Single species models with logistic growth and dissymmetric impulse dispersal

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ABSTRACT

In this paper, two classes of single-species models with logistic growth and impulse dispersal (or migration) are studied: one model class describes dissymmetric impulsive bi-directional dispersal between two heterogeneous patches; and the other presents a new way of characterizing the aggregate migration of a natural population between two heterogeneous habitat patches, which alternates in direction periodically. In this theoretical study, some very general, weak conditions for the permanence, extinction of these systems, existence, uniqueness and global stability of positive periodic solutions are established by using analysis based on the theory of discrete dynamical systems. From this study, we observe that the dynamical behavior of populations with impulsive dispersal differs greatly from the behavior of models with continuous dispersal. Unlike models where the dispersal is continuous in time, in which the travel losses associated with dispersal make it difficult for such dispersal to evolve e.g., [25,26,28], in the present study it was relatively easy for impulsive dispersal to positively affect populations when realistic parameter values were used, and a rich variety of behaviors were possible. From our results, we found impulsive dispersal seems to more nicely model natural dispersal behavior of populations and may be more relevant to the investigation of such behavior in real ecological systems.

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1. Introduction

Due to the ubiquitous prevalence of organism movements in nature and their significant impacts on species' diversity [57], population dynamics [21] and genetic polymorphisms [22], dispersal, migration, and other types of movement in a spatio-temporally heterogeneous environment, have always attracted great interest by biologists, ecologists and biomathematicians. This includes studies of persistence and extinction [35,17,19,23,14,12,27, 1,48,50,3,37,53,52,7,10,11,33,59,60] and stability of equilibria and periodic solutions [9,13,25,26,4–6,24,49,56,40].

Because of their distinctive significance, both as a basis for metapopulation theory and as the starting point for modeling multi-species interactions in patchy environment, single-species dispersal models have been extensively studied, and many important results have been obtained [13,14,12,25,26,28,4,5, 20,53,50].

A standard single-species logistic model with continuous constant dispersal rate between two heterogeneous patches can be written as follows

$$\dot{N}_1 = r_1 N_1 \left(1 - \frac{N_1}{k_1}\right) - mN_1 + m(1-\delta)N_2,$$

$$\dot{N}_2 = r_2 N_2 \left(1 - \frac{N_2}{k_2}\right) - mN_2 + m(1-\delta)N_1, \tag{1.1}$$

where $N_i(t)(i = 1, 2)$ represents the population density in the ith habitat at time t, r_i and k_i are the intrinsic rate of population increase and the carrying capacity of population i, δ is the fraction of migrants dying during migration and m is the emigration rate, a constant. Above dispersal model may be used to characterize the mobility of bird or, insect [15]. Interest for above continuous dispersal models mainly focused on the stability of equilibrium e.g.. [13], and the effect of optimal dispersal rates on population size and evolution e.g. [18,25,26,28].

Habitat heterogeneity in space has long been taught not to be sufficient to promote evolution of dispersal. In particular, [25] showed that, with sufficiently high dispersal, a population will be stable if the average over the environment of the density dependent terms indicates stability. Furthermore, [26] showed that, the conditions for stability with a low dispersal rate are more stringent than those for stability with a high dispersal rate. For any dynamics leading to an equilibrium which does exhibit spatial variation, dispersal will be selected against. Hence, selection for dispersal must include other factors. [28] found that the evolution of an optimal habitat distribution may lead to a reduction in population size, and passive

dispersal should always be selectively disadvantageous in a spatially heterogeneous but temporally constant environment.

Therefore, the question is: what are the "other factors in the above logistic dispersal model"? and is it true that passive dispersal always be selectively disadvantageous? In all of the above population dispersal models, it is assumed that migratory behavior of the modelled populations is occurring at every point in time and is occurring simultaneously between any two patches; i.e. these models are continuous bidirectional dispersal models. At the same time, authors carried into research for above models mainly by utilizing techniques of analyzing equilibrium since the model characterized here are continuous dynamic systems. Actually, real dispersal behavior is very complicated and is always influenced by environmental change and, sometimes by human activities. It usually occurs stochastically or discontinuously [44], and it is often the case that species dispersal occurs at some transitory intervals of time when individuals move among patches to search for mates, food, refuge, etc.

Animal movements between regions or patches of habitat are rarely continuous in time. They may occur during short intervals of time within seasons or within the lifetimes of animals. There are several general reasons for this.

First, the environmental conditions in the landscape matrix between habitat patches may permit normal movement patterns between patches only at certain times. This could be a result of either seasonality or random events that influence the ability of individual organisms to move between patches. For example, in marshes, high water during the wet season may restrict movement of some small mammals between drier patches, such as tree islands [45] within a seasonally flooded marsh. Conversely, fish inhabiting pools and side channels of a river system that are isolated during low water periods may be able to move back and forth among such waterbodies when water levels are higher e.g. [58,39]. In these types of cases, movement may be bidirectional when conditions permit.

Another general class of movements is connected with life cycles of organisms. Many animals may disperse long distances from their natal sites at certain stages in their life cycles, particularly between their birth and start of reproduction [16]. For example, in Florida scrub jays, the females tend to move earlier and farther [47], while among olive baboons, it is males that predominately move [41]. Juvenile male Florida panthers leave the territories of their mothers at about 14 months of age, and may travel over 100 miles to seek a territory. During the mating season, males of many species may move long distances; for example, male stoats searching for females [43]. Those movements associated with life cycles can be considered as bidirectional, as individuals may be starting from any habitat site on the landscape and moving in more or less random directions away from their natal sites.

Therefore, it is not reasonable to characterize the population movements in these cases with continuous dispersal models. This short-time scale dispersal is more appropriately assumed to be in the form of pulses in the modeling process, in order to be in much better agreement with the real ecological situation. With the developments and applications of impulsive differential equations [2,34], theories of impulsive differential equations (hybrid dynamical systems) have been introduced into population dynamics, and many important studies have been performed [3,30,32,36,51,55].

Hui and Chen [30] proposed the following single-species Lotka–Volterra model with impulsively bidirectional dispersal:

$$
\begin{cases}
\begin{rcases}
\dot{N}_1(t) = N_1(t)(a_1 - b_1 N_1(t)), \\
\dot{N}_2(t) = N_2(t)(a_2 - b_2 N_2(t)),
\end{rcases} & t \neq n\tau, \\
\begin{rcases}
\Delta N_1 = d_1(N_2(t^-) - N_1(t^-)), \\
\Delta N_2 = d_2(N_1(t^-) - N_2(t^-)),
\end{rcases} & t = n\tau,\ n = 1,2,\ldots,
\end{cases} \tag{1.2}
$$

where $a_i\, b_i\ (i = 1,2)$ are the intrinsic growth and density-dependent parameters of the population i, d_i is the net dispersal rate between

the ith patch and the jth patch ($i \neq j,\ i,j = 1,2$). $\Delta N_i = N_i(n\tau^+) - N_i(n\tau^-)$, $N_i(n\tau^+) = \lim_{t \to n\tau^+} N_i(t)$ represents the density of the population in the i-th patch after the n-th pulse dispersal at time $t = n\tau$, while $N_i(n\tau^-) = \lim_{t \to n\tau^-} N_i(t) = N_i(n\tau)$ represents the density of the population in the i-th patch before the n-th pulse dispersal event at time $t = n\tau$ (τ the period of dispersal between any two pulse events is a positive constant). The dispersal behavior of populations between two patches occurs only at the impulsive instants $n\tau(\ n = 1,2,\cdots)$. Sufficient criteria were obtained for the existence, uniqueness and global stability of positively periodic solutions by using discrete dynamical system theory.

However, in the above impulsive dispersal models, it is assumed that the dispersal occurs between homogeneous habitat patches; i.e. the dispersal rate between any two patches is equal or symmetrical [35,25,26,28] which is really too idealized for a real ecosystem. Actually, in the real world, due to the heterogeneity of the spatio-temporal distributions in nature, movement between fragments of patches is usually not the same rate in both directions. In addition, once the individuals leave their present habitat, they may not successfully reach a new one, due to predation, harvesting, or for other reasons, so that there are traveling losses. Therefore, the dispersal rates among these patches are not always the same. Rather, in real ecological situations they are different (or dissymmetrical [14,38]). Therefore, it is our basic goal to investigate single species models with dissymmetric impulse dispersal.

Based on the above considerations, in this paper, we will first consider the following single species model with logistic growth and dissymmetric impulsive bi-directional dispersal:

$$
\begin{cases}
\begin{rcases}
\dot{N}_1(t) = r_1 N_1(t)(1 - \frac{N_1(t)}{k_1}), \\
\dot{N}_2(t) = r_2 N_2(t)(1 - \frac{N_2(t)}{k_2}),
\end{rcases} & t \neq n\tau, \\
\begin{rcases}
\Delta N_1(t) = b_2 N_2(t^-) - a_1 N_1(t^-), \\
\Delta N_2(t) = b_1 N_1(t^-) - a_2 N_2(t^-),
\end{rcases} & t = n\tau,\ n = 1,2,\ldots,
\end{cases} \tag{1.3}
$$

where $a_i(i = 1,2)$ is the rate of population N_i emigrating from the ith patch, and $b_i(i = 1,2)$ is the rate of population N_i immigrating from the i-th patch. Here we assume $0 \leqslant b_i \leqslant a_i \leqslant 1$, which means that there possibly exists mortality during migration between two patches.

