Effects of Predator and Prey Dispersal on Success or Failure of Biological Control

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Abstract Biological control, defined as the reduction of pest populations by natural enemies, is often a component of integrated pest management strategies. Augmentation of natural enemy numbers by planned releases is a common biological control method, the successes and failures of which have been extensively reviewed. The effectiveness of biological control is influenced by how populations of predators and prey (or hosts and parasitoids) disperse in patchy environments. Here, we address the question of whether such dispersal leads to beneficial or detrimental pest control outcomes by developing a simple predator-prey model with constant releases of natural enemies in a two-patch environment. Theoretical and numerical results for all possible cases indicate that population dispersal has significant effects on the persistence of pests. For some ranges of dispersal rates or parameter space, dispersal is beneficial for pest control measures but this is not so for other ranges when it is detrimental. Therefore, knowledge of pest and natural enemy dispersal is crucial for understanding the effectiveness of biological control in a patchy environment. Finally, the model is generalised for multi-patch systems.

Keywords Natural enemy \cdot Pest \cdot Biological control \cdot Dispersal

1. Introduction

Biological control, defined as the reduction of pest populations by natural enemies, is one component of integrated pest management strategies. Typically, it involves an active human role, often with augmentation of natural enemies usually by supplemental releases. Biological control has been used against weeds and vertebrate pests such as rabbits as well

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as to control invertebrates including nematodes, insects, and arachnids. The controlling agents used have included insect predators and parasitoids, predatory mites, entomopathogenic nematodes, and vertebrates. The latter have included cane toads against beetles such as white-grub *Phyllophaga* spp. and Cane Beetles *Dermolepida alboatristum*, and ducks to control locusts *Locusta migratoria*. In addition, microbial agents such as bacteria, viruses, and fungi are also used in biological control programmes. Thus, biological control is an important subject in applied ecology in theory and practice. Theoretical treatments include the host-parasitoid models of Nicholson–Bailey (1935) recently expanded by Tang and Cheke (2008) and the classic predator-prey models of Lotka (1920) and Volterra (1931). However, neither Nicholson and Bailey nor Lotka and Volterra dealt specifically with dispersal, another important topic in applied ecology (see papers in DeBach and Rosen, 1991), although laboratory studies have investigated the effects of manipulating dispersal on the outcome of predator-prey interactions (Huffaker, 1958; Takafuji, 1976) and the roles of host and parasitoid dispersal have been considered theoretically (Hassell, 1978, 2000). Dispersal is also fundamental to the concept of metapopulations (Levins, 1970; Hanski and Gilpin, 1997). Several workers have elaborated on metapopulation models addressing dispersal issues and there have also been publications on dispersal applied to host-pathogen dynamics (Dwyer and Hails, 2002). Here, we link biological control models with metapopulation concepts to address the question of whether, theoretically, dispersal by predators and/or their prey promotes or inhibits the success of biological control.

Dispersal of pests and natural enemies has significant effects on pest control, but in practice, more information is required on the dispersal of both natural enemies and pests to assess the success or failure of biological control operations. Therefore, the quantification of the movement patterns of pest species is necessary information to underpin theories on spatial dynamics and pest management. For instance, dispersal is a major aspect of the life-history of many insects and is often believed to be a stabilizing force in their population dynamics (Stein et al., 1994) and dispersal patterns of herbivorous insects in agroecosystems have been associated with pest outbreaks (Kareiva, 1982). On the other hand, studies on the dispersal of natural enemies have demonstrated the importance of movement in the efficiency of inundative releases (Saavedra et al., 1997; McDougall and Mills, 1997) and in the establishment of insects introduced for insect pest control (Hopper and Roush, 1993).

The successes and failures of biological control have been extensively reviewed (DeBach and Rosen, 1991; Collier and Van Steenwyk, 2004; Stiling and Cornelissen, 2005). A number of factors can influence the effectiveness of biological control agents including agent specificity (generalist or specialist), the type of agent (predator, parasitoid, or pathogen), the timing and number of releases, the method of release, synchrony of the natural enemy with the host, field conditions, and release rate (DeBach and Rosen, 1991; Van den Driesche and Bellows, 1996; Collier and Van Steenwyk, 2004; Stiling and Cornelissen, 2005).

Many research papers have assessed the relative impact of release rates on the effectiveness of augmentative biological control. Augmentative or inundative, biological control is the release of large numbers of natural enemies to augment natural enemy populations or to inundate pest populations with natural enemies. Collier and Van Steenwyk (2004) reviewed articles in which the effectiveness of augmentative biological control agents as a function of release rates were measured. The effect of release rates on the successful implementation of augmentative biological control was assessed when parasitoids
and predators were utilized as biological control agents. In addition, the relative impact of release rates was compared with factors such as the method and timing of releases and when pesticides were used in conjunction with biological control agents.

The aim of this paper is to investigate how population dispersal affects the persistence of pests and whether it is beneficial to pest control or not. The difference between success and failure in biological control can be due to exogenous limitations or to endogenous processes. We focus on population dispersal to find more general aspects of the interactions between natural enemies and pests in a patchy environment that can be used to improve success and minimize the risks of biological control.

We propose a simple prey-predator model with constant releasing of natural enemies in a two-patch environment. Theoretical and numerical results for all possible cases indicate that population dispersal has significant effects on the persistence of pests. For some ranges of dispersal rates or parameter space, population dispersal is beneficial to pest control; for other ranges of dispersal rates, the results imply that population dispersal is detrimental to pest control. Therefore, knowledge of pest and natural enemy dispersal is crucial for understanding the effectiveness of biological control in a patchy environment. The methods developed here can be extended to a general model.

2. A simple model with constant releasing of natural enemies

Consider the classical pest and natural enemy interaction model with the addition of a constant releasing rate of natural enemies, i.e. the following Lotka–Volterra model:

\[
\begin{aligned}
\frac{dx(t)}{dt} &= ax(t) - bx(t)y(t), \\
\frac{dy(t)}{dt} &= cx(t)y(t) - dy(t) + u,
\end{aligned}
\]  

(1)

where \(x, y\) denote the number of pests and natural enemies, respectively. \(a, b, c, d,\) and \(u\) are positive constants.

The assumptions in the model (1) are: (i) The pest grows unboundedly in a Malthusian way in the absence of any predation, governed by the \(ax\) term in (1). (ii) The effect of the natural enemy is to reduce the pest’s per capita growth rate by a term proportional to the pest and natural enemy populations; this is the \(-bxy\) term. (iii) In the absence of any pest for sustenance, the natural enemy’s death rate results in exponential decay, the \(dy\) term in (1). (iv) The pest’s contribution to the natural enemy’s growth rate is \(cxy\); that is, it is proportional to the available prey as well as to the size of the predator population. (v) The release rate of natural enemies is a constant \(u\).

