Ideal Free Distribution in a System of Multiple Predator and Prey Species

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Abstract

We study mechanisms and effects of ideal free distributions (IFDs) on an ecological community consisting of $\boldsymbol{n}$ prey and $\boldsymbol{m}$ predator species, for any positive integers $\boldsymbol{n}$ and $\boldsymbol{m}$, by considering the corresponding diffusive Lotka-Volterra system with time-periodic coefficients. We define a notion of joint IFD in a time-periodic environment, and give necessary and sufficient conditions for it to be achieved by a subcollection of prey and predator species with suitable dispersal strategies. Next, we show, via construction of a Lyapunov functional, that such dispersal strategies are evolutionarily stable, in the sense that if a subcollection of prey and predator species adopts an ideal free dispersal strategy, then the total community must converge to an IFD for large time; if a unique combination of prey-predator species adopts an ideal free strategy, then it can drive all other species to extinction. Conversely, if a combination of prey-predator species adopts a non-ideal free dispersal strategy, then it can be invaded by some suitable mutant strategies. Our results provide insight into the evolution of spatial distribution of ecological communities with predator-prey interactions.

Keywords: Ideal free distribution, evolutionarily stable strategy, multi-species predator-prey system, reaction-diffusion-advection, time periodicity

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1 Introduction

Dispersal is a pivotal life-history trait that fundamentally shapes population dynamics. It mediates interactions between populations, such as predation and competition, and influences the spatiotemporal distribution of individuals. The evolutionary mechanisms underlying dispersal strategies have long fascinated both ecologists and mathematicians alike, leading to the establishment of several robust theoretical frameworks (Cantrell et al. 2006; DeAngelis et al. 2011; Dockery et al. 1998; Hutson et al. 2001; Lutscher et al. 2005; Křivan and Cressman 2009; Maynard Smith 1974; Geritz et al. 1997; Korobenko and Braverman 2014). In recent years, pairwise invasion analysis, grounded in adaptive dynamics, has become a widely used approach (Averill et al. 2012; Cantrell et al. 2017; He and Ni 2016; Lam and Lou 2014). This method assumes that two or more populations differ only in their dispersal strategies and explores strategies that can resist invasion. The key question is to seek evolutionarily stable strategies (ESS), which are strategies that enable populations adopting these strategies to resist invasion by rare mutants using any other strategies.

A related but different concept is convergent stable strategies (CSS), for which nearby mutant strategies are favored whenever they are closer to the CSS than the resident strategy. ESS and CSS are independent stability concepts and may occur in any combination.

A growing body of research has confirmed that dispersal strategies leading to ideal free distributions (IFDs) are ESS in various settings of dispersal models (Averill et al. 2012; Cantrell et al. 2007, 2010, 2012, 2022; Maciel et al. 2020; Cantrell and Cosner 2025; Křivan et al. 2008; Cressman and Křivan 2006). The IFD, introduced by Fretwell and Lucas (1969), describes how individuals distribute themselves to achieve optimal fitness. This theory is based on two key assumptions: (i) each individual has complete knowledge of its environment, and (ii) each individual can freely move to the most favorable locations. The main motivation behind the assumptions proposed by Fretwell and Lucas was the nesting behavior of birds, which typically have keen eyesight, so they have high abilities to sense the most favorable locations in the surrounding environment (ideal) and then to move to those locations at will (free). Moreover, the IFD prediction has been validated in several empirical or experimental studies (Milinski 1979; Grand 1997; Morris et al. 2004).

The evolutionary impacts of temporal periodicity combined with dispersal in population ecology have garnered significant attention, as most natural systems are influenced by seasonal cycles. Temporal periodicity has been shown to induce significantly different population dynamics. For example, in a two-species competition system with random diffusion, the slower diffuser is favored in temporally constant

environments (i.e., slower diffusion is an ESS) (Dockery et al. 1998). However, in time-periodic environments, the direction of selection can reverse, and coexistence can occur (Hutson et al. 2001; Bai et al. 2023). For further insights into the combined effects of temporal periodicity and dispersal, see (Katriel 2022; Liu et al. 2022; Lam and Lou 2024; Benaim et al. 2024; Cantrell and Cosner 2018; Cantrell et al. 2021).

In temporally constant environments, a feature of the IFD is that, at equilibrium, the reproductive fitness of all individuals is spatially equalized, which will be zero if the population is at equilibrium since no net movement occurs. Notably, the occurrence of IFD in temporally varying environments differs from that in temporally constant environments (Kamrujjaman 2019; Lou 2019; Cantrell and Cosner 2018; Cantrell et al. 2021). For example, one would generally expect a mismatch between the local population and carrying capacity, and there will inevitably be times when the population exceeds or falls short of the carrying capacity. Consequently, a natural question arises: how can one characterize IFD in temporally varying environments. This problem has been considered in a reaction-diffusion-advection model setting by Cantrell et al. (2021) and in a patch model setting by Lam and Zhang (2025) in autonomous or time-periodic environments, under a symmetry assumption on the fitness functions of the competing species. Therein, an appropriate notion of IFD based on pathwise fitness is introduced. For general ecological interaction models in time-periodic environments, it is reasonable to conjecture that a similar definition of IFD can be established.

On a broader level, the fitness of a given population depends not only on the local abiotic environment but also on the collection, or the local community of species, with which it interacts directly or indirectly (Fauth et al. 1996; McPeek 2017). In fact, the web of interactions among all the species found in a patch of forest, or in a stream or lake, forms very dense and complex networks (Winemiller 1990; Martinez 1991; Dunne et al. 2002; Bascompte et al. 2003). How does the notion of IFD factor into the selection of the local community of species? A starting point to address this question is to limit our scope to a smaller subset of interacting species embedded in the broader interaction web, i.e., the community module attributed to Holt (1997).