Moreover, to the best of our knowledge, in all of the models investigated, whether with continuous dispersal or the discontinuous dispersal considered so far, there are hardly any papers that consider the aggregate migration, or migration of the total population as a whole. Such migration usually stems from what has been termed 'seasonal hostility' or the impossibility to survive or reproduce in certain locales for part of a year [42]. In practice, in real ecological systems, with alternating seasons, many kinds of birds and mammals will migrate from cold regions to warm regions in search of a better habitat to inhabit or breed. Anadromous fish will go back from ocean to their birthplaces in stream to spawn, and vice versa for some other species. An example is the annual migration of birds between the tropics and temperate or boreal regions. For example, the blackburnian warbler is a small songbird that nests in forests of the northeastern United States and southern Canada during the spring and summer, but migrates to Central and South America to live through the winter [29]. Other examples include annual migrations of ungulates among grazing areas to follow spatio-temporal changes in rainfall, or annual movements of elk from higher to lower elevations to escape cold in winter. In these cases, movement is unidirectional during each migration period and may take place over fairly short time periods.

Obviously, this kind of discontinuous periodic migration behavior occurs extensively in nature, which prompts us to model and investigate it properly. Motivated by the above considerations, in this paper, we further characterize and research the above-men-

tioned dispersal migration by using the following single species model with logistic growth and impulsively unilateral dispersal:

$$\begin{cases} \dot{N}_1(t) = r_1 N_1(t)\left(1 - \frac{N_1(t)}{k_1}\right), & t \in (2n\tau, (2n+1)\tau), \\ \dot{N}_2(t) = r_2 N_2(t)\left(1 - \frac{N_2(t)}{k_2}\right), & t \in ((2n+1)\tau, (2n+2)\tau), \\ N_1(t^+) = b_2 N_2(t^-), & t = (2n+2)\tau, \\ N_2(t^+) = b_1 N_1(t^-), & t = (2n+1)\tau, \quad n = 0, 1, 2, \dots. \end{cases}$$
$$(1.4)$$

The population $N = (N_1, N_2)$ inhabits two patches (patch 1 and patch 2) and alternates periodically; i.e.. it lives in patch 1 during time interval $(2n\tau, (2n+1)\tau)$, and at end of time period $(2n+1)\tau$, it migrates, as a whole, to patch 2 with a success rate of b_1. From that point it lives through the time period $((2n+1)\tau, (2n+2)\tau)$, and then migrates, as a whole, back to patch 1 at time $(2n+2)\tau$ with a success rate of b_2. It continues migrating back and forth between the two patches at two different periods of time during the year, where $N_1((2n+2)\tau^+) = \lim_{t \to (2n+2)\tau^+} N_1(t)$ represents the density of population in the 1-st patch after the $(2n+2)$th pulse dispersal at time $t = (2n+2)\tau$, $N_2((2n+1)\tau^+) = \lim_{t \to (2n+1)\tau^+} N_2(t)$ represents the density of the population in the 2nd patch after the $(2n+1)$th pulse dispersal at time $t = (2n+1)\tau$. $N_i((2n+i)\tau^-) = \lim_{t \to (2n+i)\tau^-} N_i(t)$ represents the density of the population in the i-nd patch before the $(2n+i)$th pulse dispersal at time $t = (2n+i)\tau$ $(i = 1, 2)$. The parameters, b_i, where $0 \leqslant b_i \leqslant 1$ represents the successful aggregate migration rate of population N_i from the ith patch to the jth patch $(i, j = 1, 2, \ i \neq j)$.

The main purpose of this paper is to provide analytic criteria not only for the permanence versus extinction of metapopulations, but also for the existence, uniqueness and global stability of the positively periodic solutions. We compare the implications of these criteria with both continuous dispersal models and impulsive dispersal models.

This paper is organized as follows. In the next section, we introduce the definition of permanence. From discrete dynamic system theory, we establish stroboscopic maps in terms of models 1.3 and 1.4, by which we can obtain the dynamical behaviors of the systems (simultaneous bi-directional and alternating uni-directional). In Section 3.1, the results of permanence and extinction for the systems are presented. The existence and uniqueness of positive periodic solutions for the models are obtained by an analytic approach in Section 3.2. In Section 3.3, the global stability of positive periodic solutions for the systems are established by the discrete dynamic systems theory. Discussions are presented in Section 4.

2. Preliminaries

Before going into details, we first draw a very clear definition of permanence. The definitions of permanence or persistence are numerous, but here we refer to [31,54,8].

Definition 2.1. Systems (1.3) and (1.4) are said to be permanent, if there are positive constants m_i and M_i such that

$$m_i \leqslant \liminf_{t \to \infty} N_i(t) \leqslant \limsup_{t \to \infty} N_i(t) \leqslant M_i, \quad i = 1, 2,$$

for any positive solutions $N(t) = (N_1(t), N_2(t))$ of systems (1.3) and (1.4).

Next, to study the permanence, existence and uniqueness of positively periodic solutions for systems (1.3) and (1.4), we take $x = \frac{N_1}{k_1}$, $y = \frac{N_2}{k_2}$, $k = \frac{k_2}{k_1}$, which on substituting into (1.3) becomes

$$\begin{cases} \frac{dx}{dt} = r_1 x(1 - x), \\ \frac{dy}{dt} = r_2 y(1 - y), \end{cases} \quad t \neq n\tau, \\ \begin{cases} \Delta x = b_2 ky - a_1 x, \\ \Delta y = \frac{b_1}{k} x - a_2 y, \end{cases} \quad t = n\tau, \ n = 1, 2, \dots$$
$$(2.1)$$

By calculating the first two equations of system (2.1) between pulses, we have

$$\begin{cases} x(t) = \frac{1}{1 + (x(n\tau^+)^{-1} - 1)e^{r_1(n\tau - t)}}, \\ y(t) = \frac{1}{1 + (y(n\tau^+)^{-1} - 1)e^{r_2(n\tau - t)}}, \end{cases} \quad n\tau < t < (n+1)\tau. \quad (2.2)$$

Similarly, considering the last two equations of system (2.1), we obtain the following stroboscopic maps

$$\begin{cases} x_{n+1} = \frac{(1 - a_1)x_n}{x_n + (1 - x_n)c_1} + \frac{b_2 k y_n}{y_n + (1 - y_n)c_2}, \\ y_{n+1} = \frac{(1 - a_2)y_n}{y_n + (1 - y_n)c_2} + \frac{b_1 x_n}{k(x_n + (1 - x_n)c_1)}, \end{cases} \quad (2.3)$$

where $x_n = x(n\tau^+), y_n = y(n\tau^+), 0 < c_1 = e^{-r_1\tau} < 1, 0 < c_2 = e^{-r_2\tau} < 1$. By the same method, we obtain the following equations between two pulses from system (1.4)

$$\begin{cases} \frac{dx}{dt} = r_1 x(1 - x), & t \in (2n\tau, (2n+1)\tau), \\ \frac{dy}{dt} = r_2 y(1 - y), & t \in ((2n+1)\tau, (2n+2)\tau), \\ \Delta x = b_2 ky, & t = (2n+2)\tau, \\ \Delta y = \frac{b_1}{k} x, & t = (2n+1)\tau, \ n = 0, 1, 2, \dots \end{cases} \quad (2.4)$$

By integrating and solving the first two equations of (2.4) between pulses, we get

$$\begin{cases} x(t) = \frac{1}{1 + (x(2n\tau^+)^{-1} - 1)e^{r_1(2n\tau - t)}}, & t \in (2n\tau, (2n+1)\tau), \\ y(t) = \frac{1}{1 + (y((2n+1)\tau^+)^{-1} - 1)e^{r_2((2n+1)\tau - t)}}, & t \in ((2n+1)\tau, (2n+2)\tau), \end{cases} \quad (2.5)$$

and we have the following stroboscopic maps by the same method

$$\begin{cases} x_{2n+2} = \frac{b_2 k y_{2n+1}}{y_{2n+1} + (1 - y_{2n+1})c_2}, \\ y_{2n+1} = \frac{b_1 x_{2n}}{k(x_{2n} + (1 - x_{2n})c_1)}, \end{cases} \quad (2.6)$$

where $y_{2n+1} = y((2n+1)\tau^+), x_{2n+2} = x((2n+2)\tau^+)$, $0 < c_1 = e^{-r_1\tau} < 1, 0 < c_2 = e^{-r_2\tau} < 1$. The positivity of any solution with initial values $x(t_0) > 0, y(t_0) > 0$, both for systems (2.3) and (2.6), is evident. Moreover, we can see here (2.6) determines x_k for even k and y_k for odd k.

Lastly, in order to establish the global stability of positively periodic solutions, we introduce the following well known result of discrete dynamical system theory:

Lemma 2.2 [46]. *Let $F : R_+^n \to R_+^n$ be continuous, C^1 in int (R_+^n), and suppose $DF(0)$ exists with $\lim_{x \to 0^+} DF(x) = DF(0)$. In addition, assume*

(a) $DF(x) > 0$, if $x > 0$;
(b) $DF(y) < DF(x)$, if $0 < x < y$;

If $F(0) = 0$, let $\lambda = \rho(DF(0))$. If $\lambda \leqslant 1$, then for every $x \geqslant 0$, $F^{(n)}(x) \to 0$ as $n \to \infty$; if $\lambda > 1$, then either $F^{(n)}(x) \to \infty$ as $n \to \infty$ for every $x > 0$ or there exists a unique nonzero fixed point q of F. In the latter case, $q > 0$ and for every $x > 0$, $F^{(n)}(x) \to q$ as $n \to \infty$.