It is easy to see that there are two steady states: \(E^* = (0, y^*) = (0, \frac{u}{d})\), and if \(u < \frac{ad}{b}\) then there is an unique interior equilibrium \(E_*(x_*, y_*)\) with \(x_* = \frac{b}{ac}[\frac{ad}{b} - u], y_* = \frac{a}{b}\). By linearization stability analysis, we see that if \(u > \frac{ad}{b}\) then the equilibrium with pest eradication (EPE) \(E^*\) is locally stable; if \(u < \frac{ad}{b}\) then the interior equilibrium \(E_*\) is locally stable. Similarly, we can define the threshold value \(R_u = \frac{ad}{bu} = \frac{a}{by^*}\), and thus if \(R_u < 1\) then the EPE \(E^*\) is stable. Otherwise, it is unstable.
Furthermore, $E_*$ is globally stable under the existence condition $u < \frac{ad}{b}$ or $R_u < 1$. In fact, if we choose the following Lyapunov function

$$V = x_\ast\left[\frac{x}{x_\ast} - \ln\frac{x}{x_\ast}\right] + \frac{b}{c}y_\ast\left[\frac{y}{y_\ast} - \ln\frac{y}{y_\ast}\right]$$

(2)

and the following is satisfied

$$\frac{dV}{dt} = -b(x - x_\ast)(y - y_\ast) + \frac{b}{c}(y - y_\ast)\left[c(x - x_\ast) + \frac{u}{y} - \frac{u}{y_\ast}\right]$$

$$= \frac{bu}{c}(y - y_\ast)\left[\frac{1}{y} - \frac{1}{y_\ast}\right]$$

$$= -\frac{bu}{cyy_\ast}(y - y_\ast)^2 \leq 0,$$  

(3)

then the interior equilibrium $E_*$ is globally stable, if it exists. Similarly, if we choose the Lyapunov function

$$V = x + \frac{b}{c}y^\ast\left[\frac{y}{y^\ast} - \ln\frac{y}{y^\ast}\right]$$

(4)

we can prove the global stability of equilibrium $E^\ast$.

The simple model (1) implies that we can control the release rate $u$ of natural enemies such that $R_u < 1$, i.e. the EPE is globally stable, and the effect of releasing rates on the successful implementation of biological control can be assessed through the threshold condition $R_u > 1$ or $R_u < 1$.

3. Two-patch model

The main aim of this paper is to investigate how dispersal in a patchy environment influences pest control. So, let us consider the following model which allows the populations to move within two patches

$$\begin{align*}
\frac{dx_1(t)}{dt} &= a_1x_1(t) - b_1x_1(t)y_1(t) + d_{21}x_2(t) - d_{12}x_1(t), \\
\frac{dy_1(t)}{dt} &= c_1x_1(t)y_1(t) - d_1y_1(t) + u_1 + D_{21}y_2(t) - D_{12}y_1(t), \\
\frac{dx_2(t)}{dt} &= a_2x_2(t) - b_2x_2(t)y_2(t) - d_{21}x_2(t) + d_{12}x_1(t), \\
\frac{dy_2(t)}{dt} &= c_2x_2(t)y_2(t) - d_2y_2(t) + u_2 - D_{21}y_2(t) + D_{12}y_1(t),
\end{align*}$$

(5)

where $x_i$ ($i = 1, 2$) is the number of pests in patch $i$, $y_i$ is the number of natural enemies in patch $i$, $d_{12}, d_{21}, D_{12}, D_{21}$ are non-negative constants. $d_{ij}$ ($i, j = 1, 2, i \neq j$) represents the immigration rate of pests from the $i$th patch to the $j$th patch, and $D_{ij}$ ($i, j = 1, 2,$
i \neq j$) represents the immigration rate of natural enemies from the \( i \)th patch to the \( j \)th patch. All other parameters in model (5) are identical to those in model (1).

Rearranging system (5) yields

\[
\begin{aligned}
\frac{dx_1(t)}{dt} &= (a_1 - d_{12})x_1(t) - b_1x_1(t)y_1(t) + d_{21}x_2(t), \\
\frac{dx_2(t)}{dt} &= (a_2 - d_{21})x_2(t) - b_2x_2(t)y_2(t) + d_{12}x_1(t), \\
\frac{dy_1(t)}{dt} &= c_1x_1(t)y_1(t) - (d_1 + D_{12})y_1(t) + u_1 + D_{21}y_2(t), \\
\frac{dy_2(t)}{dt} &= c_2x_2(t)y_2(t) - (d_2 + D_{21})y_2(t) + u_2 + D_{12}y_1(t).
\end{aligned}
\tag{6}
\]

In the following, we will focus on model (6) and investigate its dynamical behavior and the biological implications.

3.1. Natural enemy subsystem

Let \( x_1 = 0, x_2 = 0 \) in system (6), and consider the following natural enemy subsystem

\[
\begin{aligned}
\frac{dy_1(t)}{dt} &= -(d_1 + D_{12})y_1(t) + u_1 + D_{21}y_2(t), \\
\frac{dy_2(t)}{dt} &= -(d_2 + D_{21})y_2(t) + u_2 + D_{12}y_1(t).
\end{aligned}
\tag{7}
\]

It is easy to see that the system (6) has an unique positive equilibrium \( E^* = (y_{u_1}^*, y_{u_2}^*) \) with

\[
y_{u_1}^* = \frac{D_{21}u_2 + u_1D_{21} + u_1d_2}{d_1d_2 + d_1D_{21} + D_{12}d_2}, \quad y_{u_2}^* = \frac{d_1u_2 + D_{12}u_2 + D_{12}u_1}{d_1d_2 + d_1D_{21} + D_{12}d_2}.
\]

Its characteristic equation has two negative eigenvalues, which means that \( E^* \) is globally asymptotically stable due to the model’s linearity.

3.2. The stability and threshold conditions of EPE of model (6)

Based on Section 3.1, it is seen that the two-patch system (6) has an unique EPE \( E^* \triangleq (0, 0, y_{u_1}^*, y_{u_2}^*) \) and its stability can be determined by the eigenvalues of the following Jacobian matrix:

\[
J_{E^*} = \begin{pmatrix}
(a_1 - d_{12}) - b_1y_{u_1}^* & d_{21} & 0 & 0 \\
d_1 & (a_2 - d_{21}) - b_2y_{u_2}^* & 0 & 0 \\
c_1y_{u_1}^* & 0 & -(d_1 + D_{12}) & D_{21} \\
0 & c_2y_{u_2}^* & D_{12} & -(d_2 + D_{21})
\end{pmatrix}
\triangleq \begin{pmatrix}
A & 0 \\
B & C
\end{pmatrix}
\tag{8}
\]
This is a lower block triangular matrix, and all eigenvalues of $C$ have negative real parts. Therefore, the stability of the equilibrium with pest eradication $E^r$ can be determined by the eigenvalues of matrix $A$, and its characteristic equation is

$$\lambda^2 - \beta_1 \lambda + \beta_2 = 0$$  \hspace{1cm} (9)

with

$$\beta_1 = a_1 + a_2 - d_{21} - d_{12} - b_1 y^*_u_1 - b_2 y^*_u_2$$

and

$$\beta_2 = [a_1 - d_{12} - b_1 y^*_u_1][a_2 - d_{21} - b_2 y^*_u_2] - d_{21}d_{12}.$$  \hspace{1cm} (10)