It is worth noting that most current studies on the evolution of dispersal primarily focus on two competing species. In such cases, monotone dynamical systems theory can be employed to determine asymptotic dynamics. In contrast, fewer studies have addressed systems with multiple species within the framework of adaptive dynamics. Throughout their lifespans, individuals of any species are likely to interact with multiple competitors, predators, and mutualists. Adaptive responses among multiple predator and prey species can act as stabilizing forces in large, complex food webs. In light of this, researchers have extensively studied the dynamical behaviors of predator-prey interactions (Flaxman and Lou 2009; Sadovsky and Senashova 2016; Schreiber and Saltzman 2009; Cantrell and Cosner 2025; Cantrell et al. 2007, 2012; Křivan 1996; Cressman et al. 2004; Zelenchuk and Tsybulin 2021; Frølich and Thygesen 2022). The IFD of predator-prey systems has been explored in various articles (Cantrell and Cosner 2025; Cantrell et al. 2007, 2012; Křivan 1996; Cressman et al. 2004; Zelenchuk and Tsybulin 2021; Frølich and Thygesen 2022). However, to our knowledge, the majority

of the applications of the adaptive dynamics approach to IFD in predator-prey systems are limited to environments that are static over time and to a small number of species.

In this paper, we apply pairwise invasion analysis to investigate the evolutionary stability of the IFD of a multiple predator-prey species model in time-periodic environments. The presence of multiple species raises an intriguing question: if each single species adopts a non-ideal free dispersal strategy, but the superposition of their distribution constitutes an ideal free distribution, would the so-called *joint IFD* strategy be selected or not?

Highlights of this paper

In this paper, we continue the study of the problem started in Cantrell and Cosner (2025) concerning the ideal free distribution in predator-prey species interactions:

- **(Evolution of a community of species towards IFD)** By introducing a system of equations describing n-prey and m-predator species, we study how evolution shapes a *community* of prey-predator species by bringing it closer to IFD, where the fitness of a particular prey (resp. predator) species depends on all other members in the community. Roughly speaking, we show that a community of ecologically identical species is stable if and only if it achieves IFD.
- **(IFD in time-periodic environments)** We consider the evolution of IFD in general time-periodic environments. Our argument thus includes as a particular case the evolution of a community to IFD in the autonomous framework as well.
- **(Non-IFD is selected against)** When the community does not form a joint IFD, then we show that it can possibly be invaded by mutant species, provided that species employ a suitable dispersal strategy (see Theorem 2). This shows that IFD is a necessary condition for a community to be evolutionarily stable.
- **(Selection advantage of approximate IFD)** Extending our theoretical results regarding when a joint-IFD is exactly achieved, we also investigated the situation when IFD is approximately achieved via numerical computation. For this purpose, we introduced a measure of how "close" a community is to achieving an IFD. Our numerical results demonstrate that a new species is more likely to invade and establish a viable population within an existing community if its presence can bring the community closer to achieving IFD. In the framework of adaptive dynamics, this suggests that the IFD is convergence stable as well as evolutionarily stable.

1.1 A reaction-diffusion model consisting of n prey and m predator species.

We will study the evolution of dispersal via the following Lotka-Volterra predator-prey model with n prey species and m predator species:

$$\begin{cases} \partial_t u^i = \nabla \cdot [D_u^i \nabla u^i - u^i \vec{P}^i] + u^i \left(a - b\sum_{k=1}^n u^k - c\sum_{k=1}^m v^k\right), & \text{in } \Omega \times (0,\infty), \\ \partial_t v^j = \nabla \cdot [D_v^j \nabla v^j - v^j \vec{Q}^j] + v^j \left(-d + e\sum_{k=1}^n u^k - f\sum_{k=1}^m v^k\right), & \text{in } \Omega \times (0,\infty), \\ [D_u^i \nabla u^i - \vec{P}^i u^i] \cdot \nu = [D_v^j \nabla v^j - \vec{Q}^j v^j] \cdot \nu = 0, & \text{on } \partial\Omega \times (0,\infty), \end{cases} \tag{1}$$

where Ω is a bounded smooth domain in $\mathbb{R}^N$, $i = 1, \cdots, n$ and $j = 1, \cdots, m$. Here, function $u^i(x,t)$ (resp. $v^j(x,t)$) represents the density of the i-th prey species (resp. j-th predator species) at time $t > 0$ and location $x \in \Omega$, where the set Ω is a bounded domain in $\mathbb{R}^N$ with a smooth boundary $\partial\Omega$ and an outward unit normal vector ν.

Specifically, we consider the interactions of n phenotypes of a prey species and m phenotypes of a predator species. Within the prey (resp. predator) species, we assume these phenotypes differ only by their dispersal strategies, then focus on the selection for dispersal strategies and patterns. Mathematically, the demographic rates depend on the total prey/predator population, as indicated by the appearance of $\sum_{k=1}^n u^k$ (resp. $\sum_{k=1}^m v^k$), and the coefficients a, b, c, d, e, f are independent of i and j. In other words, we assume that the fitnesses of the n prey (resp. m predator) species are symmetric.

The dispersal strategy of prey species u^i is given by $(D_u^i, \vec{P}^i)$, where $D_u^i(x,t) > 0$ is the spatial diffusion rate and the vector field $\vec{P}^i(x,t)$ describes the directed movement. A similar interpretation holds for the predator species with dispersal strategy $(D_v^j, \vec{Q}^j)$. The functions $a(x,t)$ and $d(x,t)$ represent the intrinsic growth rate of a prey species and the death rate of a specialist predator species, respectively. The functions $b(x,t)$ and $f(x,t)$ measure the strength of self-limitation, and $c(x,t)$ and $e(x,t)$ are the predation rate and the production rate of predator species, respectively.

