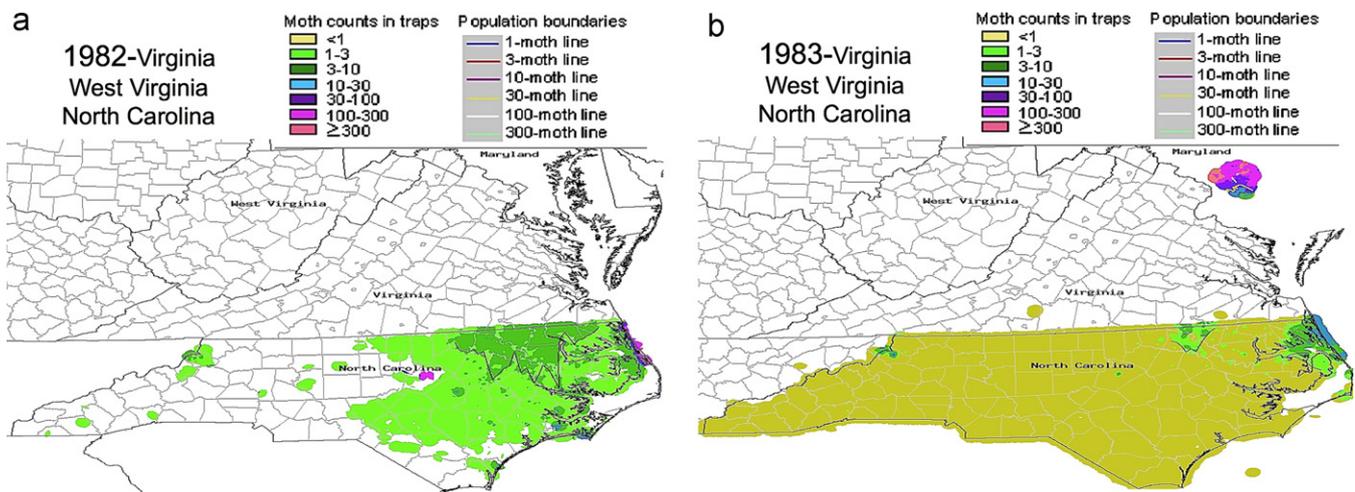


Fig. 7. The distribution of gypsy moth in Virginia, West Virginia and North Carolina in (a) 1982 and (b) 1983. The brown or light green areas are places where moth counts in traps are either less than the Allee threshold (the Allee threshold of gypsy moth is about 20 per trap, see Courchamp et al., 2009, p. 193). Thus we can technically consider that the gypsy moth populations are not established in these areas. Therefore, we only focus on the areas (e.g., the blue and purple areas) in Eastern North Carolina where the population of gypsy moths is established in 1982. By comparison, we can observe that in these infected areas, gypsy moths are either retreated or lower in density in 1983. The figures are from Decision-Support System for the Gypsy Moth-Slow the Spread Program (<http://da.ento.vt.edu/>). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

- For small intensity of dispersals l , i.e., $0 < l < 0.01$, the coupled system exhibits source–sink dynamics, about 14% (the second dot in Fig. 6) of the initial conditions in Patch I are attracted to the interior period-2 orbits for all $a = 0.98, r = 2.45, P_0^{II} = 0.25, 0.5, 0.75, 1, 1.25, 1.5, H_0^{II} = 0$.
- For intermediate intensity of dispersals l , all initial conditions in Patch I can lead to the extinction of insects in both patches. The

- following table gives the range of l that lead to the extinction of insects in both patches when $a = 0.98, r = 2.45, P_0^{II} = 0.25, 0.5, 0.75, 1, 1.25, 1.5, H_0^{II} = 0$ (Table 1).
- We observed two critical values of l based on simulations, which are $l = 0.5$ and 0.92 . Fig. 5 suggests that when the intensity of dispersal is strong ($0.2 < l < 0.5$), the size of $B_1(P_0^{II})$ is increasing with respect to l up to the critical value $l = 0.5$; while the size of

$B_1(l, P_0^I)$ is decreasing with respect to l starting from 0.5 up to the critical value $l=0.92$; and the size of $B_1(l, P_0^I)$ is increasing with respect to l when $0.92 < l < 1$; at $l=1$, the insect population becomes extinct in both patches. The biological explanation for these critical points may be as follows: Insect's populations are the same for both patches in each generation when $l = \frac{1}{2}$. This leads to the strongest synchronization between two patches, which promotes the persistence of insect population. Due to symmetry of two patches, the impact of l when it is greater than $\frac{1}{2}$ is similar to the impact when it is less than $\frac{1}{2}$, thus there is another critical point l (which is 0.92 in Fig. 5) where insect populations in both patches go to extinct. When l is very close to 1 (i.e., $l > 0.92$), the system becomes very complicated. This may be an artificial effect from complicated dynamics of discrete systems.