Let $s(A)$ be the maximum real part of the eigenvalues of matrix $A$ and $\rho(A)$ be the spectral radius of matrix $A$. It is easy to see that

$$s(A) = \frac{\beta_1 + \sqrt{\beta_1^2 - 4\beta_2}}{2}$$

$$= \frac{(a_1 - d_{12} - b_1 y^*_u_1) + (a_2 - d_{21} - b_2 y^*_u_2) + \sqrt{[(a_1 - d_{12} - b_1 y^*_u_1) - (a_2 - d_{21} - b_2 y^*_u_2)]^2 + 4d_{21}d_{12}}}{2}.$$  \hspace{1cm} (11)

Thus, if we set the threshold value $R_{u_1u_2}$ which determines the stability of the equilibrium with pest eradication $E^r$, i.e. $s(A) < 0$ if and only if $R_{u_1u_2} < 1$. It follows from the definition of $s(A)$ that $R_{u_1u_2} > 1$ if and only if $\beta_1 > 0$ or

$$\beta_1 \leq 0 \text{ and } \beta_2 < 0;$$  \hspace{1cm} (12)

$R_{u_1u_2} < 1$ if and only if

$$\beta_1 \leq 0 \text{ and } \beta_2 > 0.$$  \hspace{1cm} (13)

The condition $\beta_1 > 0$ means that the sum of intrinsic growth rates of pests in two patches is larger than the total removal rate of pest populations in two patches. According to the definitions of $y^*_u_1$, $y^*_u_2$, we can rearrange $\beta_1$ as follows:

$$\beta_1 = b_1 y^*_u_1 \left[ \frac{a_1 - d_{12}}{b_1 y^*_u_1} - 1 \right] + b_2 y^*_u_2 \left[ \frac{a_2 - d_{21}}{b_2 y^*_u_2} - 1 \right],$$  \hspace{1cm} (14)

and $\beta_2$ becomes

$$\beta_2 = b_1 b_2 y^*_u_1 y^*_u_2 \left[ \frac{a_1 - d_{12}}{b_1 y^*_u_1} - 1 \right] \left[ \frac{a_2 - d_{21}}{b_2 y^*_u_2} - 1 \right] - d_{21}d_{12}$$

$$= b_1 b_2 y^*_u_1 y^*_u_2 \left[ \left( \frac{a_1 - d_{12}}{b_1 y^*_u_1} - 1 \right) \left( \frac{a_2 - d_{21}}{b_2 y^*_u_2} - 1 \right) - \frac{d_{21}d_{12}}{b_1 b_2 y^*_u_1 y^*_u_2} \right].$$  \hspace{1cm} (15)
In expressions (13) and (14), \( \frac{a_1 - d_1}{b_1 y_1} \) can be considered as a threshold value at the first patch, and \( \frac{a_2 - d_2}{b_2 y_2} \) a threshold value at the second patch. Therefore, if \( \frac{a_1 - d_1}{b_1 y_1} < 1 \) and \( \frac{a_2 - d_2}{b_2 y_2} < 1 \), then we have \( \beta_1 < 0 \) and the sign of \( \beta_2 \) depends on the dispersal rates of the pests and natural enemies, which means that the different dispersal rates may result in different dynamical behaviour of model (6). The numerical results shown in Fig. 1 indicate how the dispersal of natural enemies affects the sign of \( \beta_2 \).

In the following, we will show that if \( s(A) < 0 \) (i.e. \( R_{u_1 u_2} < 1 \)), then the equilibrium with pest eradication \( E^r \) is globally stable. In fact, it follows from the non-negativity of solutions of system (6) that we have

\[
\begin{align*}
\frac{dy_1(t)}{dt} &\geq -(d_1 + D_{12})y_1(t) + u_1 + D_{21}y_2(t), \\
\frac{dy_2(t)}{dt} &\geq -(d_2 + D_{21})y_2(t) + u_2 + D_{12}y_1(t),
\end{align*}
\]

(15)

which means for sufficiently large \( t \) and small \( \epsilon > 0 \) that we have

\[(y_1(t), y_2(t)) > (y_{u_1}^\ast - \epsilon, y_{u_2}^\ast - \epsilon).\]
Without loss of generality, we assume that the above inequality holds true for all $t \geq 0$. Consequently, we have
\[
\begin{align*}
\frac{dx_1(t)}{dt} &\leq (a_1 - d_{12})x_1(t) - b_1x_1(t)(y_{u_1}^* - \varepsilon) + d_{21}x_2(t), \\
\frac{dx_2(t)}{dt} &\leq (a_2 - d_{21})x_2(t) - b_2x_2(t)(y_{u_2}^* - \varepsilon) + d_{12}x_1(t).
\end{align*}
\] (16)

Then it suffices to show that positive solutions of the following auxiliary system
\[
\begin{align*}
\frac{dx_1(t)}{dt} &= (a_1 - d_{12})x_1(t) - b_1x_1(t)(y_{u_1}^* - \varepsilon) + d_{21}x_2(t), \\
\frac{dx_2(t)}{dt} &= (a_2 - d_{21})x_2(t) - b_2x_2(t)(y_{u_2}^* - \varepsilon) + d_{12}x_1(t),
\end{align*}
\] (17)
tend to zero as $t$ goes to infinity. Let $A_1$ be the matrix defined by
\[A_1 = \text{diag}(-b_1, -b_2).\]

Since $s(A) < 0$ and $s(A + \varepsilon A_1)$ are continuous for small $\varepsilon$, so when $\varepsilon$ is small enough we still have $s(A + \varepsilon A_1) < 0$. Consequently, the solutions of the model (16) approach zero as $t$ tends to infinity, which implies that the equilibrium with pest eradication $E^r$ is globally stable if $R_{u_1}u_2 < 1$ holds true.

The conditions which guarantee the stability of EPE clearly show the effect of population dispersal on the persistence of the pest. We will address this in more detail in the coming sections.

3.3. Some special cases

In the absence of population dispersal between two patches, i.e. $d_{21} = d_{12} = D_{21} = D_{12} = 0$, the system (5) reduces to two independent subsystems
\[
\begin{align*}
\frac{dx_1(t)}{dt} &= a_1x_1(t) - b_1x_1(t)y_1(t), \\
\frac{dy_1(t)}{dt} &= c_1x_1(t)y_1(t) - d_1y_1(t) + u_1
\end{align*}
\] (18)
and
\[
\begin{align*}
\frac{dx_2(t)}{dt} &= a_2x_2(t) - b_2x_2(t)y_2(t), \\
\frac{dy_2(t)}{dt} &= c_2x_2(t)y_2(t) - d_2y_2(t) + u_2.
\end{align*}
\] (19)

It follows from Section 2 that the EPEs in each isolated patch are $(0, y_1^*) = (0, \frac{a_1}{b_1})$ and $(0, y_2^*) = (0, \frac{a_2}{b_2})$, respectively. Further, if the threshold values $R_{u_1} = \frac{a_1}{b_1y_1^*} < 1$ and $R_{u_2} = \frac{a_2}{b_2y_2^*} < 1$, then the EPEs $(0, y_1^*)$ and $(0, y_2^*)$ are globally stable in two isolated patches; if $R_{u_1} > 1$ and $R_{u_2} > 1$, then the pest population can be persistent in each isolated patch.
In the following, we will address how population dispersal affects the stability of EPE $E^\ast$, i.e. the persistence of pests in both patches when dispersal occurs within two patches.