If $F(0) \neq 0$, then either $F^{(n)}(x) \to \infty$ as $n \to \infty$ for every $x \geqslant 0$ or there exists a unique fixed point q of F. In the latter case, $q > 0$ and for every $x > 0, F^{(n)}(x) \to q$ as $n \to \infty$.

3. Main results

3.1. Permanence and extinction

In this subsection, we first present conditions to ensure that systems (2.3) and (2.6) are permanent (or, alternatively, go to

extinction) which will imply the permanence (or extinction) of systems (1.3) and (1.4), respectively.

Theorem 3.1. *System (2.3) is permanent (or extinct) if*

$$[b_1b_2 - (1-a_1)(1-a_2)]e^{(r_1+r_2)\tau} + e^{r_1\tau}(1-a_1) + e^{r_2\tau}(1-a_2)$$
$$> 1 \ (or \leqslant 1). \tag{3.1}$$

Proof. First, we prove that if $[b_1b_2 - (1-a_1)(1-a_2)]e^{(r_1+r_2)\tau} + e^{r_1\tau}(1-a_1) + e^{r_2\tau}(1-a_2) > 1$, then system (1.4) is permanent. Since $0 \leqslant b_i \leqslant a_i \leqslant 1$, $0 < c_i = e^{-r_i\tau} \leqslant 1 (i = 1,2)$, from the first equation of system (2.3), we have

$$x_{n+1} = \frac{1-a_1}{1+(x_n^{-1}-1)c_1} + \frac{b_2k}{1+(y_n^{-1}-1)c_2}$$
$$= \frac{1-a_1}{1-c_1+c_1x_n^{-1}} + \frac{b_2k}{1-c_2+c_2y_n^{-1}} < \frac{1-a_1}{1-c_1} + \frac{b_2k}{1-c_2}. \tag{3.2}$$

Similarly, we have

$$y_{n+1} = \frac{1-a_2}{1+(y_n^{-1}-1)c_2} + \frac{b_1}{k(1+(x_n^{-1}-1)c_1)}$$
$$= \frac{1-a_2}{1-c_2+c_2y_n^{-1}} + \frac{b_1}{k(1-c_1+c_1x_n^{-1})}$$
$$< \frac{1-a_2}{1-c_2} + \frac{b_1}{k(1-c_1)}. \tag{3.3}$$

Hence, by (3.2) and (3.3) we know that system (2.3) has an ultimate upper bound.

In system (2.3), we define the map $H_i : (0, +\infty) \to (0, +\infty)$ by

$$H_1(x_n) = \frac{1}{1+(x_n^{-1}-1)c_1}, \quad H_2(y_n) = \frac{1}{1+(y_n^{-1}-1)c_2}. \tag{3.4}$$

Thus, we have

$$x_{n+1} = (1-a_1)H_1(x_n) + b_2kH_2(y_n), y_{n+1}$$
$$= (1-a_2)H_2(y_n) + \frac{b_1}{k}H_1(x_n). \tag{3.5}$$

For any initial values $x_0 > 0$ and $y_0 > 0$, there are four cases:

Case 1: $x_0 \geqslant x_1 > 0$ and $y_0 \geqslant y_1 > 0$.
Case 2: $0 < x_0 \leqslant x_1$ and $0 < y_0 \leqslant y_1$.
Case 3: $x_1 \geqslant x_0 > 0$ and $0 < y_1 \leqslant y_0$.
Case 4: $0 < x_1 \leqslant x_0$ and $y_1 \geqslant y_0 > 0$.

For case 1, we have $H_1(x_0) \geqslant H_1(x_1)$ and $H_2(y_0) \geqslant H_2(y_1)$. From (3.2) we obtain $x_1 \geqslant x_2$ and $y_1 \geqslant y_2$. By the same argument we get that

$$x_0 \geqslant x_1 \geqslant x_2 \geqslant \cdots x_n \geqslant \cdots > 0, \quad y_0 \geqslant y_1 \geqslant y_2 \geqslant \cdots y_n \geqslant \cdots > 0.$$

For case 2, by the same argument above if $x_0 \leqslant x_1$ and $y_0 \leqslant y_1$, for sequences $\{x_n\}$ and $\{y_n\}$ we can obtain

$$0 < x_0 \leqslant x_1 \leqslant x_2 \leqslant \cdots x_n \leqslant \cdots, \quad 0 < y_0 \leqslant y_1 \leqslant y_2 \leqslant \cdots y_n \leqslant \cdots$$

For case 3, from (3.2) and (3.3) we obtain that

$$H_1(x_n) = \frac{b_2ky_{n+1} - (1-a_2)x_{n+1}}{b_1b_2 - (1-a_1)(1-a_2)}, H_2(y_n)$$
$$= \frac{\frac{b_1}{k}x_{n+1} - (1-a_1)y_{n+1}}{b_1b_2 - (1-a_1)(1-a_2)} \tag{3.6}$$

and $H_1(x_1) \geqslant H_1(x_0) > 0$ and $H_2(y_0) \geqslant H_2(y_1) > 0$. Furthermore, from (3.4) we get that

$$\frac{b_2ky_2 - (1-a_2)x_2}{b_1b_2 - (1-a_1)(1-a_2)} \geqslant \frac{b_2ky_1 - (1-a_2)x_1}{b_1b_2 - (1-a_1)(1-a_2)} > 0,$$
$$\frac{\frac{b_1}{k}x_1 - (1-a_1)y_1}{b_1b_2 - (1-a_1)(1-a_2)} \geqslant \frac{\frac{b_1}{k}x_2 - (1-a_1)y_2}{b_1b_2 - (1-a_1)(1-a_2)} > 0. \tag{3.7}$$

There are two subcases for case 3:

3a: $b_1b_2 - (1-a_1)(1-a_2) > 0.$
3b: $b_1b_2 - (1-a_1)(1-a_2) < 0.$

For subcase 3a, since $b_1b_2 - (1-a_1)(1-a_2) > 0$, from (3.7) we can get that

$$b_2k(y_2 - y_1) \geqslant (1-a_2)(x_2 - x_1), \frac{b_1}{k}(x_2 - x_1)$$
$$\leqslant (1-a_1)(y_2 - y_1). \tag{3.8}$$

Then if $y_2 \leqslant y_1$, we could get that $x_2 \leqslant x_1$, which is similar to case 1. If $y_2 \geqslant y_1$ and $x_2 \geqslant x_1$, it is similar to case 2. If $y_2 \geqslant y_1, x_2 \leqslant x_1$ and $y_2 \geqslant y_3$, then we obtain that $x_2 \geqslant x_3$, a conclusion that is similar to case 1. If $y_2 \geqslant y_1, x_2 \leqslant x_1, y_2 \leqslant y_3$, then we obtain $x_2 \leqslant x_3$, a conclusion that is similar to case 2. Therefore, we acquire that if $x_1 \geqslant x_0$ and $y_1 \leqslant y_0$, the sequences $\{x_n\}$ and $\{y_n\}$ is similar to case 1 or case 2 or there exist $\eta(\eta > 0)$, it satisfies

$$x_1 \geqslant x_2 \geqslant \cdots x_n \geqslant \cdots > 0, y_n \geqslant \eta.$$

For subcase 3b, by the same argument like subcase 3a, we get the similar conclusions of sequences $\{x_n\}$ and $\{y_n\}$.

For case 4, by a similar argument like case 3, we could obtain a similar conclusion like case 1, 2 or there exist $\xi(\xi > 0)$, such that

$$0 < y_1 \leqslant y_2 \leqslant \cdots y_n \leqslant \cdots, \quad x_n \geqslant \xi.$$

Subsequently, we prove there are constants $\xi > 0, \eta > 0$ such that

$$\liminf_{n\to\infty} x_n \geqslant \xi \quad and \quad \liminf_{n\to\infty} y_n \geqslant \eta. \tag{3.9}$$

Otherwise, one of the following cases is true:

Case (1): there exists $\eta > 0$ such that $\liminf_{n\to\infty} y_n = \eta$ and $\liminf_{n\to\infty} x_n = 0$.
Case (2): there exists $\xi > 0$ such that $\liminf_{n\to\infty} x_n = \xi$ and $\liminf_{n\to\infty} y_n = 0$.
Case (3): $\liminf_{n\to\infty} x_n = 0$ and $\liminf_{n\to\infty} y_n = 0$.

Now, we exclude these cases one by one.

For case (1), since $\liminf_{n\to\infty} y_n = \eta > 0$, from (3.4) and (3.5) we have

$$x_{n+1} = \frac{1-a_1}{1+(x_n^{-1}-1)c_1} + \frac{b_2k}{1+(y_n^{-1}-1)c_2} > \frac{b_2k}{1+(y_n^{-1}-1)c_2}$$
$$\geqslant \frac{b_2k}{1+(\eta^{-1}-1)c_2} > 0. \tag{3.10}$$

Taking the infimum limit on both sides of (3.10), we have $\liminf_{n\to\infty} x_n > 0$. This is a contradiction.