The most interesting finding in this section is that the intermediate intensity of dispersals combined with Allee-like effects may promote the extinction of the insect population, which may be a mechanism that explains why the population of gypsy moth in Eastern North Carolina retreated in 1983 relative to 1982: Fig. 7 shows the distribution of gypsy moth in Virginia, West Virginia and North Carolina in 1982 and 1983. The brown or light green areas are places where moth counts in traps are less than the Allee threshold (the Allee threshold of gypsy moth is about 20 per trap, see Courchamp et al., 2009, p. 193). Thus we can technically consider that the gypsy moth populations are not established in these areas. Therefore, we only focus on the areas in Eastern North Carolina where the gypsy moth populations are established in 1982, i.e., the areas with purple or dark blue color. These areas can be considered as the infected patch and their surrounding areas where gypsy moths population is below the Allee threshold can be considered as the uninfected patch according to our coupled system (5)–(8). Because of the moderated dispersal of gypsy moths, the density of gypsy moths in the infected patch is either retreated or has much lower density in 1983.

7. Conclusions

We have studied a two patch model for a time discrete plant–insect interaction in the form of a host–parasite model. A fundamental feature of the model is the occurrence of three different time-separated phases: plant growth is followed by a dispersal of a parasite, which is followed by the parasite's attack. The model incorporates nonlinear intra-plant competition.

We discussed the impact of the different intensities of dispersal combined with an Allee-like effect on a two-patch model. Our main interest was focused on the spread of an established insect population in Patch I into Patch II which initially has no insects. We show that for moderate coupling between the two patches (measured in our barrier parameter l), the infestation may actually disappear in both patches. Our main results can be summarized as follows:

1. If the single-patch model is permanent, then the two-patch model is permanent in both patches when the intensity of dispersal is less than $\frac{1}{2}$, i.e., $l < \frac{1}{2}$. The two-patch model has local extinction of the insect population in one patch when the intensity of dispersal is greater than $\frac{1}{2}$ and the attracting rate a of insect is large. These analytical results suggest that the dispersal may not stop the expansion of these insects to new areas; however, large dispersal and insect attacking rates may prevent spreading to new areas where there are not enough plants.
2. If the single-patch model exhibits Allee-like effects, then small intensity of dispersal generates source–sink dynamics, indicating a successful expansion. Intermediate intensity of

dispersals promotes the extinction of the insect population in both patches. This may be a mechanism that explains why forest pests retreat in some years (e.g., gypsy moth, Fig. 7), suggesting that we may be able to regulate the population of forest pests with intermediate levels of dispersal when pests suffer from Allee-like effects.

There are several highly interesting open problems that we will study to extend our results:

- We will extend the two patch model to a spatial continuum. We expect to be able to relate our results to front propagation in bistable media. There the front movement changes direction as a function of the size of the infestation (Malchov et al., 2008).
- We will study the influence of the temporal ordering of the three phases—plant growth, insect infestation and insect dispersal. We will develop differential equation models that allow for the overlap of those phases and study the influence of the stage separation.
- In nature, insects have different dispersals during their lifetime, e.g., the short-distance dispersal, which is caused by the larvae moving from one place to another and long-distance dispersal, which can be caused by human transportation. We will study how long-distance dispersals affect the speed of invasion. The resulting mathematical structure is a time discrete spatial integration kernel.
- Habitat structure has broad impacts on many biological systems. In particular, habitat fragmentation may increase the probability of species extinction, but can also lead to population outbreaks in response to a decline of natural enemies. An extreme consequence of fragmentation is the isolation of small regions of suitable habitat surrounded by a large region of hostile matrix. This scenario can be interpreted as a critical patch-size problem, well studied in a continuous-time framework, but relatively new in discrete-time models. We intend to gain understanding of how insect outbreaks are influenced by both habitat size and dispersal kernels. In particular, we examine the interaction among the pest emergence time, dispersal, and patch size in ensuring plant–insect persistence.

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Appendix A. Preliminary results

Lemma A.1. *If initial conditions are symmetric, $P_0^I = P_0^{II}$, $H_0^I = H_0^{II}$, then the uncoupled system (1)–(2) is an invariant subspace of (5)–(8). If $l=0$ or initial conditions are symmetric, i.e., $P_0^I = P_0^{II}$, $H_0^I = H_0^{II}$, then the system (5)–(8) is reduced to the uncoupled system (1)–(2).*

Lemma A.2. *The coupled system (5)–(8) is positively invariant and bounded. Moreover, the following subspaces:*

$$\{(P^I, 0, 0, 0) \in \mathbb{R}_+^4\}, \quad \{(0, 0, P^{II}, 0) \in \mathbb{R}_+^4\}, \quad \{(P, H, 0, 0) \in \mathbb{R}_+^4\}, \\ \{(0, 0, P, H) \in \mathbb{R}_+^4\}, \quad \{(P^I, 0, P^{II}, 0) \in \mathbb{R}_+^4\}$$

are positively invariant.