In the remainder of this paper, we consider system (1) with time-periodic coefficients:

(A) All coefficients are smooth and T-periodic in t, i.e.,

$$D_u^i, D_v^j, a, b, c, d, e, f \in C_{per}^\infty(\overline{\Omega} \times \mathbb{R};\ \mathbb{R}) = \{\phi \in C^\infty(\overline{\Omega} \times \mathbb{R};\ \mathbb{R}) :\ \phi(x,t) = \phi(x,t+T)\},$$

and $\vec{P}^i(x,t)$, and $\vec{Q}^j(x,t) \in C_{per}^\infty(\overline{\Omega} \times \mathbb{R};\ \mathbb{R}^N)$, and such that

$$D_u^i, D_v^j, a, b, c, d, e > 0, \quad ae > bd \quad \text{and} \quad f \geq 0 \quad \text{in } \overline{\Omega} \times \mathbb{R}.$$

1.2 IFD in autonomous system

The ideal free distribution was originally formulated as a theoretical description of how a population would be distributed in space at equilibrium if individuals could sense the availability at every location of some spatially distributed resource such as food or nesting sites which would be reduced by crowding (ideal information) and could move to the currently most favorable location (free movement).

Denote the dispersal operators by

$$L^i\phi = D_u^i \nabla \cdot [\nabla\phi - \phi\vec{P}^i], \quad A^j\psi = D_v^j \nabla \cdot [\nabla\psi - \psi\vec{Q}^j]. \tag{2}$$

We recall the notion of IFD in temporally constant environments is a population distribution (i) which is at equilibrium and (ii) at which the reproductive fitness is spatially equalized. Indeed, if (ii) does not hold, then some individuals would move to locations where resource availability would be higher and in doing so alter the distribution. Since the reproductive fitness is constant in space, it must be zero due to (i).

As introduced in Cantrell and Cosner (2025), we say that $(u^{1*}(x), v^{1*}(x))$ forms an IFD of the system (1) with temporally constant coefficients (in case $n = m = 1$) if it is a positive equilibrium solution of (1) and the fitness functions given by

$$F_{prey} := a - bu^{1*} - cv^{1*}, \qquad \text{and} \qquad F_{predator} := -d + eu^{1*} - fv^{1*} \tag{3}$$

vanish identically in Ω. This definition is consistent with the definition of the IFD used in all previous work on competing species with symmetric local fitness functions in autonomous systems (Averill et al. 2012; Cantrell et al. 2010; Maciel et al. 2020). We also assume the following technical assumptions.

(Ha) $f(x) > 0$ in $\overline{\Omega}$ and there exists a constant $\kappa_1 > 0$ such that

$$\sup_{x\in\overline{\Omega}} \left[|\kappa_1 c(x) - e(x)|^2 - 4\kappa_1 b(x) f(x)\right] < 0.$$

(Hb) $f(x) \equiv 0$ in $\overline{\Omega}$ and there exists a constant $\kappa_2 > 0$ such that $e(x) = \kappa_2 c(x)$.
(Hc) There is a constant $C_v \in [0, 1)$ such that the IFD population densities satisfy

$$\begin{cases} \dfrac{L^2 u^{1*}}{cu^{1*}} + (1 - C_v)v^{1*} \geq 0, \\ A^2 \left[\dfrac{L^2 u^{1*}}{cu^{1*}} + (1 - C_v)v^{1*} \right] = 0. \end{cases}$$

where (L^2, A^2) is given by (2).

Remark 1 Condition **(Ha)** (resp. **(Hb)**) guarantees the positive (resp. semi-positive) definiteness of the quadratic form associated with the matrix

$$\mathcal{A} = \begin{pmatrix} \kappa_1 b & \kappa_1 c \\ -e & f \end{pmatrix}.$$

Theorem 1 *(Cantrell and Cosner 2025) Consider system (1) with time-independent coefficients, where $m = n = 2$, $\vec{P}^i$, and $\vec{Q}^i$ are the gradients of some functions. Suppose that the first predator-prey pair forms an IFD, while the second pair does not; then the following statements hold.*

(i) *If* **(Ha)** *holds, then the steady state $\left(u^{1*}(x), 0, v^{1*}(x), 0\right)$ is globally asymptotically stable among nonnegative and nontrivial initial conditions.*
(ii) *If* **(Hb)** *holds, but* **(Hc)** *does not, then the steady state $(u^{1*}(x), 0, v^{1*}(x), 0)$ is globally asymptotically stable among nonnegative and nontrivial initial conditions.*

The second closely related result concerns a model of three competing species, written as follows:

$$\begin{cases} \partial_t u^i = D_u^i \nabla \cdot [\nabla u^i - u^i \nabla P^i(x)] + u^i \left(a(x) - \sum_{k=1}^3 u^k \right), & \text{in } \Omega \times (0,\infty), \\ [\nabla u^i - u^i \nabla P^i(x)] \cdot \nu = 0, & \text{on } \partial\Omega \times (0,\infty), \end{cases}$$

for $i = 1, 2, 3$, where $D_u^i > 0, 0 < P^i(x) \in C^2(\overline{\Omega})$, and furthermore, that $a(x)$ is positive and nonconstant. If $\exp(P^1(x)) = k_0 a(x)$ for some $k_0 > 0$, then the corresponding equilibrium of the single species exactly matches the availability of resources, i.e. $u^i(x) \equiv a(x)$, and hence is an IFD. Similarly, we say that (u^i, u^j) forms an IFD pair if $a(x) \in \text{span}\{\exp(P^i), \exp(P^j)\}$. Then it is proved in Theorems 2.2 and 2.3 (Lou and Munther 2012) that

(i) If species 1 achieves an IFD, and species 2 and 3 do not form an ideal free pair, then species 1 excludes species 2 and 3.
(ii) If species 1 and 2 form an IFD pair, and species 3 does not achieve an IFD, then species 1 and 2 exclude species 3.