Similarly, we can exclude case (2).

Based on the arguments above in Case 1 to 4, we know the sequences $\{x_n\}$ and $\{y_n\}$ are either monotone increasing or monotone decreasing or bounded. Therefore, for case (3), we know sequences $\{x_n\}$ and $\{y_n\}$ must be monotone decreasing. So, we have $0 < x_{n+1} \leqslant x_n$ and $0 < y_{n+1} \leqslant y_n$, by (3.4) and (3.5) we have

$$\frac{1-a_1}{1+(x_n^{-1}-1)c_1} + \frac{b_2k}{1+(y_n^{-1}-1)c_2} \leqslant x_n,$$
$$\frac{1-a_2}{1+(y_n^{-1}-1)c_2} + \frac{b_1}{k(1+(x_n^{-1}-1)c_1)} \leqslant y_n. \tag{3.11}$$

Thus, we have

$$\frac{(1-c_1)x_n + c_1 - 1 + a_1}{1 + (x_n^{-1} - 1)c_1} \geqslant \frac{b_2 k}{1 + (y_n^{-1} - 1)c_2},$$
$$\frac{(1-c_2)y_n + c_2 - 1 + a_2}{1 + (y_n^{-1} - 1)c_2} \geqslant \frac{b_1}{k(1 + (x_n^{-1} - 1)c_1)}, \tag{3.12}$$

which imply that

$$[(1-c_1)x_n + c_1 - 1 + a_1][(1-c_2)y_n + c_2 - 1 + a_2] - b_1 b_2 \geqslant 0. \tag{3.13}$$

Taking the infimum limit on both sides of (3.13), we obtain

$$(c_1 - 1 + a_1)(c_2 - 1 + a_2) - b_1 b_2 \geqslant 0. \tag{3.14}$$

That is

$$b_1 b_2 - (c_1 - 1 + a_1)(c_2 - 1 + a_2) \leqslant 0, \tag{3.15}$$

which contradicts $b_1 b_2 - (c_1 - 1 + a_1)(c_2 - 1 + a_2) > 0$, i.e.. $[b_1 b_2 - (1 - a_1)(1 - a_2)]e^{(r_1 + r_2)\tau} + e^{r_1 \tau}(1 - a_1) + e^{r_2 \tau}(1 - a_2) > 1$. Finally, we can determine there exist constants $\alpha_i, \beta_i (0 < \alpha_i < \beta_i)(i = 1, 2)$, such that $\alpha_1 \leqslant \liminf_{n \to \infty} x_n \leqslant \limsup_{n \to \infty} x_n \leqslant \beta_1$ and $\alpha_2 \leqslant \liminf_{n \to \infty} y_n \leqslant \limsup_{n \to \infty} y_n \leqslant \beta_2$.

Therefore, system (1.4) is permanent if $[b_1 b_2 - (1 - a_1)(1 - a_2)]e^{(r_1 + r_2)\tau} + e^{r_1 \tau}(1 - a_1) + e^{r_2 \tau}(1 - a_2) > 1$.

Next, we prove if

$$[b_1 b_2 - (1 - a_1)(1 - a_2)]e^{(r_1 + r_2)\tau} + e^{r_1 \tau}(1 - a_1) + e^{r_2 \tau}(1 - a_2) \leqslant 1, \tag{3.16}$$

then system (1.4) goes to extinct. Corresponding to (2.3), let us consider the following system

$$F(x, y) = \begin{cases} f_1(x, y) = \frac{(1-a_1)x}{x + (1-x)c_1} + \frac{b_2 k y}{y + (1-y)c_2} \\ f_2(x, y) = \frac{(1-a_2)y}{y + (1-y)c_2} + \frac{b_1}{k(1 + (x^{-1} - 1)c_1)}. \end{cases} \tag{3.17}$$

Obviously, $F(x, y) \in C^1$ in int (R_+^2) and $F(0, 0) = 0$. We have

$$DF(x, y) = \begin{bmatrix} \frac{c_1(1-a_1)}{[(1-c_1)x + c_1]^2} & \frac{b_2 c_2 k}{[(1-c_2)y + c_2]^2} \\ \frac{b_1 c_1}{k[(1-c_1)x + c_1]^2} & \frac{c_2(1-a_2)}{[(1-c_2)y + c_2]^2} \end{bmatrix} \tag{3.18}$$

$$DF(0, 0) = \begin{bmatrix} \frac{(1-a_1)}{c_1} & \frac{b_2 k}{c_2} \\ \frac{b_1}{kc_1} & \frac{(1-a_2)}{c_2} \end{bmatrix}. \tag{3.19}$$

Obviously, $DF(x, y) > 0$ if $(x, y) > (0, 0)$, $DF(x_1, y_1) < DF(x_2, y_2)$ if $(x_1, y_1) > (x_2, y_2) > (0, 0)$, and $\lim_{(x,y) \to (0,0)} DF(x, y) = DF(0, 0)$. We have the characteristic equation

$$\lambda^2 - \left(\frac{1-a_1}{c_1} + \frac{1-a_2}{c_2}\right)\lambda + \frac{(1-a_1)(1-a_2)}{c_1 c_2} - \frac{b_1 b_2}{c_1 c_2} = 0. \tag{3.20}$$

Let ρ be the spectral radius of above linearized matrix (3.19), then

$$\rho = \frac{\frac{1-a_1}{c_1} + \frac{1-a_2}{c_2} + \sqrt{\left(\frac{1-a_1}{c_1} + \frac{1-a_2}{c_2}\right)^2 - 4\left(\frac{(1-a_1)(1-a_2)}{c_1 c_2} - \frac{b_1 b_2}{c_1 c_2}\right)}}{2}$$
$$= \frac{\frac{1-a_1}{c_1} + \frac{1-a_2}{c_2} + \sqrt{\left(\frac{1-a_1}{c_1} - \frac{1-a_2}{c_2}\right)^2 + 4\frac{b_1 b_2}{c_1 c_2}}}{2} \tag{3.21}$$

Assume $\rho > 1$, then by (3.21) we can obtain

$$\frac{1-a_1}{c_1} + \frac{1-a_2}{c_2} + \frac{b_1 b_2}{c_1 c_2} > 1 + \frac{(1-a_1)(1-a_2)}{c_1 c_2} \tag{3.22}$$

i.e.

$$[b_1 b_2 - (1 - a_1)(1 - a_2)]e^{(r_1 + r_2)\tau} + e^{r_1 \tau}(1 - a_1) + e^{r_2 \tau}(1 - a_2) > 1, \tag{3.23}$$

which contradicts with (3.16), therefore we have $\rho \leqslant 1$, by Lemma 2.2, we have $F^n(x, y) \to (0, 0)$ as $n \to \infty$, which means

that system (2.3) is extinct. This completes the proof of Theorem 3.1. □

Remark 3.2. Based on the assumptions and the actual biological meanings of parameters b_i, r_i and a_i ($i = 1, 2$), involving the migration period τ, condition (3.1) in Theorem 3.1 is very weak and easy to verify. Even if there exists a low rate of migration a_i between two patches and a high rate of mortality during migration b_i, the metapopulation can be permanent (or, alternatively, goes to extinction), which differs from the results of continuous dispersal models [25,28], where only a high rate of migration between patches and a low rate of mortality during migration can stabilize the population and the metapopulation might persist. Therefore, our result means that the evolution of natural populations in a patchy environment with discontinuous bilateral dispersal has a greater number of outcomes that should be realizable in nature, which nicely matches what occurs in the real ecological environment. Moreover, we can easily conclude that $\Lambda = [b_1 b_2 - (1 - a_1)(1 - a_2)]e^{(r_1 + r_2)\tau} + e^{r_1 \tau}(1 - a_1) + e^{r_2 \tau}(1 - a_2)$ is a threshold value for the persistence of system (2.3), i.e.. if $\Lambda > 1$ it will be permanent and if $\Lambda \leqslant 1$ it will go to extinction.