Proof. According to (5)–(8), for any $(P_n^I, H_n^I, P_n^{II}, H_n^{II}) \in \mathbb{R}_+^4$, we have follows:

$$0 \leq P_{n+1}^I = P_n^I e^{r(1-P_n^I) - aH_{n+d}^I} \leq \max_{P \geq 0} \{P e^{r(1-P)}\} = \frac{e^{r-1}}{r}$$

$$0 \leq H_{n+1}^I = P_n^I e^{r(1-P_n^I)} [1 - e^{-aH_{n+d}^I}] \leq \max_{P \geq 0} \{P e^{r(1-P)}\} = \frac{e^{r-1}}{r}$$

Similarly, we can show that

$$0 \leq P^{II} \leq \frac{e^{r-1}}{r}, \quad 0 \leq H^{II} \leq \frac{e^{r-1}}{r}$$

It is easy to check that

$$\{P^I = 0\}, \quad \{P^{II} = 0\}, \quad \{P^I = H^I = 0\}, \quad \{P^{II} = H^{II} = 0\}$$

are positively invariant respectively. \square

Lemma A.3 (Elaydi and Sacker, 2004). If $\{P_i\}_{i=1}^k$ is a period- k -orbit of the Ricker map $P_{n+1} = P_n e^{r(1-P_n)}$, then $\sum_{i=1}^k P_i/k = 1$. If, in addition, the inequality $|\prod_{k=1}^n (1-rP_k)| < 1$ holds, then it is a stable period- k -orbit. In particular, if $0 < r \leq 2$, then the map has global stability at $P=1$. If $2 < r < 2.52$, then it has a locally stable period-2 orbit that attracts all initial conditions in \mathbb{R}_+ except a Lebesgue measure 0 set.

Lemma A.4. If $0 < r < 2$ and $a(1-l) > 1$, then the system (9)–(10) is permanent. In particular, there exists a positive number $\varepsilon > 0$, such that for any $(P_0^I, H_0^I) \in \mathbb{R}_+^2$, the following equality and inequality hold:

$$\lim_{n \rightarrow \infty} r_{P_0^I}^n = \lim_{n \rightarrow \infty} \frac{\ln \frac{P_0^I}{P_0^I}}{n} = 0$$

and

$$\limsup_{n \rightarrow \infty} \frac{\sum_{k=0}^{n-1} H_k^I}{n} \leq \frac{r(1-\varepsilon)}{a(1-l)}$$

Proof. For $0 < r < 2$ and $a(1-l) > 1$, Kang and Chesson (2010) and Salceanu and Smith (2009) shows that the system (9)–(10) is permanent. Thus, there exists a positive number $\varepsilon > 0$, such that for any $P_0^I > 0$ and $H_0^I > 0$, we have as follows:

$$\varepsilon < \liminf_{n \rightarrow \infty} \min\{P_n^I, H_n^I\} \leq \limsup_{n \rightarrow \infty} \max\{P_n^I, H_n^I\} < \max\{1, r/a\} \quad (19)$$

For any $P_0^I > 0$ and $H_0^I > 0$, we have the mean growth rate

$$r_{P_0^I}^n := \frac{\ln \frac{P_0^I}{P_0^I}}{n} = r \left(1 - \frac{\sum_{k=0}^{n-1} P_k^I}{n} \right) - a(1-l) \frac{\sum_{k=0}^{n-1} H_k^I}{n} \quad (20)$$

From (19), we can see that $\ln P_n^I / P_0^I$ is bounded, thus,

$$\lim_{n \rightarrow \infty} r_{P_0^I}^n = \lim_{n \rightarrow \infty} \frac{\ln \frac{P_0^I}{P_0^I}}{n} = 0$$

In addition, from (20), we have

$$\frac{\sum_{k=0}^{n-1} H_k^I}{n} = r \left(1 - \frac{\sum_{k=0}^{n-1} P_k^I}{a(1-l)n} \right) - \frac{r_{P_0^I}^n}{a(1-l)}$$

Thus

$$\limsup_{n \rightarrow \infty} \frac{\sum_{k=0}^{n-1} H_k^I}{n} = \limsup_{n \rightarrow \infty} \left(\frac{r \left(1 - \frac{\sum_{k=0}^{n-1} P_k^I}{n} \right)}{a(1-l)} - \frac{r_{P_0^I}^n}{a(1-l)} \right) \leq \frac{r(1-\varepsilon)}{a(1-l)} \quad \square$$

Proposition A.1. For the four boundary equilibria: $(0,0,0,0)$, $(1,0,0,0)$, $(0,0,1,0)$, and $(1,0,1,0)$ of the system (5)–(8) we find:

- $(0,0,0,0)$, $(1,0,0,0)$, and $(0,0,1,0)$ are always unstable;
- $(1,0,1,0)$ is locally stable if $0 < r < 2$ and $0 < a < 1$; it is unstable if $r > 2$ or $a > 1$.