Assume first that the pest population can be persistent in each isolated patch, i.e., $R_{u_i} > 1, i = 1, 2$. It follows from (10) that we have

$$2s(A) = \left( a_1 - d_{12} - b_1 y_{u_1}^\ast \right) + \left( a_2 - d_{21} - b_2 y_{u_2}^\ast \right)$$

$$+ \sqrt{\left[ \left( a_1 - d_{12} - b_1 y_{u_1}^\ast \right) - \left( a_2 - d_{21} - b_2 y_{u_2}^\ast \right) \right]^2 + 4d_{21}d_{12}}. \quad (20)$$

If $d_{21} = d_{12}$, then we have

$$2s(A) = \left( a_1 - b_1 y_{u_1}^\ast \right) + \left( a_2 - b_2 y_{u_2}^\ast \right) - 2d_{21}$$

$$+ \sqrt{\left[ \left( a_1 - b_1 y_{u_1}^\ast \right) - \left( a_2 - b_2 y_{u_2}^\ast \right) \right]^2 + 4d_{21}^2}$$

$$\geq \left( a_1 - b_1 y_{u_1}^\ast \right) + \left( a_2 - b_2 y_{u_2}^\ast \right)$$

$$= a_1 \left[ 1 - \frac{1}{R_{u_1}} \frac{d_2 + D_{21} + D_{21}u_2/u_1}{d_2 + D_{21} + D_{12}d_2/d_1} \right]$$

$$+ a_2 \left[ 1 - \frac{1}{R_{u_2}} \frac{d_1 + D_{12} + D_{12}u_1/u_2}{d_1 + D_{12} + D_{21}d_1/d_2} \right]. \quad (21)$$

Thus, if the parameters $D_{12}, D_{21}, d_1, d_2, u_1, u_2$ satisfy the balance equation

$$\frac{D_{21}u_2}{d_2} = \frac{D_{12}u_1}{d_1}, \quad (22)$$

then we have $s(A) > 0$, i.e. $R_{u_1u_2} > 1$ holds true. Of course, the balance equation is satisfied if $D_{21} = D_{12}, d_1 = d_2, u_1 = u_2$. Therefore, we can conclude that if the dispersal rates of the pest populations in the two patches are equal (i.e. $d_{12} = d_{21}$), and the parameters $D_{12}, D_{21}, d_1, d_2, u_1, u_2$ related to natural enemies in two patches satisfy the balance equation (22), then the dispersal of populations does not affect the persistence of the pest population, i.e. the pest population can also be persistent in both patches when population dispersal occurs and $R_{u_i} > 1, i = 1, 2$. Thus, during the lifetime of the predator with persistence of the pest assumed, the values of the fractions on each side of Eq. (22) could be equivalent, leading to a balance, even though the dispersal rates, death rates, and rates of release could differ in each patch. If this holds true, it means that the end result of dispersal and additions from releases in one patch is the same as in the other patch over the lifetime of the predator in both patches. We also note that if $D_{21} = D_{12} = 0$ (i.e. the predator populations cannot disperse between the two patches) and $d_{21} = d_{12} > 0$, it is easily obtained that $s(A) > 0$, i.e. $R_{u_1u_2} > 1$ holds true when $R_{u_i} > 1, i = 1, 2$.

Now suppose that the pest has been eradicated in each isolated patch, i.e. $R_{u_i} < 1, i = 1, 2$. Similarly, if $d_{12} = d_{21}$, then we have

$$2s(A) = \left( a_1 - b_1 y_{u_1}^\ast \right) + \left( a_2 - b_2 y_{u_2}^\ast \right) - 2d_{21}$$

$$+ \sqrt{\left[ \left( a_1 - b_1 y_{u_1}^\ast \right) - \left( a_2 - b_2 y_{u_2}^\ast \right) \right]^2 + 4d_{21}^2}$$.  

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\[
= (a_1 - b_1 y_{u_1}^*) + (a_2 - b_2 y_{u_2}^*) \\
+ \frac{[(a_1 - b_1 y_{u_1}^*) - (a_2 - b_2 y_{u_2}^*)]^2}{\sqrt{[(a_1 - b_1 y_{u_1}^*) - (a_2 - b_2 y_{u_2}^*)]^2 + 4d_2^2 + 2d_1}} \\
\leq (a_1 - b_1 y_{u_1}^*) + (a_2 - b_2 y_{u_2}^*) + |(a_1 - b_1 y_{u_1}^*) - (a_2 - b_2 y_{u_2}^*)| \\
= 2\max\{a_1 - b_1 y_{u_1}^*, a_2 - b_2 y_{u_2}^*\} \\
= 2\max\left\{a_1 \left[ 1 - \frac{1}{R_{u_1}} \frac{d_2 + D_{21} + D_{21u_2}/u_1}{d_2 + D_{21} + D_{12}d_2/d_1} \right], \right. \\
\left. a_2 \left[ 1 - \frac{1}{R_{u_2}} \frac{d_1 + D_{12} + D_{12u_1}/u_2}{d_1 + D_{12} + D_{21}d_1/d_2} \right] \right\}. \quad (23)
\]

Therefore, if the balance equation (22) holds true or more specifically if \(D_{21} = D_{12}, d_1 = d_2, u_1 = u_2\), then we have \(s(A) < 0\), i.e. \(R_{u_1}u_2 < 1\). It follows that the pest population has also been eradicated in both patches when population dispersal occurs. In this case, if the natural enemy population cannot disperse between the two patches, i.e. \(D_{12} = D_{21}\), it is easy to show that \(s(A) < 0\), i.e. \(R_{u_1}u_2 < 1\) holds true when \(R_{u_i} < 1, i = 1, 2\). Therefore, we also see that in this special case the dispersal of populations does not affect the persistence of the pest population in two patches.

Finally, let us consider \(R_{u_1} > 1\) and \(R_{u_2} < 1\) (or \(R_{u_1} < 1\) and \(R_{u_2} > 1\)), and see how the dispersal affects control of the pest. For this case, we consider the following special cases.