Theorem 1 indicates that predator-prey species achieving an IFD can exclude the non-IFD ones. The results of Lou and Munther (2012) further demonstrate that species forming an IFD, or collectively forming an IFD, will dominate during multi-species competition. A similar result for an arbitrary number of competing species in temporally constant patchy environments was obtained in Cantrell, Cosner, and Lou (2012).

Inspired by these results, we delve into the selection mechanisms behind dispersal when including time periodicity. Specifically, we will generalize the definitions of IFD in Cantrell and Cosner (2025); Cantrell et al. (2021) and ideal free pairs in Lou and Munther (2012) to system (1), where multiple interacting prey-predator species in a time-periodic environment are considered. We then perform a pairwise invasion analysis to determine whether a subset of prey species $\{1, \cdots, n\}$ and a subset of predator species $\{1, \cdots, m\}$ using an ideal free dispersal strategy can resist invasion by the remaining species using other dispersal strategies. The time periodicity brings a challenge for constructing Lyapunov functions for (1). We handle this problem with the generalized relative entropy method (Lam and Lou 2022, Chapter 4).

1.3 The definition of joint IFD for system (1)

In environments that vary in time as well as space, it would not be reasonable to expect the population density to remain constant in time, even with spatial movement. In the time-periodic case, we can sometimes expect a model to have a periodic steady state, but it is too much to expect the existence of a steady state where fitness is constant in space and time. It turns out that it is reasonable to look for a steady state that has fitness constant in space, that is, not depending on the space variable at any given time, but possibly depending on the time variable. (A related formulation is that at a steady state, the integral of fitness along any T-periodic path through space is the same (Cantrell et al. 2021)).

To define a notion of IFD, we recall that the fitness functions given in (3), which are symmetric among all prey (resp. predator) species, are now functions of both spatial and time variables. If $(u^*(x,t), v^*(x,t))$ are prey-predator population densities which is a time-periodic solution of (1), and they correspond to a Nash equilibrium of the evolutionary game, then the payoff of any representative individual should be indifferent to any dispersal strategy. This motivates the following definition based on the simultaneous equilibration of fitness functions in space, but not in time. (A related formulation is that, at a T-periodic steady state, the integral of fitness along any T-periodic path through space is independent of the chosen path; See (Cantrell et al. 2021, Definition 2.1).

Definition 1 Let (u^{1*}, v^{1*}) be a positive T-periodic solution of system (1) with $n = m = 1$, we say (u^{1*}, v^{1*}) is an IFD if

$$(x,t) \mapsto a - bu^{1*} - cv^{1*} \quad \text{and} \quad (x,t) \mapsto -d + eu^{1*} - fv^{1*} \quad \text{are independent of } x. \tag{4}$$

Moreover, we say the corresponding dispersal coefficients form an IFD strategy.

Remark 2 When the coefficients are time-independent, (4) means that there are constants C_1, C_2 such that

$$a - bu^{1*} - cv^{1*} = C_1 \quad \text{and} \quad -d + eu^{1*} - fv^{1*} = C_2.$$

Substituting this, together with no net movement condition, i.e., $\nabla \cdot [D_u^1 \nabla u - u\vec{P}^1] = 0$ and $\nabla \cdot [D_v^1 \nabla v - v\vec{Q}^1] = 0$, into the equilibrium system associated with (1) with $n = m = 1$ yields $C_1 = C_2 = 0$, i.e. the local fitness functions vanish. In this way, it is consistent with the IFD condition for the autonomous system.

Remark 3 Consider the special case where the coefficients satisfy

$$ae > bd, \qquad \partial_t \int_\Omega \frac{af + cd}{bf + ec} dx = 0 \quad \text{and} \quad \partial_t \int_\Omega \frac{ea - bd}{bf + ec} dx = 0,$$

and define

$$(u_0^*, v_0^*) = \left(\frac{af + cd}{bf + ce}, \frac{ae - bd}{bf + ce} \right).$$

For each t, define the functions $p_0(\cdot, t), q_0(\cdot, t)$

$$\Delta p_0 = \partial_t u_0^* \text{ in } \Omega, \quad \nabla p_0 \cdot \nu = 0 \text{ on } \partial\Omega,$$
$$\Delta q_0 = \partial_t v_0^* \text{ in } \Omega, \quad \nabla q_0 \cdot \nu = 0 \text{ on } \partial\Omega.$$

One can verify that the dispersal strategy

$$\vec{P}_0^*(x,t) = \frac{1}{u_0^*} \left(D_u(x,t) \nabla u_0^* - \nabla p_0(x,t) \right) \quad \text{and} \quad \vec{Q}_0^*(x,t) = \frac{1}{v_0^*} \left(D_v(x,t) \nabla v_0^* - \nabla q_0(x,t) \right),$$

makes (u_0^*, v_0^*) a T-periodic solution of (1) with $n = m = 1$. Moreover, $a - bu_0^* - cv_0^* \equiv -d + eu_0^* - fv_0^* \equiv 0$. Thus, (u_0^*, v_0^*) is an IFD, and $(D_u, \vec{P}_0^*, D_v, \vec{Q}_0^*)$ is an ideal free dispersal strategy.