Proof. We consider the following three cases:

- The eigenvalues of the Jacobian at the origin $(0,0,0,0)$ are $\lambda_1 = \lambda_3 = e^r$ and $\lambda_2 = \lambda_4 = 0$. Hence $(0,0,0,0)$ is always a saddle independent of the dispersal parameter l .
- The eigenvalues of the Jacobian at $(1,0,0,0)$ and $(0,0,1,0)$ are $\lambda_1 = 1-r, \lambda_3 = e^r, \lambda_2 = a(1-l), \lambda_4 = 0$. Since $r > 0$ these equilibria are always saddles.
- The eigenvalues of the Jacobian at $(1,0,1,0)$ are $\lambda_1 = \lambda_3 = 1-r, \lambda_2 = a, \lambda_4 = a(1-2l)$. This indicates that the boundary equilibrium $(1,0,1,0)$ is locally stable if $0 < r < 2$ and $0 < a < 1$; otherwise, if $r > 2$ or $a > 1$, then $(1,0,1,0)$ becomes unstable.

Therefore, the statement holds. \square

Proposition A.2. If the single-patch model (1)–(2) has no interior equilibrium, then the coupled system (5)–(8) has no interior equilibria either.

Proof. If the single-patch model (1)–(2) has no interior equilibrium, then the coupled system (5)–(8) cannot have (P, H, P, H) where $P > 0$ and $H > 0$ as its interior equilibrium according to Lemma A.1. In addition, the following two equations have no solution for any $(P, H) \in \mathbb{R}_+^2$.

$$\begin{aligned} 0 &= r(1-P) - aH \Rightarrow P = 1 - \frac{aH}{r} \\ H &= P[e^{aH} - 1] \Rightarrow P = \frac{H}{e^{aH} - 1} \end{aligned}$$

This implies that

$$\frac{H}{e^{aH} - 1} - \left(1 - \frac{aH}{r} \right) > 0 \quad \text{for any } H > 0$$

Thus, we have

$$H > \left(1 - \frac{aH}{r} \right) [e^{aH} - 1] \quad \text{for any } H > 0 \quad (21)$$

Now assume that the coupled system (5)–(8) has a positive asymmetric equilibrium

$$(P^I, H^I, P^{II}, H^{II}) \quad \text{where } P^i > 0, r/a > H^i > 0, i = I, II$$

Then

$$0 = r(1-P^I) - a(1-l)H^I - aH^{II} \quad (22)$$

$$0 = r(1-P^{II}) - a(1-l)H^{II} - aH^I \quad (23)$$

$$H^I = P^I [e^{a(1-l)H^I + aH^{II}} - 1] \quad (24)$$

$$H^{II} = P^{II} [e^{a(1-l)H^{II} + aH^I} - 1] \quad (25)$$

If $P^I = P^{II}$, then from (22) and (23), we can conclude that $H^I = H^{II}$. Similarly, if $H^I = H^{II}$, then from (22) and (23), we can conclude that $P^I = P^{II}$. Therefore,

$$P^I \neq P^{II}, \quad H^I \neq H^{II} \quad \text{and} \quad l \neq 1/2.$$

For convenience, let

$$U^I = (1-l)H^I + lH^{II} \quad \text{and} \quad U^{II} = (1-l)H^{II} + lH^I.$$

Then (22)–(25) becomes

$$0 = r(1-P^I) - aU^I \Rightarrow P^I = 1 - \frac{aU^I}{r} \quad (26)$$

$$0 = r(1-P^{II}) - aU^{II} \Rightarrow P^{II} = 1 - \frac{aU^{II}}{r} \quad (27)$$

$$U^I = (1-l)P^I [e^{aU^I} - 1] + lP^{II} [e^{aU^{II}} - 1] \quad (28)$$

$$U^{II} = (1-l)P^{II} [e^{aU^{II}} - 1] + lP^I [e^{aU^I} - 1] \quad (29)$$

where

$$H^I = \frac{(1-l)U^I - lU^{II}}{(1-l)^2 - l^2} \quad \text{and} \quad H^{II} = \frac{(1-l)U^{II} - lU^I}{(1-l)^2 - l^2}$$

Then, from (26) and (27), we can simplify (28) and (29) as

$$U^I = (1-l) \left(1 - \frac{aU^I}{r} \right) [e^{aU^I} - 1] + l \left(1 - \frac{aU^I}{r} \right) [e^{aU^{II}} - 1] \quad (30)$$

$$U^{II} = (1-l) \left(1 - \frac{aU^{II}}{r} \right) [e^{aU^{II}} - 1] + l \left(1 - \frac{aU^I}{r} \right) [e^{aU^I} - 1] \quad (31)$$

Defining the function $f(U) = (1-aU/r)[e^{aU} - 1]$, we find

$$U^I = \frac{(1-l)U^{II}}{l} + \frac{(2l-1)f(U^{II})}{l} \quad (32)$$

$$U^{II} = \frac{(1-l)U^I}{l} + \frac{(2l-1)f(U^I)}{l} \quad (33)$$

Let $F(U) = (1-l)U/l + (2l-1)f(U)/l$. Then the solutions of equalities (32)–(33) are fixed points of the map $F \cdot F$. However, for any $0 < U < r/a$, from (21), we have $0 < f(U) < U$. Thus,

if $l < 1/2$, then $F(U) > U > f(U) > 0$; while if $l > 1/2$, then $U > F(U) > f(U) > 0$