Assume that \(d_{21} = d_{12} = 0, D_{12} > 0\) and \(D_{21} > 0\), then we have

\[
2s(A) = (a_1 - b_1 y_{u_1}^*) + (a_2 - b_2 y_{u_2}^*) + \sqrt{[(a_1 - b_1 y_{u_1}^*) - (a_2 - b_2 y_{u_2}^*)]^2} \\
= (a_1 - b_1 y_{u_1}^*) + (a_2 - b_2 y_{u_2}^*) + |(a_1 - b_1 y_{u_1}^*) - (a_2 - b_2 y_{u_2}^*)| \\
= 2\max\{a_1 - b_1 y_{u_1}^*, a_2 - b_2 y_{u_2}^*\} \\
= 2\max\left\{a_1 \left[ 1 - \frac{1}{R_{u_1}} \frac{d_2 + D_{21} + D_{21u_2}/u_1}{d_2 + D_{21} + D_{12}d_2/d_1} \right], \right. \\
\left. a_2 \left[ 1 - \frac{1}{R_{u_2}} \frac{d_1 + D_{12} + D_{12u_1}/u_2}{d_1 + D_{12} + D_{21}d_1/d_2} \right] \right\}. \quad (24)
\]

If

\[
s(A) = a_1 \left[ 1 - \frac{1}{R_{u_1}} \frac{d_2 + D_{21} + D_{21u_2}/u_1}{d_2 + D_{21} + D_{12}d_2/d_1} \right], \quad (25)
\]

then the sign of \(s(A)\) is determined by the sign of

\[
1 - \frac{1}{R_{u_1}} \frac{d_2 + D_{21} + D_{21u_2}/u_1}{d_2 + D_{21} + D_{12}d_2/d_1},
\]

from which we can define the threshold value \(R_0 = R_{u_1} \frac{d_2 + D_{21} + D_{21u_2}/u_1}{d_2 + D_{21} + D_{12}d_2/d_1}\). Thus, if \(R_0 > 1\), then the pest population is persistent. Otherwise, it will be eradicated. Therefore, if
\( R_{u_1} > 1 \) and \( R_{u_2} < 1 \), i.e. the predator in the first patch has a higher chance to attack the prey than those in the second patch. So, the predator populations are more likely to move from the second patch to the first patch, which clarifies that the dispersal rate \( D_{21} \) should be larger than \( D_{12} \). If so, we can choose \( D_{12} \) as a parameter, and fix all others in \( R_0 \), then \( R_0 < 1 \) implies that

\[
\frac{d_2 + D_{21} + D_{12}d_2/d_1}{d_2 + D_{21} + D_{21}u_2/u_1} < 1, \tag{26}
\]

i.e.

\[
D_{12} < \frac{d_1 (d_1 + D_{21})(1 - R_{u_1}) + D_{21}u_2/u_1}{R_{u_1}}. \tag{27}
\]

If

\[
s(A) = a_2 \left[ 1 - \frac{1}{R_{u_2}} \frac{d_1 + D_{12} + D_{12}u_1/u_2}{d_1 + D_{12} + D_{12}d_1/d_2} \right]. \tag{28}
\]

we can also define the threshold value \( R_0 = R_{u_2} \frac{d_1 + D_{12} + D_{12}d_1/d_2}{d_1 + D_{12} + D_{12}u_1/u_2} \) and obtain results similar to the above.

Based on the above discussion, we obtain that \( s(A) < 0 \) (\( R_{u_1}<1 \)) if and only if \( R_0 < 1 \) and \textit{vice versa}. These results imply that we can control the dispersal rates \( D_{12} \) and \( D_{21} \) such that \( R_{u_1}<1 \) or \( R_{u_2}<1 \), which means whether the pest population will be eradicated in both patches or not depends on the dispersal rates, even if the pest is persistent in a single isolated patch. The results also clarify that predator population dispersal reduces pest outbreaks and is beneficial to pest control. Similarly, when \( R_{u_1} < 1 \) and \( R_{u_2} > 1 \) we can obtain the same results.

Now assume that \( D_{12} = D_{21} = 0, d_{12} > 0, d_{21} > 0 \), then \( y^*_{u_1} = y^*_1 = \frac{u_1}{d_1}, y^*_{u_2} = y^*_2 = \frac{u_2}{d_2} \).

If \( R_{u_1} = \frac{a_1}{b_1} y^*_1 > 1 \) and \( R_{u_2} = \frac{a_2}{b_2} y^*_2 < 1 \), according to the formulae for \( \beta_1 \) and \( \beta_2 \) given in (13) and (14), we have

\[
\beta_1 = b_1 y^*_1 \left[ \frac{a_1 - d_{12}}{b_1 y^*_1} - 1 \right] + b_2 y^*_2 \left[ \frac{a_2 - d_{21}}{b_2 y^*_2} - 1 \right]
= a_1 \left[ 1 - \frac{1}{R_{u_1}} \right] + a_2 \left[ 1 - \frac{1}{R_{u_2}} \right] - d_{12} - d_{21}; \tag{29}
\]

and

\[
\beta_2 = b_1 b_2 y^*_1 y^*_2 \left[ \frac{a_1 - d_{12}}{b_1 y^*_1} - 1 \right] \left[ \frac{a_2 - d_{21}}{b_2 y^*_2} - 1 \right] - d_{21} d_{12}
= \left[ a_1 \left( 1 - \frac{1}{R_{u_1}} \right) - d_{12} \right] \left[ a_2 \left( 1 - \frac{1}{R_{u_2}} \right) - d_{21} \right] - d_{12} d_{21}. \tag{30}
\]

Thus, according to the sufficient and necessary conditions which guarantee the \( s(A) > 0 \), in this special case we can easily get the threshold conditions such that \( s(A) > 0 \) (\( R_{u_1 u_2} > 1 \)) or \( s(A) < 0 \) (\( R_{u_1 u_2} < 1 \), or \( \beta_1 \leq 0 \) and \( \beta_2 > 0 \)) from the formulae for \( \beta_1 \).
and $\beta_2$ given by (29) and (30). In particular, we can obtain the threshold values of dispersal rates of the pest populations such that they disappear in both patches. Therefore, the results also clarify that pest dispersal reduces their outbreaks and is beneficial to pest control in certain parameter spaces. But we also note that population dispersal may result in more severe outbreaks of pests. This indicates that population dispersal can also be detrimental to pest control and this will be addressed in more detail in the coming section.

4. Numerical investigations and biological implications

Knowledge of pest and natural enemy dispersal and population dynamics are crucial for understanding and predicting pest outbreaks and for developing pest management and control strategies. In the previous section, we theoretically investigated how population dispersal affects the persistence of pests. For the simple system (5), the results obtained in Section 3 imply that we can only obtain the threshold conditions at which the pest may or may not outbreak for some special cases, and it was not easy to get the threshold conditions under the complete parameter space. Thus, in the following, we address how the dispersal of pest and natural enemy populations affects the extinction and persistence of the pest numerically. In particular, we focus on the following three cases:

Case 1 $R_{u_1} > 1$ and $R_{u_2} < 1$, i.e. the pest can be persistent in the first isolated patch and dies out in the second isolated patch.

If we fix the parameters as follows:

\[
\begin{align*}
a_1 &= 4, & b_1 &= 0.7, & c_1 &= 0.2, & d_1 &= 0.1, & a_2 &= 1, \\
b_2 &= 0.3, & c_2 &= 0.2, & d_2 &= 0.1, & u_2 &= 0.5, & u_1 &= 0.5, \\
d_{12} &= 0.4, & d_{21} &= 0.4
\end{align*}
\]  

(31)

and let $D_{12}, D_{21}$ vary; it follows that we have $R_{u_1} = 1.1429, R_{u_2} = 0.6667$, which means that the pest can be persistent in the first isolated patch and dies out in the second isolated patch. Now let $D_{12}$ and $D_{21}$ vary from 0 to 1, and we numerically calculate the values of $s(A)$ as shown in Fig. 2(A). The results shown in Fig. 2(A) clarify the effects of dispersal of natural enemies on the sign of $s(A)$, i.e. the persistence of the pest depends on the dispersal rates of natural enemies.