Theorem 3.3. *Assume that $b_1 b_2 e^{(r_1 + r_2)\tau} > 1$ or $(\leqslant 1)$, then system (2.6) is permanent (or extinct).*

Proof. First, we prove if $b_1 b_2 e^{(r_1 + r_2)\tau} > 1$ then system (2.6) is permanent. Since $0 \leqslant b_i \leqslant 1$ and $0 \leqslant c_i = e^{-r_i \tau} \leqslant i (i = 1, 2)$, from system (2.6) we have

$$x_{2n+2} = \frac{b_2 k}{1 - c_2 + c_2 y_{2n+1}^{-1}} < \frac{b_2 k}{1 - c_2}, \tag{3.24}$$

$$y_{2n+1} = \frac{b_1}{k(1 - c_1 + c_1 x_{2n}^{-1})} < \frac{b_1}{k(1 - c_1)}. \tag{3.25}$$

Next, in system (2.6), we have

$$x_{2n+2} = \frac{b_1 b_2 k}{b_1(1 - c_2) + c_2 k(1 - c_1) + c_1 c_2 k x_{2n}^{-1}}. \tag{3.26}$$

Let

$$\phi(x_{2n}) = \frac{b_1 b_2 k}{b_1(1 - c_2) + c_2 k(1 - c_1) + c_1 c_2 k x_{2n}^{-1}}. \tag{3.27}$$

From (3.24) we see that the sequence $\{x_{2n}\}$ is bounded above and $\phi'(x) > 0$. Since $\alpha \equiv b_1(1 - c_1) + c_1 k(1 - c_1) > 0$, (3.26) yields

$$x_{2n} < \frac{b_1 b_2}{c_1 c_2} x_{2n}. \tag{3.28}$$

If there exists N such that $x_{2N+2} \leqslant x_{2N}$. Then $x_{2n+2} \leqslant x_{2n}$ for all $n \geqslant N$ because ϕ is an increasing function. From $\phi(x_{2n}) < x_{2n}$, we have

$$b_1 b_2 k < \alpha x_{2n} + c_1 c_2 k. \tag{3.29}$$

Dividing (3.29) by $c_1 c_2 k$, we have

$$\frac{b_1 b_2}{c_1 c_2} < \alpha x_{2n} + 1. \tag{3.30}$$

Therefore, by $b_1 b_2 e^{(r_1 + r_2)\tau} = \frac{b_1 b_2}{c_1 c_2} > 1$ we have

$$x_{2n} > \frac{\frac{b_1 b_2}{c_1 c_2} - 1}{\alpha} > 0. \tag{3.31}$$

Therefore, we have

$$\liminf x_{2n} > \frac{\frac{b_1 b_2}{c_1 c_2} - 1}{\alpha} > 0. \tag{3.32}$$

Similarly, in system (2.6),

$$y_{2n+1} = \frac{b_1 b_2}{kb_2(1-c_1) + c_1(1-c_2) + c_1 c_2 y_{2n-1}^{-1}}. \tag{3.33}$$

By the same arguments like above, we can conclude

$$\liminf y_{2n+1} > \frac{\frac{b_1 b_2}{c_1 c_2} - 1}{\beta} > 0, \tag{3.34}$$

where $\beta \equiv kb_2(1-c_1) + c_1(1-c_2) > 0$. Based on above arguments, we can see system (2.6) is permanent.

Next if $b_1 b_2 e^{(r_1+r_2)\tau} \leqslant 1$, by (3.28), we can see

$$x_{2n+2} < x_{2n}. \tag{3.35}$$

Therefore, the sequence $\{x_{2n}\}$ is non-increasing. Let the limit of $\{x_{2n}\}$ be γ, then $\gamma \geqslant 0$. Take limit for two sides of (3.26), we can obtain

$$\gamma = \frac{b_1 b_2 k - c_1 c_2 k}{b_1(1-c_2) + c_2 k(1-c_1)} \leqslant 0. \tag{3.36}$$

Therefore, $\gamma = 0$, i.e. $\lim x_{2n} = 0$

Similarly, by the same arguments like above, we can conclude $\lim y_{2n+1} = 0$. Therefore, if $b_1 b_2 e^{(r_1+r_2)\tau} \leqslant 1$, system (2.6) is extinct. This completes the proof of Theorem 3.3. □

Remark 3.4. The assumption $b_1 b_2 e^{(r_1+r_2)\tau} > 1$ in Theorem 3.3 is very simple and easy to verify too, which means that a higher successful rate of migration b_i $(i = 1, 2)$, a higher growth rate r_i and a longer migration period τ (that is, enough time to be restored, mature, breed, etc.) will greatly enhance the survival of natural populations, which is consistent with the real environment. The result implies that the behavior of aggregate migration alternating periodically between patches according to changes in the environment is the best way for natural populations to subsist and evolve. This strategy will evolve by natural selection and will continue from generation to generation, as in many natural populations. Furthermore, we can easily conclude that $\Lambda = b_1 b_2 e^{(r_1+r_2)\tau}$ is a threshold value of persistence for above system (2.6), i.e. if $\Lambda > 1$ it will be permanent, if $\Lambda \leqslant 1$ it will be extinct.

3.2. Existence and uniqueness of positive periodic solutions

In this part, we will prove the existence and uniqueness of the fixed points of systems (2.3) and (2.6), which means that systems (1.3) and (1.4) have uniquely positive periodic solutions.

Corresponding to (2.3), let us consider the following system

$$\begin{cases} x = \frac{(1-a_1)x}{x+(1-x)c_1} + \frac{b_2 ky}{y+(1-y)c_2}, \\ y = \frac{(1-a_2)y}{y+(1-y)c_2} + \frac{b_1}{k(1+(x^{-1}-1)c_1)}. \end{cases} \tag{3.37}$$

From (3.37), we have

$$\begin{cases} (1-c_1)x + c_1 - 1 + a_1 = b_2 k \frac{1+(x^{-1}-1)c_1}{1+(y^{-1}-1)c_2}, \\ (1-c_2)y + c_2 - 1 + a_2 = \frac{b_1}{k} \frac{1+(y^{-1}-1)c_2}{1+(x^{-1}-1)c_1}. \end{cases} \tag{3.38}$$

Thus,

$$(1-c_1)x + c_1 - 1 + a_1][(1-c_2)y + c_2 - 1 + a_2] = b_2 b_1. \tag{3.39}$$

From the first equation of (3.38) we have

$$y = \frac{c_2[(1-c_1)x + c_1 - 1 + a_1]}{b_2 k[1 + (x^{-1} - 1)] + (c_2 - 1)[(1-c_1)x + c_1 - 1 + a_1]}, \tag{3.40}$$

which may be put into (3.39). After some algebraic manipulation this reduces to

$$(1-c_1)^2(1-c_2)(1-a_2)x^3 + (1-c_1)[b_2 k(c_2 - 1 + a_2)(1 - c_1) + 2(1-c_2) \times (1-a_2)(c_1 - 1 + a_1) + b_1 b_2(1 - c_2)]x^2 + [b_2 k(2c_1 - 1 + a_1)(c_2 - 1 + a_2) \times (1 - c_1) + (1 - c_2)(1 - a_2)(c_1 - 1 + a_1)^2 - b_1 b_2^2 k(1 - c_1) + b_1 b_2(1 - c_2) \times (c_1 - 1 + a_1)]x - [b_1 b_2^2 kc_1 - kc_1 b_2(c_1 - 1 + a_1) \times (c_2 - 1 + a_2)]$$
$$= 0. \tag{3.41}$$

Let

$$f(x) = \phi_1 x^3 + \phi_2 x^2 + \phi_3 x - \phi_4, \tag{3.42}$$

where

$$\begin{aligned} \phi_1 &= (1-c_1)^2(1-c_2)(1-a_2), \\ \phi_2 &= (1-c_1)[b_2 k(c_2 - 1 + a_2)(1 - c_1) + 2(1-c_2)(1-a_2) \\ &\quad \times (c_1 - 1 + a_1) + b_1 b_2(1 - c_2)], \\ \phi_3 &= b_2 k(2c_1 - 1 + a_1)(c_2 - 1 + a_2)(1 - c_1) + (1 - c_2)(1 - a_2) \\ &\quad \times (c_1 - 1 + a_1)^2 - b_1 b_2^2 k(1 - c_1) + b_1 b_2(1 - c_2)(c_1 - 1 + a_1), \\ \phi_4 &= b_1 b_2^2 kc_1 - kc_1 b_2(c_1 - 1 + a_1)(c_2 - 1 + a_2). \end{aligned} \tag{3.43}$$

Then

$$f'(x) = 3\phi_1 x^2 + 2\phi_2 x + \phi_3. \tag{3.44}$$

Let $f'(x) = 0$, we have

$$x_{1,0} = \frac{-\phi_2 + \sqrt{\Delta}}{3\phi_1}, \quad x_{2,0} = \frac{-\phi_2 - \sqrt{\Delta}}{3\phi_1}, \tag{3.45}$$

where

$$\begin{aligned} \Delta = \phi_2^2 - 3\phi_1 \phi_3 &= (1-c_1)^2 \Big[b_2^2 k^2(c_2 - 1 + a_2)^2(1 - c_1)^2 + (1 - c_2)^2 \\ &\quad \times (1-a_2)^2(c_1 - 1 + a_1)^2 + b_1^2 b_2^2(1 - c_2)^2 + b_2 k(1 - c_2)(1 - a_2)(1 - c_1) \\ &\quad \times (c_2 - 1 + a_2)(-2c_1 - 1 + a_1) + b_1 b_2^2 k(c_2 - 1)(1 - c_1)(a_2 - 1 - 2c_2) \\ &\quad + b_1 b_2(1 - a_2)(1 - c_2)^2(c_1 - 1 + a_1) \Big]. \end{aligned} \tag{3.46}$$

Obviously, the following conclusion is true: $f(x) \to -\infty$ as $x \to -\infty, f(x) \to +\infty$ as $x \to +\infty, f(x)(x \in R)$ is a continuous function.

Theorem 3.5. *There exists a unique positive fixed point (ξ, η) of system (2.3) if one of the following conditions is true:*

(1) $1 - c_1 - a_1 > 0, 1 - c_2 - a_2 > 0, \phi_2 \geqslant 0$;
(2) $1 - c_1 - a_1 < 0, 1 - c_2 - a_2 < 0, \phi_4 > 0$ and
    $(1-c_2)(c_1 - 1 + a_1) - b_2 k(1 - c_1) > 0$;
(3) $(1 - c_1 - a_1)(1 - c_2 - a_2) \leqslant 0$.