Therefore, for any $0 < U < r/a$, we have

$$F(F(U)) < F(U) < U \quad \text{if } l < 1/2, \quad F(F(U)) > F(U) > U \quad \text{if } l > 1/2$$

This implies that $F \cdot F$ has no fixed point for $U > 0$. Therefore, the coupled system (5)–(8) has no interior equilibrium. \square

Proposition A.3. *If $a(1-l) > 1$, then the coupled system (5)–(8) has boundary equilibria $(P^0, H^0, 0, 0)$ and $(0, 0, P^0, H^0)$ with $P^0 > 0$ and $H^0 > 0$. If, in addition, the equalities (14) hold, then $(P^0, H^0, 0, 0)$ and $(0, 0, P^0, H^0)$ are locally stable.*

Proof. From Lemma A.2, we know that the space $P_n^{II} = H_n^{II} = 0$ is positively invariant, then the coupled system (5)–(8) reduces to the system (9)–(10) in this invariant manifold, i.e.,

$$P_{n+1}^I = P_n^I e^{r(1-P_n^I) - a(1-l)H_n^I}$$

$$H_{n+1}^I = P_n^I e^{r(1-P_n^I)} [1 - e^{-a(1-l)H_n^I}]$$

which gives a fixed point (P^0, H^0) that satisfies

$$0 = r(1-P^0) - a(1-l)H^0 \quad (34)$$

$$H^0 = P^0 [e^{a(1-l)H^0} - 1] \quad (35)$$

By applying Proposition 3.2 of Kang et al. (2008), we can conclude that if $a(1-l) > 1$, then the equations (34)–(35) have a unique positive solution (P^0, H^0) . Thus the coupled system (5)–(8) has boundary equilibria $(P^0, H^0, 0, 0)$ and $(0, 0, P^0, H^0)$ with $P^0 > 0$ and $H^0 > 0$. \square

The eigenvalues of the Jacobian matrix at the equilibria $(P^0, H^0, 0, 0)$ are

$$\lambda_1 = 0, \quad \lambda_2 = e^{r-aH^0}, \quad \lambda_3 + \lambda_4 = 1 + P^0(a(1-l) - r) \quad \text{and} \\ \lambda_3 \lambda_4 = aP^0 e^{a(1-l)H^0} (1-l)(1-rP^0).$$

By applying the Jury test (Edelstein-Keshet, 2005, p. 57) to λ_3 and λ_4 , we can conclude that the boundary equilibria $(P^0, H^0, 0, 0)$ and $(0, 0, P^0, H^0)$ are locally stable if the inequalities (14) hold.

Proposition A.4. *Assume that the single-patch model (1)–(2) has a locally stable steady state at (P, H) . If the inequalities (13) hold, then the*

coupled system (5)–(8) is locally stable at the synchronized steady state (P, H, P, H) .

Proof. The single-patch model (1)–(2) at the steady state (P, H) has the Jacobian matrix

$$J_{(P,H)} = \begin{bmatrix} 1-rP & -aP \\ (1-rP)(e^{aH}-1) & aP \end{bmatrix} \quad (36)$$

with the following conditions on the eigenvalues:

$$\lambda_1 + \lambda_2 = 1 + P(a-r) \quad \text{and} \quad \lambda_1 \lambda_2 = aPe^{aH}(1-rP).$$

The Jacobian matrix of the coupled system (5)–(8) at the synchronized steady state (P, H, P, H) can be represented as

$$J_{P_{(P,H,P,H)}} = \begin{bmatrix} 1-rP & -aP & 0 & 0 \\ (1-rP)(e^{aH}-1) & aP & 0 & 0 \\ 0 & 0 & 1-rP & -aP \\ 0 & 0 & (1-rP)(e^{aH}-1) & aP \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1-l & 0 & l \\ 0 & 0 & 1 & 0 \\ 0 & l & 0 & 1-l \end{bmatrix}$$

with conditions on the eigenvalues

$$\lambda_1 + \lambda_2 = 1 + P(a-r), \quad \lambda_1 \lambda_2 = aPe^{aH}(1-rP)$$

$$\lambda_3 + \lambda_4 = 1 + P(a(1-2l) - r), \quad \lambda_3 \lambda_4 = aPe^{aH}(1-2l)(1-rP)$$

Since the single-patch model (1)–(2) is locally stable steady state at (P, H) , thus, $|\lambda_i| < 1, i = 1, 2$. Apply the Jury test (Edelstein-Keshet, 2005, p. 57) to λ_3 and λ_4 again, we can see that $|\lambda_i| < 1, i = 3, 4$ if the inequalities (14) hold. \square