For this case, in order to reduce the number of pests in the first patch such that $s(A) < 0$ ($R_{u_1u_2} < 1$, i.e. the pest dies out in both patches), intuitively the dispersal rate $D_{21}$ should be larger than the dispersal rate $D_{12}$ because the pest can outbreak or has a larger number in the first patch, and the results shown in Fig. 2(A) confirm this. But if we further increase the dispersal rate $D_{21}$ of natural enemies from the second patch to the first patch and maintain the dispersal rate $D_{12}$ relatively small, the results shown in Fig. 2(A) imply that the pests can be persistent in both patches. In fact, if $D_{21} \gg D_{12}$, then most of the natural enemies in the second patch move from this patch to the first patch such that populations of local natural enemies in the second patch are too low and cannot suppress the pests in the second patch any more. Consequently, the pests outbreak in both patches.

Similarly, we can fix $D_{12}, D_{21}$ and study the effects of varying dispersal rates of the pests on their persistence in both patches. For example, if we choose $d_{21}, d_{12}$ as parameters, and fix $D_{21} = D_{12} = 0.4$ and the others are as given in (31). The values of $s(A)$ with
Fig. 2 The effects of population dispersal on the persistence ($s(A) > 0$) of pests. (A) The effects of predator dispersal on the pest persistence, where $D_{12}, D_{21}$ vary from 0 to 1 and all other parameters are as given in (31). (B) The effects of pest dispersal on its persistence, where $d_{12}, d_{21}$ vary from 0 to 1 and all other parameters are as given in (31).
respect to $d_{12}$ and $d_{21}$ imply that in this case the pests can only be eradicated if their dispersal rate from the first patch to the second patch is relatively large and the dispersal rate of pests from the second patch to the first patch is relatively small (Fig. 2(B)).

If $R_{u_1} < 1$ and $R_{u_2} > 1$, i.e. the pests can be persistent in the second isolated patch and die out in the first isolated patch, we can obtain results similar to those shown in Case 1.

**Case 2** $R_{u_1} > 1$ and $R_{u_2} > 1$, i.e. the pests can be persistent in each isolated patch.

What we want to know in this case is whether we can control the dispersal rates of the pests and natural enemies such that the EPE is stable (i.e. $s(A) < 0$ or $R_{u_1} R_{u_2} < 1$). To address this question, we fix parameters as follows:

\[
\begin{align*}
a_1 &= 4, & b_1 &= 0.7, & c_1 &= 0.2, & d_1 &= 0.1, & a_2 &= 2, \\
b_2 &= 0.35, & c_2 &= 0.2, & d_2 &= 0.1, & u_1 &= 0.5, & u_2 &= 0.5, \\
d_{12} &= 0.05, & d_{21} &= 0.95
\end{align*}
\]  

and let $D_{12}$ vary from 0 to 0.8, and $D_{21}$ vary from 0 to 1. It follows from the formulae for $R_{u_1}$ and $R_{u_2}$ that we have $R_{u_1} = 1.1429$, $R_{u_2} = 1.1429$, i.e. the pests outbreak in both isolated patches.

The results shown in Fig. 3(A) clearly indicate that $s(A)$ is negative for some plane parameter ranges of $D_{12}$ and $D_{21}$, and this is more likely to happen only when $D_{12} \approx D_{21}$. Note also that if we choose $d_{21} \gg d_{12}$, i.e. the dispersal rate of the pest from the second patch to the first patch is significantly larger than its dispersal rate from the second patch to the first patch, then extensive numerical investigations imply that this is one of two ways to eradicate the pests in this case. The other way is to control the dispersal rates $d_{12}$ and $d_{21}$ such that $d_{21} \ll d_{12}$.

From a biological point of view, when the pests are persistent in any single isolated patch and the aim is to eradicate them by controlling their dispersal rates, we can limit their dispersal from the first patch to the second patch but allow them to move from the second patch to the first patch at high rates, i.e. $d_{21} \gg d_{12}$. At the same time, the natural enemies can freely move between the two patches with the same dispersal rates. If so, the pests can be quickly eradicated in the second patch. Consequently, the pest may die out in both patches even if they could have been persistent in each isolated patch. This result clarifies that field boundaries can act as barriers to limit the pest movement, and such barriers could change the population dynamics of the pests by influencing their movement between fields, and further have an impact on a pest control programme.

**Case 3** $R_{u_1} < 1$ and $R_{u_2} < 1$, i.e. the pests die out in both isolated patches.

For this case, can the pests be eradicated no matter how large the dispersal rates are? Or can the pests be persistent in both patches if they have different dispersal rates in each patch? To answer these questions, we fix parameters as follows:

\[
\begin{align*}
a_1 &= 2, & b_1 &= 0.5, & c_1 &= 0.2, & d_1 &= 0.1, & a_2 &= 1, \\
b_2 &= 0.3, & c_2 &= 0.2, & d_2 &= 0.1, & u_1 &= 0.5, & u_2 &= 0.5, \\
d_{12} &= 0.4, & d_{21} &= 0.4
\end{align*}
\]
Fig. 3  The effects of population dispersal on the persistence of pests. (A) The effects of predator dispersal on the pest’s persistence, where $D_{12}$ varies from 0 to 0.8, $D_{21}$ varies from 0 to 1, and all other parameters are as given in (32). (B) The effects of pest dispersal on its persistence, where $D_{12}, D_{21}$ vary from 0 to 1 and all other parameters are as given in (33).
and let $D_{12}$, $D_{21}$ vary from 0 to 1. It follows from the formulae of $R_{u_1}$ and $R_{u_2}$ that we have $R_{u_1} = 0.8$, $R_{u_2} = 0.6667$, i.e. the pests can be eradicated in both isolated patches.

Numerical results shown in Fig. 3(B) imply that $s(A)$ may be positive for some plane parameter ranges of $D_{12}$ and $D_{21}$, and the results also imply that this happens only if the difference between $D_{12}$ and $D_{21}$ is quite big, i.e. $D_{12} \gg D_{21}$ or $D_{12} \ll D_{21}$. Otherwise, the pests will also die out in both patches if they are extinct in both isolated patches.

It follows from all of the above three cases that whether the pest population is persistent or not depends on the dispersal rates of the pest population or the natural enemy population. These results imply that reducing or increasing population dispersal could both allow the pest species to explode to much higher levels, and so be more difficult to eradicate, or to maintain a low population, and hence be easier to eradicate.