The proof of Theorem 3.5 will be given in Appendix A.

Remark 3.6. Although the conditions and development in Theorem 3.5 are somewhat long and complicated compared with the symmetrical pulse dispersal model [30], they are still very easy to satisfy and understand. However, with the eye to the real migratory behavior of natural populations, it is reasonable because there are so many nondeterministic factors which can greatly impact and change the evolving trajectories of migratory populations, such as the matching of periods between aggregate migration and individual reproduction (or growth), the delay (or advance) of emigration from present patch or arrival to the new region, to say nothing of natural disasters and man-made inter-

ventions. Actually, the trajectories of natural populations in heterogeneous environments are very subtly affected by many factors, so there are hardly any purely periodic trajectories.

Corresponding to system (2.6), we have the following.

Theorem 3.7. *System (2.6) has a unique positive fixed point (ξ, η) if $b_1 b_2 e^{(r_1 + r_2)\tau} > 1$.*

Proof. Let ξ is the fixed point of (3.26), we have

$$\xi = \frac{(b_1 b_2 - c_1 c_2)k}{b_1(1 - c_2) + c_2 k(1 - c_1)} > 0, \tag{3.47}$$

Similarly, let η is the fixed point of (3.33), we have

$$\eta = \frac{b_1 b_2 - c_1 c_2}{k b_2(1 - c_1) + c_1(1 - c_2)} > 0. \tag{3.48}$$

Therefore, there exists a unique positive fixed point (ξ, η) for system (2.6). The proof is complete. $\square$

Remark 3.8. Condition in Theorem 3.7 further proves that the strategy of aggregate migration alternating periodically between patches according to environmental changs in natural populations is not only a very effective way for survival and orbit stability but also can be easy to realize in the natural environment, which is less influenced and restricted by nature than any other kinds of migration, and which is why it is prevalent in many natural populations.

3.3. Stability

Now, we prove that the positive fixed points (ξ, η) of (2.3) and (2.6) are globally stable by using Lemma 2.2, which means that the positive periodic solutions of system (1.3) and (1.4) are globally stable.

Firstly for system (2.3) we have the following

Theorem 3.9. *If conditions of Theorem 3.5 hold, then for every $(x, y) > (0, 0)$, $F^{(n)}(x, y) \to (\xi, \eta)$ as $n \to \infty$.*

Proof. In order to apply Lemma 2.2 we need to show that anyone of conditions (1), (2), or (3) in Theorem 3.5 imply that system (2.3) is permanent. If condition (1) of Theorem 3.5 holds, then by

$$\phi_2 = (1 - c_1)[b_2 k(c_2 - 1 + a_2)(1 - c_1) + b_1 b_2(1 - c_2) \\ + 2(1 - c_2)(1 - a_2)(c_1 - 1 + a_1)] \geqslant 0, \tag{3.49}$$

we have

$$2(1 - c_2)(1 - a_2)(c_1 - 1 + a_1) + b_1 b_2(1 - c_2) > 0. \tag{3.50}$$

Then, we have

$$b_1 b_2 > -2(1 - a_2)(c_1 - 1 + a_1), \tag{3.51}$$

so

$$b_1 b_2 - (c_1 - 1 + a_1)(c_2 - 1 + a_2) \\ > 2(a_2 - 1)(c_1 - 1 + a_1) - (c_2 - 1 + a_2)(c_1 - 1 + a_1) \\ = (a_2 - 1 - c_2)(c_1 - 1 + a_1) \\ = (c_2 - 1 + a_2)(c_1 - 1 + a_1) - 2c_2(c_1 - 1 + a_1) > 0. \tag{3.52}$$

If condition (2) holds, we have

$$\phi_4 = b_1 b_2^2 k c_1 - k c_1 b_2 (c_1 - 1 + a_1)(c_2 - 1 + a_2) \\ = b_2 k c_1 [b_1 b_2 - (c_1 - 1 + a_1)(c_2 - 1 + a_2)] > 0. \tag{3.53}$$

Therefore, we have $b_1 b_2 - (c_1 - 1 + a_1)(c_2 - 1 + a_2) > 0$.

If condition (3) holds, obviously, we can see $b_1 b_2 - (c_1 - 1 + a_1)(c_2 - 1 + a_2) > 0$.

Therefore, if conditions of Theorem (3.5) hold, we always have $b_1 b_2 - (c_1 - 1 + a_1)(c_2 - 1 + a_2) > 0$, i.e. (3.1). Therefore, we have system (2.3) is permanent. As similar as the arguments in Theorem (3.1), we have $F(x, y)$ defined in (3.17) satisfies all conditions in Lemma (2.2). From (3.17), let ρ be the spectral radium of (3.19). Assume $\rho \leqslant 1$, by (3.21) we can obtain

$$\frac{1 - a_1}{c_1} + \frac{1 - a_2}{c_2} + \frac{b_1 b_2}{c_1 c_2} \leqslant 1 + \frac{(1 - a_1)(1 - a_2)}{c_1 c_2}, \tag{3.54}$$

i.e.

$$[b_1 b_2 - (1 - a_1)(1 - a_2)]e^{(r_1 + r_2)\tau} + e^{r_1 \tau}(1 - a_1) + e^{r_2 \tau}(1 - a_2) \leqslant 1,$$

which contradicts with (3.1), therefore, we have $\rho > 1$, where $0 < c_i = e^{-r_i \tau} \leqslant 1$ $(i = 1, 2)$. By Lemma 2.2, we have $F^{(n)}(x, y) \to (\xi, \eta)$ as $\to \infty$. This completes the proof of Theorem 3.9.

For system (2.6) on the global stability, we have the following.

Theorem 3.10. *If $b_1 b_2 e^{(r_1 + r_2)\tau} > 1$, then for every $(x, y) > (0, 0)$, $F^{(n)}(x, y) \to (\xi, \eta)$ as $n \to \infty$.*

Proof. Corresponding to (2.6), let us consider the following system

$$x = \frac{b_1 b_2 k x}{[b_1(1 - c_1) + c_2 k(1 - c_2)]x + c_1 c_2 k}, \\ y = \frac{b_1 b_2 y}{[k b_2(1 - c_1) + c_1(1 - c_2)]y + c_1 c_2}. \tag{3.55}$$

From (3.55) we obtain that

$$F(x) = \frac{b_1 b_2 k x}{[b_1(1 - c_1) + c_2 k(1 - c_2)]x + c_1 c_2 k}, \\ F(y) = \frac{b_1 b_2 y}{[k b_2(1 - c_1) + c_1(1 - c_2)]y + c_1 c_2}. \tag{3.56}$$

Obviously, $F(x) \in C^1$ in int (R_+) and $F(0) = 0$. We have

$$DF(x) = \frac{b_1 b_2 c_1 c_2 k^2}{\{[b_1(1 - c_2) + c_2 k(1 - c_1)]x + c_1 c_2 k\}^2}, \tag{3.57}$$

$$DF(0) = \frac{b_1 b_2}{c_1 c_2}. \tag{3.58}$$

Obviously, $\lim_{x \to 0} DF(x) = DF(0)$, $DF(x) > 0$ for any $x > 0$ and $DF(x_1) < DF(x_2)$ if $x_1 > x_2 > 0$. Let ρ be the spectral radius of $\rho(DF(0))$, then

$$\rho = \frac{b_1 b_2}{c_1 c_2}. \tag{3.59}$$

Since $b_1 b_2 e^{(r_1 + r_2)\tau} > 1$, we have $\rho > 1$, therefore from Lemma 2.2, we have $F^n(x) \to \xi$ as $n \to \infty$. Similarly, we could obtain that $F^n(y) \to \eta$ as $n \to \infty$ for $b_1 b_2 e^{(r_1 + r_2)\tau} > 1$. This completes the proof of Theorem 3.10. $\square$

Remark 3.11. Theorems 3.9 and 3.10 show that the orbits of migrating populations are principally inclined to be attracted by their ideal periodic orbit providing it exists. Namely, the globally stable states of migrating populations are mostly determined by their own accurate harmony with the real environment, long term coincident dispersal periods, instantaneous emigration (immigration) from one patch and arrival (departure) to another patch. In other words, stability of orbits greatly depends on the long-range constants of the environmental parameters.

Remark 3.12. In this paper, we mainly study two kinds of impulsive dispersal models of single species, and focus on comparing the results between autonomous continuous dispersal model with constant migration rates (e.g. model (1.1)) and autonomous discontinuous dispersal models with constant periodic migration rates (models (1.2)). However, in the real world, we know there is hardly any real constant environment, therefore, non-autonomous impulsive dispersal model with time-periodic variable migration rates will be very reasonable and match well with the real ecosystem. Therefore, there is an open question, i.e.. what is the dynamical difference between non-autonomous discontinuous dispersal model with time-periodic variable migration rates and non-autonomous continuous dispersal model with time-periodic variable migration rates.