As shown in Lou and Muther (2012); Cantrell, Cosner, and Lou (2012), a specific combination of distributions for multiple species may form IFD even when no single species forms IFD. This motivates the following notion of a joint IFD for predator-prey systems with arbitrarily many species, which is a generalization of Definition 1.

Definition 2 Let $\mathcal{S}$ be a nonempty subset of $\{1,\cdots,n\}$, and let $\mathcal{K}$ be a nonempty subset of $\{1,\cdots,m\}$. We say that system (1) has a $\mathcal{S}$-$\mathcal{K}$ joint IFD $(\vec{u}^*,\vec{v}^*) = (u^{1*},\cdots,u^{n*},v^{1*},\cdots,v^{m*})$ if $(\vec{u}^*,\vec{v}^*)$ is a T-periodic solution of (1) satisfying

$$u^{i*}>0 \text{ for } i\in\mathcal{S}, \quad u^{i*}\equiv 0 \text{ for } i\in\{1,\cdots,n\}\setminus\mathcal{S}:=\mathcal{S}^c,$$
$$v^{j*}>0 \text{ for } j\in\mathcal{K}, \quad v^{j*}\equiv 0 \text{ for } j\in\{1,\cdots,m\}\setminus\mathcal{K}:=\mathcal{K}^c,$$

and

$$a-b\sum_{i=1}^{n}u^{i*}-c\sum_{j=1}^{m}v^{j*} \quad\text{and}\quad -d+e\sum_{i=1}^{n}u^{i*}-f\sum_{j=1}^{m}v^{j*} \text{ are independent of } x. \tag{5}$$

Unless otherwise specified, $\mathcal{S}$ is always a nonempty subset of $\{1,\cdots,n\}$ and $\mathcal{K}$ a nonempty subset of $\{1,\cdots,m\}$. Moreover, $\mathcal{S}^c=\{1,\cdots,n\}\setminus\mathcal{S}$ and $\mathcal{K}^c=\{1,\cdots,m\}\setminus\mathcal{K}$.

1.4 Main results

In competitive systems, species failing to form IFD may be invaded by rare mutant species with different dispersal strategies (Cantrell et al. 2021; Lam and Zhang 2025). We address such a problem for prey-predator system (1). The result implies the necessity of IFD even in the autonomous systems case of Cantrell and Cosner (2025). Without loss of generality, we illustrate it in the setting of $m=n=2$. The result can be stated as follows.

Theorem 2 *Let $m=n=2$ for system (1). Suppose that time-periodic solution (u^{1*},v^{1*}) is not an IFD. Then there exists a dispersal strategy $(D_u^2,\vec{P}^2)$ or $(D_v^2,\vec{Q}^2)$ such that $(u^{1*},0,v^{1*},0)$ is unstable for system (1).*

This indicates that if a pair of resident prey and predator species does not form an IFD, then they can be invaded, i.e., any dispersal strategy that fails to produce IFD is not evolutionarily stable. One can similarly prove the instability of any non-IFD periodic solutions consisting of n prey and m predator species, with $n+m>2$.

Next, we generalize Theorem 1 to the time-periodic system (1) with arbitrarily many prey and predator species. It turns out that we need to solve an auxiliary non-autonomous predator-prey ODE system (see (7)). We will prove that if a $\mathcal{S}$-$\mathcal{K}$ joint IFD exists, then under certain assumptions on the environmental coefficients $\mathcal{A}:=(a,b,c,d,e,f)$, it is stable in the evolutionary sense. To state the assumptions on $\mathcal{A}$, we need to use positive time-periodic functions $(M(t),N(t))$, which can be defined entirely in terms of $\mathcal{A}$. First, we introduce the generalization of conditions **(Ha)-(Hb)**.

(Ha') $\inf\limits_{(x,t)\in\overline{\Omega}\times\mathbb{R}} f(x,t)>0$ and there is a constant $\rho_1>0$ such that

$$\sup_{(x,t)\in\overline{\Omega}\times\mathbb{R}}\left[\left(\frac{\rho_1 c}{M}-\frac{e}{N}\right)^2-4\frac{\rho_1 bf}{MN}\right]<0.$$

(Hb') $f(x,t)\equiv 0$ in $\overline{\Omega}\times\mathbb{R}$ and $\frac{e(x,t)M(t)}{c(x,t)N(t)}$ is constant in $\overline{\Omega}\times\mathbb{R}$.

where $(M(t), N(t))$ are positive quantities derived entirely in terms of the coefficients $\mathcal{A} := (a, b, c, d, e, f)$. The definition of $(M(t), N(t))$ is contained in Subsection 2.2.

Remark 4 Condition **(Ha')** (resp. **(Hb')**) guarantees the positive (resp. semi-positive) definiteness of the quadratic form associated with the matrix

$$\mathcal{A} = \begin{pmatrix} \rho_1 b(x,t)/M(t) & \rho_1 c(x,t)/M(t) \\ -e(x,t)/N(t) & f(x,t)/N(t) \end{pmatrix}.$$

Remark 5 If $\rho_0 := \frac{e(x,t)M(t)}{c(x,t)N(t)}$ is constant in $\overline{\Omega} \times \mathbb{R}$ and $\inf f > 0$, then **(Ha')** holds for ρ_1 sufficiently close to ρ_0.

Remark 6 When $a, b, c, d, e > 0$ and $f \geq 0$ are time-independent, $M(t)$ and $N(t)$ are positive constants (see Appendix A). Then assumptions **(Ha')-(Hb')** reduce to **(Ha)-(Hb)**. In particular, if an autonomous system satisfies **(Ha)**, then any periodic perturbation of the system satisfies **(Ha')**.