We also note that from a practical point of view, it is interesting to consider the case in which one patch is a farmland and the other is a wasteland or an abandoned farmland. Assume that natural enemies are only released in the farmland (i.e. $u_2 > 0$), that pests in the neighboring wasteland immigrate into the farmland (i.e. $d_{12} > 0$) and that the parameter values are fixed as follows:

$$
\begin{align*}
    a_1 &= 2, & b_1 &= 0.35, & c_1 &= 0.2, & d_1 &= 0.1, & a_2 &= 2, \\
    b_2 &= 0.35, & c_2 &= 0.2, & d_2 &= 0.1, & u_1 &= 0.01, & u_2 &= 0.8, \\
    d_{12} &= 0.7, & d_{21} &= 0.
\end{align*}
$$

This could represent the first patch as wasteland and the second as farmland. Note that we choose $u_1$ sufficiently small (here $u_1 = 0.01$) rather than $u_1 = 0$ such that the wasteland has a pest-free equilibrium. Numerical results shown in Fig. 4(A) imply that $s(A)$ is positive for all dispersal rates of natural enemies, and consequently the pest outbreaks in both patches if $u_2$ is relatively small. If we hope to control the pest, the releasing rate of natural enemies in the farmland (i.e. $u_2$) should be large enough. This means that if we further increase the releasing rate $u_2$ such that it reaches a certain threshold value (for example $u_2 = 1.4$ here), we may control the pest such that it dies out in both patches, as shown in Fig. 4(B). These results indicate that the release of natural enemies may or may not be effective for this practical case.

5. Further development

In previous sections, we investigated the simplest predator-prey model for pest control by releases of natural enemies at constant rates. However, all of the methods developed previously can be used to study the following quite general predator-prey model in isolated patch $i$:

$$
\begin{align*}
    \frac{dx_i}{dt} &= f_i(x_i) x_i - g_i(x_i, y_i) y_i, \\
    \frac{dy_i}{dt} &= y_i g_i(x_i, y_i) y_i - d_i y_i + u_i,
\end{align*}
$$

where $x_i$ and $y_i$ are the population abundances of pests and natural enemies, respectively, $f_i(x_i)$ is the per capita net rate of increase, $d_i$ represents the per capita death rate of
Fig. 4  The effects of natural enemy dispersal and releasing rate on the persistence of pests, where $D_{12}$ and $D_{21}$ vary from 0 to 1 and all other parameters are as given in (34). (A) $\nu_2 = 0.8$. (B) $\nu_2 = 1.4$. 
the predator population, and \( y_i \) denotes the conversion efficiency of pests to predator, \( g_i(x_i, y_i) \) is the per capita functional response of the predator or the rate of pest attack. For example, we assume that the production of pests (in the absence of natural enemies) follows the usual logistic growth, and the pest-dependent functional response is of the Holling type II form (Holling, 1965), i.e. we have

\[
f_i(x_i) = r_i \left(1 - \frac{x_i}{K_i}\right), \quad g_i(x_i, y_i) = \frac{\alpha_i x_i}{1 + \alpha_i T_{hi} x_i}
\]

where \( \alpha_i \) is the instantaneous search rate, i.e. the average number of encounters with pests per predator per unit of searching time and \( T_{hi} \), the handling time, i.e. the time between a pest being encountered and search being resumed. We should emphasize here that many other growth functions including the Beverton–Holt (Beverton and Holt, 1956; Cooke et al., 1999) and the Gompertz growth (Gompertz, 1925) functions have been proposed for the pest population, as have several other pest-dependent functional response functions such as Holling’s types I and III. Different combinations of those functions result in different predator-prey systems and different dynamical behaviour.

From a biological point of view, the general assumptions on \( f_i(x_i) \) and \( g_i(x_i, y_i) \) are as follows:

(A1) \( f_i \in C'([0, \infty), R) \), \( f_i(0) > 0 \) and there exists \( K > 0 \) such that \( f_i(K) = 0 \).

(A2) \( g_i \in C'([0, \infty) \times [0, \infty), R) \), \( g_i(0, y_i) = 0 \) and \( \frac{\partial g_i}{\partial x_i} > 0 \) for all \( x_i > 0 \), \( y_i > 0 \).

Now consider pest and natural enemy populations that disperse among \( n \) patches, we have the following general model:

\[
\begin{align*}
\frac{dx_i}{dt} &= f_i(x_i)x_i - g_i(x_i, y_i)y_i + \sum_{j=1}^{n} d_{ji} x_j, \quad 1 \leq i \leq n, \\
\frac{dy_i}{dt} &= \gamma_i g_i(x_i, y_i)y_i - d_i y_i + u_i + \sum_{j=1}^{n} D_{ji} y_j, \quad 1 \leq i \leq n,
\end{align*}
\] (36)

where \( d_{ii}, D_{ii}, 1 \leq i \leq n, \) are non-positive constants, \( d_{ji} \) and \( D_{ji} \) (\( i \neq j \)) are non-negative constants. \( d_{ii} = -\sum_{j=1, j \neq i}^{n} d_{ij} \) and \( D_{ii} = -\sum_{j=1, j \neq i}^{n} D_{ij} \) represent the emigration rates of pests and natural enemies in the \( i \)th patch, respectively; \( d_{ji} \) and \( D_{ji} \) (\( i \neq j \)) denote the immigration rate of pests and natural enemies from the \( j \)th patch to the \( i \)th patch, respectively. If we further assume that there are no births and deaths of the individuals during the dispersal process, then we have

\[
\sum_{j=1}^{n} d_{ji} - \sum_{j=1}^{n} d_{ij} = 0, \quad \sum_{j=1}^{n} D_{ji} - \sum_{j=1}^{n} D_{ij} = 0.
\]

For the system (36), the EPE satisfies the following equation

\[
-(d_i - D_{ii}) y_i + u_i + \sum_{j=1, j \neq i}^{n} D_{ji} y_j = 0, \quad 1 \leq i \leq n.
\] (37)
Denote
\[
D = \begin{pmatrix}
-(d_1 - D_{11}) & D_{21} & \cdots & D_{n1} \\
D_{12} & -(d_2 - D_{22}) & \cdots & D_{n2} \\
\vdots & \vdots & \ddots & \vdots \\
D_{1n} & D_{2n} & \cdots & -(d_n - D_{nn}) 
\end{pmatrix},
\]
\[
Y = \begin{pmatrix}
y_1 \\
y_2 \\
\vdots \\
y_n
\end{pmatrix}, \quad U = \begin{pmatrix}
u_1 \\
u_2 \\
\vdots \\
u_n
\end{pmatrix}
\]
then Eq. (37) becomes
\[
DY + U = 0. \tag{39}
\]
Therefore, if we assume that \(D\) is a non-singular matrix, then we have \(Y^* = D^{-1}U\). Clearly, \(D\) is irreducible and has non-negative off-diagonal elements. Then \(s(D)\) is a simple eigenvalue of \(D\) with a positive eigenvector. In the following, we always assume that \(s(D) < 0\), i.e. \(Y^*\) is globally stable due to the linearity of the subsystem.