Appendix B. Proofs of Theorems

B.1. Proof of Theorem 3.1

Proof. The statement follows from Propositions A.1 and A.2 directly. \square

B.2. Proof of Theorem 3.2

Proof. The statement follows from Propositions A.3 and A.4 directly. \square

B.3. Proof of Theorem 4.1

Proof. If $0 < r < 2$ and $a(1-l) > 1$, then applying Lemma A.4, we can conclude that the system (9)–(10) is permanent. Notice that the system (9)–(10) is equivalent to the coupled system (5)–(8) restricted to the invariant manifold $P^{II} = H^{II} = 0$ or $P^I = H^I = 0$ from Lemma A.1. According to Proposition A.3 and Jury test, we can see that the system (9)–(10) has a unique interior equilibrium (P^0, H^0) which is locally stable if the inequality

$$2 > 1 + aP^0 e^{a(1-l)H^0} (1-l)(1-rP^0) > |1 + P^0(a(1-l) - r)|$$

holds. If a and l are large enough such that $alH^0 > r$, then according to Proposition A.3, we know that the coupled system (5)–(8) has locally stable boundary equilibria $(P^0, H^0, 0, 0)$ and $(0, 0, P^0, H^0)$, which implies that the coupled system has at least two attractors. Therefore, the first part of the theorem is true.

The plant population persists if its average long-term growth rate is positive when its population density is low. From Lemma A.1, we can see that if $P_0^I = 0$ then $H_n^I = 0$ for all positive integer $n \in \mathbb{Z}^+$. Thus, if we take an initial condition $(0, 0, P_k^I, H_k^I) \in \mathbb{R}_+^4$ with $P_k^I > 0$, then its positive orbit can be written as $\{(0, 0, P_k^I, H_k^I)\}_{k=0}^\infty$ with $P_k^I > 0$ for all

k. Then the average growth rate of plant in Patch I can be defined as

$$r_{PI}^n = \frac{\ln \frac{P_0^{PI}}{P_0}}{n} = r \left(1 - \frac{\sum_{k=0}^{n-1} P_k^{PI}}{n} \right) - \frac{a(1-l) \sum_{k=0}^{n-1} H_k^{PI}}{n}$$

This implies that

$$\frac{\sum_{k=0}^{n-1} H_k^{PI}}{n} = \frac{r \left(1 - \frac{\sum_{k=0}^{n-1} P_k^{PI}}{n} \right) - r_{PI}^n}{a(1-l)}$$

Thus, the average long-term growth rate of plant in Patch I when it is rare can be defined as

$$\begin{aligned} r_{PI} &= \limsup_{n \rightarrow \infty} \frac{\ln \frac{P_0^{PI}}{P_0}}{n} = r - \limsup_{n \rightarrow \infty} \frac{a \sum_{k=0}^{n-1} H_k^{PI}}{n} \\ &= r - \limsup_{n \rightarrow \infty} \frac{r l \left(1 - \frac{\sum_{k=0}^{n-1} P_k^{PI}}{n} \right) - r_{PI}^n}{(1-l)} \\ &= \frac{r(1-2l)}{1-l} + \limsup_{n \rightarrow \infty} \frac{r l \sum_{k=0}^{n-1} P_k^{PI} + l r_{PI}^n}{(1-l)} \\ &\geq \frac{r(1-2l)}{1-l} + \frac{r l}{1-l} \liminf_{n \rightarrow \infty} \frac{\sum_{k=0}^{n-1} P_k^{PI}}{n} + \liminf_{n \rightarrow \infty} \frac{l r_{PI}^n}{1-l} \end{aligned}$$

If $l < 1/2$, then according to Lemma A.4, we have

$$r_{PI} \geq \frac{r(1-2l)}{1-l} + \frac{r l \varepsilon}{1-l} > 0.$$

Since the coupled system (5)–(8) is dissipative from Lemma A.2, the plant population is persistent in Patch I following from Theorem 2.2 of Hutson’s (1984) by defining an average Lyapunov function $h(P^I, H^I, P^{II}, H^{II}) = P^I$. Similarly, we can show that the plant population is persistent in Patch II. Thus, we have shown that plant population is persistent in both patches if

$$0 < r < 2, \quad a(1-l) > 1 \quad \text{and} \quad 0 < l < 1/2.$$

The persistence of plants in both patches allows us to restrict the coupled system to the space

$$X = \{(P^I, H^I, P^{II}, H^{II}) \in \mathbb{R}_+^4 : P^I > \varepsilon, P^{II} > \varepsilon\} \quad \text{for some } \varepsilon > 0.$$

Notice that the fact $0 < r < 2$ implies that when the coupled system (5)–(8) is restricted to the invariant manifold $H^I = H^{II} = 0$, it has global stability at $(1, 0, 1, 0)$. Thus, the omega limit set of the invariant manifold is

$$\Omega(\{(P^I, H^I, P^{II}, H^{II}) \in X : H^I = 0\}) = \{(1, 0, 1, 0)\}$$

This allows us to apply Theorem 2.2 and its Corollary 2.3 by Hutson (1984) to obtain persistence of the herbivore population in Patch I in the coupled system by using an average Lyapunov function $h(P^I, H^I, P^{II}, H^{II}) = H^I$. Similarly, we can show that the herbivore population is persistent in Patch II. Therefore, if $0 < r < 2, a(1-l) > 1$ and $0 < l < 1/2$, then the coupled system is permanent in both patches. □

B.4. Proof of Theorem 5.1

Proof. Let $\{P_i\}_{i=1}^k$ be a period-k orbit of the Ricker map $P_{n+1} = P_n e^{r(1-P_n)}$, then

$$\{(P_i, 0, 0, 0)\}_{i=1}^k, \quad \{(0, 0, P_i, 0)\}_{i=1}^k \quad \text{and} \quad \{(P_i, 0, P_i, 0)\}_{i=1}^k$$

are period-k orbit of the coupled system (5)–(8). From Lemma A.3, we know that $\sum_{i=1}^k P_i/k = 1$.