4. Discussion

For system (2.1), we can easily find that the population dynamics between two heterogeneous patches are not greatly influenced by periodically bilateral impulse migration, no matter if there is a high rate of migration (with low mortality rate during migration) or a low rate of migration (with high mortality rate during migration), with highly frequent migration or infrequent migration. The survival and stability (or extinction) of metapopulations are only determined by threshold value Λ. In general, populations moving between patches will steadily persist according to the behavior they exhibit in each patch providing $\Lambda > 1$ even with the occurrence of periodic migration, but will lead to extinction if $\Lambda \leqslant 1$. These results are different from some earlier results about continuous dispersal model with constant migration rates of single species [25,26,28]. Those authors found that only a high rate of dispersal between patches and low mortality during migration can lead to stability of population trajectories and persistence of the metapopulations. Therefore, our result means that the evolution of natural populations in a patchy environment with discontinuous bilateral dispersal has a greater number of outcomes that should be realizable in nature, which nicely matches what occurs in the real ecological environment.

For model (2.4), we found that the survival and stability (or extinction) are depends on the threshold value $\Lambda = b_1 b_2 e^{(r_1+r_2)\tau} > 1$ (or $\leqslant 1$), which is very simple and easy to be satisfied in the real environment. The result implies that the behavior of aggregate migration alternating periodically between patches according to changes in the environment is the best way for natural populations to subsist and evolve. This strategy will evolve by natural selection and will continue from generation to generation, as in many natural populations.

In brief, depending on whether there is simultaneous bi-directional impulse dispersal (migration) or aggregate migration (periodic back and forth migration of the whole population), the form of the dispersal plays different roles in the dynamics of metapopulations. The form of the dispersal affects simultaneous bi-directional dispersal relatively little, but greatly impacts periodic back-and-forth migration when there is an assumption of constancy of environmental parameters. Comparing these results with those of continuous dispersal models, we conclude that impulse dispersal models encompass more realistic features of nature that are difficult to analyze by continuous models, which means the hybrid dynamical models will be a better choice to model and investigate the dynamics of metapopulations.

Appendix A. Proof of Theorem 3.4

Proof. If (1) is true, since $\phi_2 \geqslant 0$, we have

$$(1 - c_1)[b_2 k(c_2 - 1 + a_2)(1 - c_1) + b_1 b_2(1 - c_2) + 2(1 - c_2)$$
$$\times (1 - a_2)(c_1 - 1 + a_1)] \geqslant 0. \tag{A.1}$$

Thus,

$$b_2 k(c_2 - 1 + a_2)(1 - c_1)(c_1 - 1 + a_1) + 2(1 - c_2)(1 - a_2)$$
$$\times (c_1 - 1 + a_1)^2 \leqslant -b_1 b_2(1 - c_2)(c_1 - 1 + a_1). \tag{A.2}$$

Hence,

$$\phi_3 \leqslant b_2 k(2c_1 - 1 + a_1)(c_2 - 1 + a_2)(1 - c_1) + (1 - c_2)(1 - a_2)$$
$$\times (c_1 - 1 + a_1)^2 - b_1 b_2^2 k(1 - c_1) - b_2 k(c_2 - 1 + a_2)(1 - c_1)$$
$$\times (c_1 - 1 + a_1) - 2(1 - c_2)(1 - a_2)(c_1 - 1 + a_1)^2$$
$$= b_2 k c_1(c_2 - 1 + a_2)(1 - c_1) - b_1 b_2^2 k(1 - c_1)$$
$$- (1 - c_2)(1 - a_2)(c_1 - 1 + a_1)^2 < 0. \tag{A.3}$$

From the definition of ϕ_2, we have

$$2(1 - c_2)(1 - a_2)(c_1 - 1 + a_1) + b_1 b_2(1 - c_2) > 0, \tag{A.4}$$

then

$$b_1 b_2 > -2(1 - a_2)(c_1 - 1 + a_1), \tag{A.5}$$

which implies that

$$\phi_4 > c_1 b_2 k[2(a_2 - 1)(c_1 - 1 + a_1) - (c_2 - 1 + a_2)(c_1 - 1 + a_1)]$$
$$= c_1 b_2 k(a_2 - 1 - c_2)(c_1 - 1 + a_1) > c_1 b_2 k(c_2 - 1 + a_2)(c_1 - 1 + a_1)$$
$$> 0. \tag{A.6}$$

Because $\phi_3 < 0$, we obtain $\sqrt{\Delta} > |\phi_2|$. From the above analysis, we have $x_{1,0} > 0, x_{2,0} < 0$ and $f(0) = -\phi_4 < 0$. Since $f(x)(x \in (-\infty, +\infty))$ is continuous, there exists a unique $\xi \in (0, +\infty)$ such that $f(\xi) = 0$ by intermediate value theorem. From $\phi_4 > 0$ and the image of (3.40), we know that $\xi > \frac{1-c_1-a_1}{1-c_1}$ and $\eta = y(\xi) > \frac{1-c_2-a_2}{1-c_2} > 0$. Thus, there is a unique (ξ, η).

If (2) is true, we could obtain that $\phi_2 > 0$. Now, we let

$$x_1^* = \frac{1 - c_1 - a_1}{1 - c_1}, \quad x_2^* = \frac{1}{1 - c_1}\left[\frac{b_1 b_2}{c_2 - 1 + a_2} - c_1 + 1 - a_1\right]. \tag{A.7}$$

We get that $x_1^* < x_2^*$, $y(0) = \frac{1}{1-c_2}\left[\frac{b_1 b_2}{c_1 - 1 + a_1} - c_2 + 1 - a_2\right]$, $y(x_2^*) = 0$. For any

$$\xi \in (0, x_2^*), \quad \text{we have} \quad y(\xi)$$
$$\in \left(0, \frac{1}{1 - c_2}\left[\frac{b_1 b_2}{c_1 - 1 + a_1} - c_2 + 1 - a_2\right]\right). \tag{A.8}$$

Hence, $y(\xi) > 0$. We have

$$f(x_2^*) = \phi_1 x_2^{*3} + \phi_2 x_2^{*2} + \phi_3 x_2^* - \phi_4$$
$$= \phi_1 x_2^{*3} + \phi_2 x_2^{*2} + \phi_3 x_2^* - b_2 k c_1(1 - c_1)(c_2 - 1 + a_2)x_2^*$$
$$= \phi_1 x_2^{*3} + \phi_2 x_2^{*2} + \bar{\phi}_3 x_2^* \tag{A.9}$$

where

$$\bar{\phi}_3 = b_2 k(2c_1 - 1 + a_1)(c_2 - 1 + a_2)(1 - c_1) + (1 - c_2)(1 - a_2)$$
$$\times (c_1 - 1 + a_1)^2 - b_1 b_2^2 k(1 - c_1) + b_1 b_2(1 - c_2)(c_1 - 1 + a_1)$$
$$- b_2 k c_1(1 - c_1)(c_2 - 1 + a_2)b_2 k(1 - c_1)(c_2 - 1 + a_2)(c_1 - 1 + a_1)$$
$$+ (1 - c_2)(1 - a_2)(c_1 - 1 + a_1)^2 + b_1 b_2[(1 - c_2)(c_1 - 1 + a_1)$$
$$- b_2 k(1 - c_1)] > 0. \tag{A.10}$$

Since $\phi_1 > 0, \phi_2 > 0, \bar{\phi}_3 > 0, \phi_4 > 0$ and $x_2^* > 0$, we obtain that $f(x_2^*) > 0, f(0) = -\phi_4 < 0$. If $\Delta \geqslant 0$, then $x_{2,0} < 0$, by intermediate value theorem, we could find a unique $\xi \in (0, x_2^*)$ such that $f(\xi) = 0$ and $\eta = y(\xi)$, where

$$\eta = y(\xi) \in \left(0, \frac{1}{1-c_2}\left[\frac{b_1 b_2}{c_1 - 1 + a_1} - c_2 + 1 - a_2\right]\right). \tag{A.11}$$

If $\Delta < 0$, then $f(x)$ is monotone increasing for all $x \in (-\infty, +\infty)$. Therefore, by the same arguments above, there exists a unique ξ and η satisfying the conclusion. If (3) is true, we give the proof in the following cases:

case 1: $(1 - c_1 - a_1)(1 - c_2 - a_2) < 0$.
case 2: $(1 - c_1 - a_1)(1 - c_2 - a_2) = 0$.