Thus, \(E' = (0, 0, \ldots, 0, y_1^*, y_2^*, \ldots, y_n^*)\) is an unique EPE of the system (36). The Jacobian matrix of system (36) at point \(E'\) can be calculated as follows:
\[
J_{E'} \triangleq \begin{pmatrix}
F - V & 0 \\
B & D
\end{pmatrix}, \tag{40}
\]
where \(D\) is given by (38), \(F = \text{diag}(f_1(0), f_2(0), \ldots, f_n(0))\),
\[
B = \text{diag}\left(y_1 y_1^* \frac{\partial g_1}{\partial x_1}(0, y_1^*), y_2 y_2^* \frac{\partial g_2}{\partial x_2}(0, y_2^*), \ldots, y_n y_n^* \frac{\partial g_n}{\partial x_n}(0, y_n^*)\right)
\]
and
\[
V = \begin{pmatrix}
y_1^* \frac{\partial g_1}{\partial x_1}(0, y_1^*) - d_{11} & -d_{21} & \cdots & -d_{n1} \\
-d_{12} & y_2^* \frac{\partial g_2}{\partial x_2}(0, y_2^*) - d_{22} & \cdots & -d_{n2} \\
\vdots & \vdots & \ddots & \vdots \\
-d_{1n} & -d_{2n} & \cdots & y_n^* \frac{\partial g_n}{\partial x_n}(0, y_n^*) - d_{nn}
\end{pmatrix}. \tag{41}
\]
It follows that the matrix \(F\) is non-negative and \(V\) has the Z sign pattern (Van den Driessche and Watmough, 2002). Let \(R_U = \rho(FV^{-1})\), then it follows from the methods given by Van den Driessche and Watmough (2002) and Wang and Zhao (2004) that we have the following two sufficient and necessary conditions:
\[
R_U > 1 \quad \text{iff} \quad s(F - V) > 0, \quad R_U < 1 \quad \text{iff} \quad s(F - V) < 0. \tag{42}
\]
In particular, when \(n = 2\) we can easily use the above two sufficient and necessary conditions to study the stability of EPE and obtain the expected results such as those shown in Section 3.
Another possible way to develop the model is to include more than one control strategy into it, i.e. other integrated control tactics like chemical and cultural control such as have been considered in a general system (Tang and Chen, 2004; Tang and Cheke, 2005; Tang et al., 2005; Van Lenteren, 1995, 2000). We leave this for our future work.

6. Discussion

The aim of this paper was to understand how dispersal in a patchy environment influences the stability properties of pest and natural enemy interaction models. So, we have proposed simple two-patch model to investigate the effects of a population dispersal between two patches on the persistence of pests. The theoretical results obtained here imply that reducing or increasing dispersal of pests or natural enemies may not only result in more severe pest outbreaks, but also can be beneficial for pest control. Therefore, knowledge about pest dispersal, natural enemy dispersal and population dynamics can be used to predict pest outbreaks and to develop optimal pest management strategies. We note that the effects of spatial heterogeneity on the competition model and foodweb model have been extensively investigated by Amarasekare and Nisbet (2001) and Amarasekare (2008). Their main results imply that competitive asymmetry (or foodweb complexity) and the dispersal rates have strong effects on local dynamics. Our model formulation, compared with their models, involves a biological control mechanism (i.e. the releasing rates $u_1, u_2$). Thus, our models not only can be used to investigate effect of dispersal pattern on the persistence or extinction of pests, but also can be used to design the optimal pest control strategies.

The extensive numerical investigations shown in this paper clarify that the dispersal rates of insect pests and natural enemies may dramatically change the dynamical behaviour, i.e. the persistence of the insect population. Three special cases were considered: Case 1 indicates that if the pest can be persistent in any one of the isolated patches and dies out in the other patch, we can control the dispersal rate of the pest or the dispersal rate of the natural enemy within a certain range such that the pest dies out in both patches. However, the results implied that biological control may be unsuccessful if the dispersal rate of the predator from the isolated patch where the pest dies out to the patch where the pest is persistent is too large. Case 2 shows that if the pests can be persistent in both isolated patches, we still can control the dispersal rates of the pest or the predator such that the pest dies out in both patches. However, in order to realize this goal, the difference between dispersal rates of the predator or the pest in the two patches must be quite big. On the other hand, if the pests dies out in both isolated patches and the difference in dispersal rates of the predator or the pest in both patches is quite large, the pest can outbreak in both patches. The numerical results obtained in Case 3 clarify this point. In summary, whether the pest population is persistent or not depends on the dispersal rates of the pest population or the natural enemy population. These results imply that reducing or increasing population dispersal could both allow the pest species to explode to much higher levels, and so be more difficult to eradicate, or to maintain a low population and hence be easier to eradicate.

The numerical investigations also clarify that knowledge about pest dispersal and population dynamics can be used to predict pest outbreaks and to develop pest management
strategies. Therefore, dispersal of pest and predator populations is a topic of great concern to individuals developing various integrated pest management programmes (Van Lenteren, 1995; Van Lenteren and Woets, 1988), and the interplay between environmental heterogeneity and individual movement is an extremely important aspect of ecological dynamics.

The results given here indicate that the dispersal of pests and natural enemies could be either beneficial or detrimental to pest control, depending on a number of factors such as the dispersal rates or the status of any single patch (extinction or persistence). These results indicate that knowledge of pest and natural dispersal and the dynamical behaviour of predator-prey systems in patchy environments is crucial for understanding the effectiveness of biological control.

From a practical point of view, we also numerically investigate the case in which one patch is a farmland and the other is a wasteland or an abandoned farmland, and assume that the natural enemies are released only in farmlands (here $u_1 \ll u_2$ in the model). The results indicate that the pest may outbreak in both patches if the releasing rate $u_2$ in the farmland is relatively small or below some threshold value; whilst the pest is controlled if $u_2$ is greater than the threshold value. So, in order to control the pest the releasing rate of natural enemies in farmland must be large enough. Consequently, we can conclude that the releasing of natural enemies may or may not be effective.

The results presented here are supported by empirical investigations. In his classic experiments involving predatory mites *Typhlodromus occidentalis* attacking *Eotetranychus sexmaculatus* prey mites on oranges, Huffaker (1958) experienced extinction of both mites or co-existence with cycles depending upon how he manipulated the system. In some cases, when the prey went extinct in one habitat patch, they re-established themselves by migrating to new patches before being attacked again by predators. Similarly, Takafuji (1976) investigated dispersal behaviour in a predacious phytoseiid mite *Phytoseiulus persimilis* in relation to the density of its prey *Tetranychus kanzawai* while changing the ability of either species to disperse by introducing bridges or barriers between habitat patches. With all prey patches available to the predator, the prey became extinct but coexistence was possible using barriers to reduce the dispersal of the predators and allowing more chances for the prey to disperse. The effects of dispersal on the outcome of predator-prey models has also been investigated by Crowley (1981), Jansen and Sabelis (1992), and Pels and Sabelis (1999), amongst others.

However, biological control is only one component of an integrated pest management (IPM) strategy (Greathead, 1992; Hoffmann and Froodsham, 1993; Neuenschwander and Herren, 1988; Parker, 1971). It is known that overuse of a single control tactic is discouraged to avoid or delay the development of resistance by the pest to the control tactic, to minimize damage to non-target organisms, and to preserve the quality of the environment. So, in order to control the pest and protect the environment, IPM has been shown by experiments to be more effective than classical methods (such as biological or chemical control only). Therefore, in the future, we will take into account IPM strategies and study the effects of dispersal on pest control in a wider context.

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