The transversal stability of these period-k orbits follow from the eigenvalues and their associated eigenvectors of the Jacobian matrix evaluated at these periodic orbits.

1. At $\{(P_i, 0, 0, 0)\}_{i=1}^k$ and $\{(0, 0, P_i, 0)\}_{i=1}^k$: Due to the symmetry of the coupled system, we will only focus on the eigenvalues and their associated eigenvectors of the Jacobian matrix evaluated at the period-k orbit $\{(P_i, 0, 0, 0)\}_{i=1}^k$. Similar results can be deduced for the period-k orbit $\{(0, 0, P_i, 0)\}_{i=1}^k$. The eigenvalues of the Jacobian matrix evaluated at the period-k orbit $\{(P_i, 0, 0, 0)\}_{i=1}^k$ are

$$\begin{aligned} \lambda_1 &= 0, \quad \lambda_2 = e^{kr} > 1, \quad \lambda_3 = \prod_{i=1}^k (1-rP_i), \\ \lambda_4 &= a^k (1-l)^k \prod_{i=1}^k P_i \leq a^k (1-l)^k \left(\frac{\sum_{i=1}^k P_i}{k} \right)^k \leq a^k (1-l)^k \end{aligned}$$

2. The eigenvalues of the Jacobian matrix evaluated $\{(P_i, 0, P_i, 0)\}_{i=1}^k$ are

$$\begin{aligned} \lambda_1 &= a^k \prod_{i=1}^k P_i \leq a^k, \quad \lambda_2 = a^k (1-2l)^k \prod_{i=1}^k P_i \leq a^k (1-2l)^k \\ \lambda_3 &= \lambda_4 = \prod_{i=1}^k (1-rP_i) \end{aligned}$$

where the values of λ_1 and λ_2 indicate the transversal stability of the period-k orbit $\{(P_i, 0, P_i, 0)\}_{i=1}^k$, i.e., if $|\lambda_1| < 1$ and $|\lambda_2| < 1$, then the period-k orbit $\{(P_i, 0, P_i, 0)\}_{i=1}^k$ is transversal stable in the invariant manifold $H^I = H^{II} = 0$. Since $a < 1$ ensures that $|\lambda_1| < 1$ and $|\lambda_2| < 1$. Any periodic orbits $\{(P_i, 0, P_i, 0)\}_{i=1}^k$ on the invariant manifold $H^I = H^{II} = 0$ of the coupled system (5)–(8) are transversally stable.

If, in addition, $2 < r < 2.52$ holds, then according to Lemma A.3 we can conclude that the coupled (5)–(8) has a locally stable period-2 orbits

$$(P_1, 0, P_1, 0), (P_2, 0, P_2, 0) \quad \text{where } P_i > 0, i = 1, 2 \quad \text{and} \\ |(1-rP_1)(1-rP_2)| < 1. \quad \square$$

References

Ackleh, A.S., Allen, L.J.S., Carter, J., 2007. Establishing a beachhead: a stochastic population model with an allee effect applied to species invasion. *Theoretical Population Biology* 71, 290–300.

Adler, R.F., 1993. Migration alone can produce persistence of host–parasitoid models. *The American Naturalist* 141, 642–650.

Allen, J.C., 1975. Mathematical models of species interactions in time and space. *The American Naturalist* 109, 319–342.

Amarasekare, P., 1998. Allee effects in metapopulation dynamics. *The American Naturalist* 152, 298–302.

Amarasekare, P., 2000. The geometry of coexistence. *Biological Journal of the Linnean Society* 71, 1–31.

Amarasekare, P., 2004. The geometry of coexistence. *Journal of Theoretical Biology* 226, 159–168.

Amezcu, A.B., Holyoak, M., 2000. Empirical evidence for predator–prey source-sink dynamics. *Ecology* 81, 3087–3098.

Briggs, C.J., Hoopes, M.F., 2004. Stabilizing effects in spatial parasitoid–host and predator–prey models: a review. *Theoretical Population Biology* 65, 299–315.

Comins, H.N., Hassell, M.P., 1976. Predation in multi-prey communities. *Journal of Theoretical Biology* 62, 93–114.

Courchamp, F., Berec, L., Gascoigne, J., 2009. *Allee Effects in Ecology and Conservation*. Oxford University Press.

Doebeli, M., 1997. Genetic variation and the persistence of predator–prey interactions in the Nicholson–Bailey model. *Journal of Theoretical Biology* 188, 109–120.