The following results show the evolutionary advantage of IFDs when the system is with or without self-limitation of the predator species (i.e, $f(x,t) > 0$ or $f(x,t) \equiv 0$ for all $(x,t) \in \overline{\Omega} \times \mathbb{R}$). Specifically, a combination of species will be selected when it is the unique combination that forms an IFD. This is the special case of Theorems 10 and 11 that are discussed in Sections 4 and 5, respectively.

Theorem 3 (With self-limitation) *Consider D_u^i, P^i, D_v^j, Q^j, and a, b, c, d, e, and f satisfying* **(A)** *and* **(Ha')**. *Suppose there exists a unique combination $\mathcal{S} \subseteq \{1, \cdots, n\}$ and $\mathcal{K} \subseteq \{1, \cdots, m\}$ such that the system (1) has a $\mathcal{S}'$-$\mathcal{K}'$ joint IFD if and only if $(\mathcal{S}', \mathcal{K}') = (\mathcal{S}, \mathcal{K})$. Then for each positive solution $(\vec{u}, \vec{v})$ to the initial value problem (1), we have*

$$\lim_{t\to\infty} \left[\sum_{i=1}^{n} \left\| u^i(\cdot,t) - u^{i*}(\cdot,t) \right\|_{C(\bar{\Omega})} + \sum_{j=1}^{m} \left\| v^j(\cdot,t) - v^{j*}(\cdot,t) \right\|_{C(\bar{\Omega})} \right] = 0, \tag{6}$$

where $(\vec{u}^*, \vec{v}^*)$ is the $\mathcal{S}$-$\mathcal{K}$ joint IFD.

An immediate consequence of Theorem 3 is the following.

Corollary 4 Under the assumptions of Theorem 3, suppose in addition that $\mathcal{S} = \{1\}$ and $\mathcal{K} = \{1\}$ are the unique subsets of prey-predator species that jointly support an IFD. Then

$$\begin{cases} \left\| u^1(\cdot,t) - u^{1*}(\cdot,t) \right\|_{C(\bar{\Omega})} + \left\| v^1(\cdot,t) - v^{1*}(\cdot,t) \right\|_{C(\bar{\Omega})} \to 0 \\ \sum_{i=2}^{n} \left\| u^i(\cdot,t) \right\|_{C(\bar{\Omega})} + \sum_{j=2}^{m} \left\| v^j(\cdot,t) \right\|_{C(\bar{\Omega})} \to 0 \end{cases}$$

as $t \to \infty$, where (u^{1*}, v^{1*}) is the IFD.

Theorem 5 (Without self-limitation) *Let D_u^i, P^i, D_v^j, Q^j and a, b, c, d, e, f satisfy* **(A)** *and* **(Hb')**. *Suppose there exists a unique combination $\mathcal{S} \subseteq \{1, \cdots, n\}$ and $\mathcal{K} \subseteq \{1, \cdots, m\}$ such that the system (1) has a $\mathcal{S}'$-$\mathcal{K}'$ joint IFD if and only only if $(\mathcal{S}', \mathcal{K}') = (\mathcal{S}, \mathcal{K})$. Assume, in addition, that (1) has no nontrivial periodic solutions $(\vec{U}, \vec{V})$ such that $U^i \equiv 0$ for all $i \in \mathcal{S}$, and*

$$\partial_x \left(-d + e \sum_{i=1}^{n} U^i \right) \equiv 0 \quad \text{in} \quad \Omega \times \mathbb{R}.$$

Then for each positive solution of the system (1), the convergence (6) holds.

In case a, b, c, d, e, f are independent of time, then we have generalized Theorem 1 to the case of $m \geq 2$ and $n \geq 2$.

1.5 Organization of the paper

In Section 2, we present some preliminary results such as the characterization of IFD in terms of $(M(t), N(t), K^{(1)}(x,t), K^{(2)}(x,t))$, which are quantities derived from the environmental coefficients. Section 3 is devoted to the existence of IFD, which is different from the case of temporally constant environments (Cantrell and Cosner 2025). The time-periodic environments may sometime contain "generalized sinks" that prevent the species from adopting an IFD. We give necessary and sufficient conditions for a given environment $(\Omega, a, b, c, d, e, f)$ to achieve an IFD. In Sections 4 and 5, we show the evolutionary stability of IFD with and without predator self-limitation, respectively. We prove Theorem 2 in Section 6. In Section 7, we demonstrate numerically that being able to approximate the conditions for IFD is utilitarian and confers advantage to the community of species, i.e. the evolutionary stability of IFD is in this sense robust. This complements and extends our analytical results. Finally, we discuss and interpret our results in the context of evolutionary community ecology in Section 8.

2 Preliminary

2.1 Well-posedness

As in Proposition 1 of Cantrell and Cosner (2018), we can transform system (1) into a reaction-diffusion-advection system with Robin boundary conditions, which admits a comparison principle (Lam and Lou 2022). Then, following standard theory (Lunardi 1995), we have the global existence and uniform boundedness of classical solutions to (1).

Theorem 6 *Suppose that* **(A)** *holds. Then system (1) with nonnegative, continuous initial data $(\vec{u}(x,0), \vec{v}(x,0))$ has a global positive solution $(\vec{u}(x,t), \vec{v}(x,t))$, and for any $\gamma \in (0,1)$,*

$$\|\vec{u}\|_{C^{1+\gamma,(1+\gamma)/2}(\overline{\Omega}\times[1,\infty))} + \|\vec{v}\|_{C^{1+\gamma,(1+\gamma)/2}(\overline{\Omega}\times[1,\infty))} \leq K$$

for some constant $K > 0$.