For case 1, if $(1 - c_1 - a_1) < 0$, $(1 - c_2 - a_2) > 0$, we obtain $\phi_4 > 0$ and

$$\Delta \geqslant (1 - c_1)^2 \{b_2 k(c_2 - 1 + a_2)(1 - c_1)(1 - c_2)(1 - a_2)(-3c_1) \\ + b_1 b_2^2 k(1 - c_2) \times (1 - c_1)(2 + c_2 - 2a_2) + 2b_1 b_2(1 - a_2) \\ \times (1 - c_2)^2 (c_1 - 1 + a_1)\} > 0. \tag{A.12}$$

If $\phi_2 \geqslant 0$, then $x_{2,0} < 0, f(0) = -\phi_4 < 0$. By the same argument with (1), we conclude that there exists a unique pair (ξ, η), where

$$\xi \in (0, +\infty), \quad \eta = y(\xi) > \frac{1 - c_2 - a_2}{1 - c_2} > 0. \tag{A.13}$$

If $\phi_2 < 0$, then

$$(1 - c_1)[b_2 k(c_2 - 1 + a_2)(1 - c_1) + 2(1 - c_2)(1 - a_2)(c_1 \\ - 1 + a_1) + b_1 b_2(1 - c_2)] \\ < 0. \tag{A.14}$$

This implies that

$$b_2 k(c_2 - 1 + a_2)(1 - c_1)(c_1 - 1 + a_1) + 2(1 - c_2)(1 - a_2)(c_1 - 1 + a_1)^2 \\ < -b_1 b_2(1 - c_2)(c_1 - 1 + a_1) \tag{A.15}$$

and

$$\phi_3 < b_2 k(2c_1 - 1 + a_1)(c_2 - 1 + a_2)(1 - c_1) + (1 - c_2) \\ \times (1 - a_2)(c_1 - 1 + a_1)^2 - b_1 b_2^2 k(1 - c_1) - b_2 k(c_2 - 1 + a_2) \\ \times (1 - c_1)(c_1 - 1 + a_1) - 2(1 - a_2)(1 - c_2)(c_1 - 1 + a_1)^2 \\ = b_2 k c_1(c_2 - 1 + a_2)(1 - c_1) - (1 - c_2)(1 - a_2)(c_1 - 1 + a_1)^2 \\ - b_1 b_2^2 k(1 - c_1) < 0. \tag{A.16}$$

Furthermore, $\sqrt{\Delta} > |\phi_2|$. So, $x_{1,0} > 0$, $x_{2,0} < 0, f(0) < 0$. Similarly, by the intermediate value theorem, there is a unique (ξ, η), where $\xi \in (0, +\infty)$, $\eta = y(\xi) > \frac{1 - c_2 - a_2}{1 - c_2} > 0$.

If $(1 - c_1 - a_1) > 0$, $(1 - c_2 - a_2) < 0$, we obtain $\phi_4 > 0$ and

$$\Delta > (1 - c_1)^2 [b_2 k(1 - c_2)(1 - a_2)(1 - c_1)(c_2 - 1 - a_2)(1 - c_1 - a_1) \\ + b_2 k(1 - c_2)(1 - c_1)(1 - a_2)(c_2 - 1 + a_2)(-2c_1 - 1 + a_1) \\ + b_1 b_2^2 k(1 - c_2)(1 - c_1)(c_2 - 1 + a_2) + b_1 b_2^2 k(c_2 - 1)(1 - c_1) \\ \times (a_2 - 1 - 2c_2)] = (1 - c_1)^2 [b_2 k(c_2 - 1 + a_2)(1 - c_1)(1 - c_2) \\ \times (1 - a_2)(-3c_1) + 3c_2 b_1 b_2^2 k(1 - c_2)(1 - c_1)] > 0. \tag{A.17}$$

Therefore, $x_{1,0}$, $x_{2,0}$ exist. From (3.40), we have

$$f(x_1^*) = \phi_1 x_1^{*3} + \phi_2 x_1^{*2} + \phi_3 x_1^* - \phi_4 \\ = \phi_1 \left[\frac{1 - c_1 - a_1}{1 - c_1}\right]^3 + \phi_2 \left[\frac{1 - c_1 - a_1}{1 - c_1}\right]^2 \\ + \left[\phi_3 \frac{1 - c_1 - a_1}{1 - c_1}\right] - \phi_4 \\ = b_1 b_2^2 k(a_1 - 1) < 0. \tag{A.18}$$

From system (3.36), we obtain that if $x < \frac{1 - c_1 - a_1}{1 - c_1}$ then $y < \frac{1 - c_2 - a_2}{1 - c_2} < 0$. Thus, we only consider $x > \frac{1 - c_1 - a_1}{1 - c_1}$. Since

$$f(x_2^*) = \frac{1}{(1 - c_1)(c_2 - 1 + a_2)^3} \Big[c_2 b_1^3 b_2^3 (1 - c_2) + c_2 b_1^2 b_2^2 (c_2 - 1 + a_2) \\ \times \big(c_1 - 1 + a_1\big)(c_2 - 1) - 2b_2 k c_1(c_2 - 1 + a_2)^4 (1 - c_1)(c_1 - 1 + a_1) \\ - \big(1 - c_2\big)(1 - a_2)(c_1 - 1 + a_1)^3 (c_2 - 1 + a_2)^3 \Big] > 0, \tag{A.19}$$

by the intermediate value theorem, there exists a unique (ξ, η), such that $\xi \in (x_1^*, x_2^*), \eta \in (0, +\infty)$ and $f(\xi) = 0$.

For case 2, if $1 - c_1 - a_1 > 0$, $1 - c_2 - a_2 = 0$, we have

$$\phi_2 = (1 - c_1)[2(1 - c_2)(1 - a_2)(c_1 - 1 + a_1)^2 - b_1 b_2(c_2 - 1)] > 0, \\ \Delta \geqslant 3c_2 b_1 b_2^2 k(1 - c_1)^3 (1 - c_2) > 0, \\ \phi_4 = c_1 b_1 b_2^2 k > 0, \quad f(0) = -c_1 b_1 b_2^2 k < 0. \tag{A.20}$$

We know that $x_{2,0} < 0$. Furthermore, since $f(x_1^*) < 0$, we acquire a unique (ξ, η) by the intermediate value theorem, such that

$$\eta = y(\xi) \left(\xi \in \left(\frac{1 - c_1 - a_1}{1 - c_1}, +\infty\right), \eta \in (0, +\infty)\right). \tag{A.21}$$

If $1 - c_1 - a_1 = 0$, $1 - c_2 - a_2 > 0$, we obtain that

$$\phi_3 = b_2 k c_1(c_2 - 1 + a_2)(1 - c_1) - b_1 b_2^2 k(1 - c_1) < 0, \tag{A.22}$$

$f(0) = -c_1 b_1 b_2^2 k < 0$ and $\sqrt{\Delta} > |\phi_2|$. So, there exist $x_{1,0} > 0$, $x_{2,0} < 0$. Furthermore, by the intermediate value theorem, there exists a unique (ξ, η), such that $\eta = y(\xi) > 0$, where $\xi \in (0, +\infty)$, and $\eta \in (\frac{1 - c_2 - a_2}{1 - c_2}, +\infty)$.

If $1 - c_1 - a_1 < 0$, $1 - c_2 - a_2 = 0$, it implies that

$$\phi_2 = (1 - c_1)[2(1 - c_2)(1 - a_2)(c_1 - 1 + a_1)^2 + b_1 b_2(1 - c_2)] > 0,$$

$$\Delta \geqslant (1 - c_1)^2 \{3c_2 b_1 b_2^2 k(1 - c_2)(1 - c_1) + 2b_1 b_2 \times (1 - a_2) \\ \times (1 - c_2)^2 (c_1 - 1 + a_1)\} \\ > 0, \tag{A.23}$$

$f(0) = -c_1 b_1 b_2^2 k < 0.$

Thus, by the intermediate value theorem we obtain $x_{2,0} < 0$ and there exists a unique positive (ξ, η), where $\xi \in (0, +\infty)$, $\eta \in (0, \frac{b_1 b_2}{(1 - c_2)(c_1 - 1 + a_1)})$, such that $\eta = y(\xi) > 0$. If $1 - c_1 - a_1 = 0, 1 - c_2 - a_2 < 0$, we have

$$\phi_2 = (1 - c_1)[b_2 k(1 - c_1)(c_2 - 1 + a_2) - b_1 b_2(c_2 - 1)] > 0,$$

$$f(x_2^*) = \frac{c_2 b_1^3 b_2^3 (1 - c_2)}{(1 - c_1)(c_2 - 1 + a_2)^3} > 0, \tag{A.24}$$

$$f(0) = -c_1 b_1 b_2^2 k < 0,$$

$$\Delta \geqslant (1-c_1)^2\{b_2 k(c_2-1+a_2)(1-c_1)(1-c_2)(1-a_2)(-3c_1)$$

$$+3c_2 b_1 b_2^2 k(1-c_2)(1-c_1)\}.$$

If $\Delta \geqslant 0$, then $x_{2,0} < 0$, by the intermediate value theorem, we could find a unique $\xi \in (0, x_2^*)$ such that $f(\xi) = 0$ and $\eta = y(\xi)$, where

$$\eta = y(\xi) \in \left(0, \frac{1}{1-c_2}\left[\frac{b_1 b_2}{c_1-1+a_1}-c_2+1-a_2\right]\right). \quad (A.25)$$

If $\Delta < 0$, then we have $f(x)$ as monotone increasing for all $x \in (-\infty, +\infty)$. Therefore, by the same arguments above, we find there exists a unique (ξ, η) satisfying the conclusion. If $1-c_1-a_1 = 0, 1-c_2-a_2 = 0$, since

$$\phi_2 = b_1 b_2(1-c_1)(1-c_2) > 0, \quad \phi_3 = -b_1 b_2^2 k(1-c_1)$$

$$< 0, \quad \phi_4 > 0, \quad (A.26)$$

we get $\sqrt{\Delta} > |\phi_2|, x_{1,0} > 0, x_{2,0} < 0$ and $f(0) < 0$. Hence there exists a unique (ξ, η), such that $\xi \in (0, +\infty)$ by intermediate value theorem, where $\eta \in (0, +\infty))$, $\eta = y(\xi)$. The proof is complete. $\quad \square$

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