Drake, J.M., 2004. Allee effects and the risk of biological invasion. *Risk Analysis* 24, 795–802.

Edelstein-Keshet, L., 2005. *Mathematical Models in Biology*. SIAM Classics in Applied Mathematics.

Elaydi, S.N., Sacker, R., 2004. Basin of attraction of periodic orbits of maps in the real line. *Journal of Difference Equations & Applications* 10, 881–888.

Guckenheimer, J., Holmes, P., 1983. *Non-linear Oscillations, Dynamical Systems and Bifurcation of Vector Fields*. Springer-Verlag, New York.

- Gyllenberg, M., Söderbacka, G., Ericsson, S., 1993. Does migration stabilize local population dynamics? Analysis of a discrete metapopulation model. *Mathematical Biosciences* 118, 25–49.
- Hastings, A., 1993. Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology* 75, 1362–1372.
- Hirsch, M., Smale, S., 1974. *Differential Equations, Dynamical Systems, and Linear Algebra*. Academic Press, New York.
- Holt, R.D., 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28, 181–208.
- Hutson, V., 1984. A theorem on average Liapunov functions. *Monatshefte für Mathematik* 98, 267–275.
- Kang, Y., Chesson, P., 2010. Relative nonlinearity and permanence. *Theoretical Population Biology* 78, 26–35.
- Kang, Y., Lanchier, N., in press. Expansion or extinction: deterministic and stochastic two-patch models with Allee effects. *Journal of Mathematical Biology*, doi:10.1007/s00285-010-0359-3.
- Kang, Y., Armbruster, D., Kuang, Y., 2008. Dynamics of a plant–herbivore model. *Journal of Biological Dynamics* 2, 89–101.
- Kawasaki, K., Shigesada, N., 2007. An integrodifference model for biological invasions in a periodically fragmented environment. *Japan Journal of Industrial and Applied Mathematics* 24, 3–15.
- Kon, R., 2006. Multiple attractors in host–parasitoid interactions: coexistence and extinction. *Mathematical Biosciences* 201, 172–183.
- Kuang, J.J., Chesson, P., 2008. Predation–competition interactions for seasonally recruiting species. *The American Naturalist* 171, 119–133.
- Leung, B., Drake, J.M., Lodge, D.M., 2004. Predicting invasions: propagule pressure and the gravity of allee effects. *Ecology* 85, 1651–1660.
- Levin, S.A., 1974. Dispersion and population interactions. *The American Naturalist* 108, 207–228.
- Liebholt, A., Tobin, P.C., 2008. Population ecology of insect invasions and their management. *Annual Review of Entomology* 53, 387–408.
- Liebholt, A.M., Macdonald, W.L., Bergdahl, D., Mastro, V.C., 1995. Invasion by exotic forest pests: a threat to forest ecosystems. *Forest Science Monographs* 30.
- Malchow, H., Petrovskii, S.V., Venturino, E., 2008. *Spatiotemporal Patterns in Ecology and Epidemiology*. Chapman & Hall, Boca Raton.
- Maynard Smith, J., Slatkin, M., 1973. The stability of predator–prey systems. *Ecology* 54, 384–391.
- Nicholson, A.J., Bailey, V.A., 1935. The balance of animal populations, Part I. *Proceedings of the Zoological Society of London* 3, 551–598.
- Nishimura, K., Kishida, O., 2001. Coupling of two competitive systems via density dependent migration. *Ecological Research* 16, 359–368.
- Reeve, J.D., 1988. Environmental variability, migration, and persistence in host–parasitoid systems. *The American Naturalist* 132, 810–836.
- Salceanu, P.L., Smith, H., 2009. Lyapunov exponents and persistence in some discrete dynamical systems. *Discrete and Continuous Dynamical Systems Series B* 12, 187–203.
- Selgrade, J.F., Roberds, J.H., 2005. Results on asymptotic behaviour for discrete, two-patch metapopulations with density-dependent selection. *Journal of Difference Equations and Applications* 11, 459–476.
- Taylor, A.D., 1988. Parasitoid competition and the dynamics of host–parasitoid models. *The American Naturalist* 132, 417–436.
- Taylor, C.M., Hastings, A., 2005. Allee effects in biological invasions. *Ecology Letter* 8, 895–908.
- Yakubu, A.-A., 2000. Searching predator and prey dominance in discrete predator–prey systems with dispersion. *SIAM Journal of Applied Mathematics* 61, 870–888.
- Yakubu, A.-A., Castillo-Chavez, C., 2002. Interplay between local dynamics and dispersal in discrete-time metapopulation models. *Journal of Mathematical Biology* 218, 273–288.
- Zhou, S.-R., Wang, G., 2004. Allee-like effects in metapopulation dynamics. *Mathematical Biosciences* 189, 103–113.
- Zhou, S.-R., Liu, Y.-F., Wang, G., 2005. The stability of predator–prey systems subject to the Allee effects. *Theoretical Population Biology* 67, 23–31.