2.2 Definition of $M(t), N(t)$ in terms of environmental coefficients

We will define the quantities $(M(t), N(t))$ as a positive T-periodic solution to the auxiliary ODE system

$$\begin{cases} M'(t) = \frac{1}{D(t)} M(t) \left[A_1(t) - M(t) B_{11}(t) - N(t) B_{12}(t) \right], \\ N'(t) = \frac{1}{D(t)} N(t) \left[A_2(t) + M(t) B_{21}(t) - N(t) B_{22}(t) \right], \end{cases} \tag{7}$$

where A_i, B_{ij} (with $B_{ij} \geq 0$) are given entirely in terms of the environmental coefficients a, b, c, d, e, f:

$$\begin{cases} A_1(t) = \displaystyle\int_\Omega \frac{af+dc}{bf+ce} dx \int_\Omega \frac{b}{bf+ce} dx + \int_\Omega \frac{c}{bf+ce} dx \int_\Omega \frac{ae-bd}{bf+ce} dx, \\ A_2(t) = \displaystyle\int_\Omega \frac{ae-bd}{bf+ce} dx \int_\Omega \frac{f}{bf+ce} dx - \int_\Omega \frac{af+dc}{bf+ce} dx \int_\Omega \frac{e}{bf+ce} dx, \\ B_{11}(t) = \displaystyle\int_\Omega \frac{b}{bf+ce} dx, \qquad B_{12}(t) = \int_\Omega \frac{c}{bf+ce} dx, \\ B_{21}(t) = \displaystyle\int_\Omega \frac{e}{bf+ce} dx, \qquad B_{22}(t) = \int_\Omega \frac{f}{bf+ce} dx, \\ D(t) = \displaystyle\int_\Omega \frac{f}{bf+ce} dx \int_\Omega \frac{b}{bf+ce} dx + \int_\Omega \frac{e}{bf+ce} dx \int_\Omega \frac{c}{bf+ce} dx. \end{cases} \tag{8}$$

To motivate system (7), we begin by observing that whenever (u^*, v^*) is an IFD according to Definition 1, then $\left(\int_\Omega u^*(x,t)\, dx, \int_\Omega v^*(x,t)\, dx \right)$ is a positive solution of (7).

Indeed, denote

$$(M(t), N(t)) := \left(\int_\Omega u^*(x,t)\, dx, \int_\Omega v^*(x,t)\, dx \right),$$

and observe that $a - bu^* - cv^*$ and $-d + eu^* - fv^*$ are independent of x and

$$\begin{cases} \partial_t u^* = \nabla \cdot [D_u \nabla u^* - u^* \vec{P}] + u^*(a - bu^* - cv^*), & \text{in } \Omega \times (0, \infty), \\ \partial_t v^* = \nabla \cdot [D_v \nabla v^* - v^* \vec{Q}] + v^*(-d + eu^* - fv^*), & \text{in } \Omega \times (0, \infty), \\ [D_u \nabla u^* - u^* \vec{P}] \cdot \nu = [D_v \nabla v^* - v^* \vec{Q}] \cdot \nu = 0, & \text{on } \partial\Omega \times (0, \infty). \end{cases}$$

Integrating the above equation over Ω yields

$$\frac{M'(t)}{M(t)} = a - bu^* - cv^*, \quad \frac{N'(t)}{N(t)} = -d + eu^* - fv^*. \tag{9}$$

Multiply the first equation of (9) by f and the second one by c, subtract the resulting equations, and integrate over Ω to yield

$$\int_\Omega \frac{af+dc}{bf+ce} dx - M(t) = \frac{M'(t)}{M(t)} \int_\Omega \frac{f}{bf+ce} dx - \frac{N'(t)}{N(t)} \int_\Omega \frac{c}{bf+ce} dx. \tag{10}$$

Repeat, but multiply the first equation of (9) by e and the second one by b, then we similarly get

$$\int_\Omega \frac{ae-bd}{bf+ce}dx - N(t) = \frac{M'(t)}{M(t)}\int_\Omega \frac{e}{bf+ce}dx + \frac{N'(t)}{N(t)}\int_\Omega \frac{b}{bf+ce}dx. \tag{11}$$

The equations (10) and (11), are equivalent to (7).

The existence of positive T-periodic $(M(t), N(t))$ is equivalent to the uniform persistence of both species (Smith and Thieme 2011), which has been studied extensively, e.g., see Teng (1999); Butler and Freedman (1981); Ding et al. (1995). To be more specific, we next give some sufficient conditions.

Lemma 7 System (7) has at least one positive T-periodic solution $(M(t), N(t))$ provided one of the following conditions holds:

(i) $a, b, c, d, e, f > 0$ are time-independent and satisfy $\frac{d}{a} < \frac{e}{b}$ for all $x \in \overline{\Omega}$.

(ii) $(a, b, c, d, e, f)(x, t) = (\tilde{a}, \tilde{b}, \tilde{c}, \tilde{d}, \tilde{e}, \tilde{f})(x, \frac{t}{T})$, where $\tilde{a}, \tilde{b}, \tilde{c}, \tilde{d}, \tilde{e}, \tilde{f} > 0$ are given 1-periodic functions such that $\frac{\tilde{d}}{\tilde{a}} < \frac{\tilde{e}}{\tilde{b}}$ for all $(x, t) \in \overline{\Omega} \times [0, 1]$ and $T \gg 1$.

(iii) $b, c, e, f > 0$ are independent of x and

$$\frac{\int_0^T \int_\Omega d(x,t)dxdt}{\int_0^T \int_\Omega a(x,t)dxdt} < \min_{t\in[0,T]} \frac{e(t)}{b(t)}. \tag{12}$$

(iv) System (1) has a $\mathcal{S} - \mathcal{K}$ joint IFD.

Moreover, if one of assumptions **(Ha')** and **(Hb')** holds, then $(M(t), N(t))$ is unique.

Proof Indeed, if the system has a $\mathcal{S}$-$\mathcal{K}$ joint IFD $(\vec{u}^*, \vec{v}^*)$, we can argue as in the beginning of Subsection (2.2) that $(M(t), N(t)) = \left(\sum_{i=1}^n \int_\Omega u^i\, dx, \sum_{j=1}^m \int_\Omega v^j\, dx\right)$ solves (7). Note from condition (ii) that $(a, b, c, d, e, f)(x, t+T) = (\tilde{a}, \tilde{b}, \tilde{c}, \tilde{d}, \tilde{e}, \tilde{f})(x, \frac{t}{T} + 1)$. Thus, when $T \gg 1$, the temporal variation occurs on a slow time scale since the time derivatives of the coefficients are of order $1/T$. This allows the auxiliary system (7) to be treated as a slow periodic perturbation of the autonomous case. The detailed proofs of sufficient conditions (i)-(iii) are postponed to Appendix and that of (iv) is given in Theorem 9, and the uniqueness under **(Ha')** (resp. **(Hb')**) is a result of Theorem 10 (resp. Theorem 11). □

Definition of $K^{(1)}, K^{(2)}$ in terms of $(M(t), N(t))$

For a given positive solution $(M(t), N(t))$ of (7), we define $\left(K^{(1)}_{MN}, K^{(2)}_{MN}\right)$ as follows

$$\begin{aligned} K^{(1)}_{MN}(x,t) &= \frac{(a - M'/M)f + (d + N'/N)c}{(bf+ec)M}, \\ K^{(2)}_{MN}(x,t) &= \frac{(a - M'/M)e - (d + N'/N)b}{(bf+ec)N}. \end{aligned} \tag{13}$$

Note that we may sometimes suppress the subscript of $K^{(i)}_{MN}$ to simplify notations.

Since $(M(t), N(t))$ satisfies (10) and (11), it is easy to verify that $K^{(i)}(x,t)$ satisfies

$$\int_\Omega K^{(1)}(x,t)dx = \int_\Omega K^{(2)}(x,t)dx = 1 \text{ for all } t \in \mathbb{R}.$$

2.3 An auxiliary lemma

The following lemma plays an essential role in the evolutionary stability analysis. The proof of this lemma is the same as Lemma 1.2 in Lam and Zhang (2025), so we omit it.

Lemma 8 Suppose $d(x,t)$ and $\vec{h}(x,t)$ are smooth and T-periodic in t. Then

$$\begin{cases} \partial_t \phi = \nabla \cdot [d\nabla\phi - \phi\vec{h}], & \text{in } \Omega \times \mathbb{R}, \\ [d\nabla\phi - \phi\vec{h}] \cdot \nu = 0, & \text{on } \partial\Omega \times \mathbb{R}, \\ \int_\Omega \phi(x,0)dx = 1 \end{cases} \tag{14}$$

has a unique positive and T-periodic solution $\phi(x,t) \in C^{\gamma+2,1+\gamma/2}_{loc}(\overline{\Omega}\times\mathbb{R})$ for any $\gamma \in (0,1)$, where $C^{\gamma+2,1+\gamma/2}_{loc}(\overline{\Omega} \times \mathbb{R})$ denotes the space of all functions $u : \overline{\Omega} \times \mathbb{R} \to \mathbb{R}$ such that $u|_K \in C^{\gamma+2,1+\gamma/2}(K)$ for every compact $K \subset \overline{\Omega} \times \mathbb{R}$. Moreover, $\int_\Omega \phi(x,t)dx = 1$ for all t.

Definition 3 For $1 \le i \le n$ (resp. $1 \le j \le m$), we define $\phi^i_1(x,t)$ (resp. $\phi^j_2(x,t)$) to be the unique positive T-periodic solution of (14) with $d = D^i_u$ and $\vec{h} = \vec{P}^i$ (resp. $d = D^j_v$ and $\vec{h} = \vec{Q}^j$).

3 Dispersal strategies that produce IFD

In this section, we investigate whether IFD is possible in a given environment. More precisely, for given environmental parameters $(\Omega, a, b, c, d, e, f)$, we determine whether there exist dispersal strategies $(D^i_u, \vec{P}^i, D^j_v, \vec{Q}^j)$, such that a $\mathcal{S}$-$\mathcal{K}$ joint IFD for system (1) can be achieved.

The following result gives the necessary and sufficient conditions for (1) to have an IFD including an arbitrary number of species.

Theorem 9 *The following statements are equivalent:*

(i) *System (1) has a $\mathcal{S}$-$\mathcal{K}$ joint IFD $(\vec{u}^*, \vec{v}^*) = (u^{1*}, \cdots, u^{n*}, v^{1*}, \cdots, v^{m*})$.*

(ii) *System (7) has a positive solution $(M(t), N(t))$ and the corresponding $K^{(1)}(x,t)$ and $K^{(2)}(x,t)$ defined by (13) are positive.*

Moreover,

$$\left(\sum_{i=1}^n u^{i*}, \sum_{j=1}^m v^{j*}\right) = \left(M(t)K^{(1)}(x,t), N(t)K^{(2)}(x,t)\right). \tag{15}$$

Proof We first prove "(i)⇒(ii)". By Definition 2, $(\vec{u}^*, \vec{v}^*)$ satisfies

$$a - b\sum_{i=1}^{n} u^{i*} - c\sum_{j=1}^{m} v^{j*} = F(t) \quad \text{and} \quad -d + e\sum_{i=1}^{n} u^{i*} - f\sum_{j=1}^{m} v^{j*} = G(t)$$

for T-periodic functions $F(t)$ and $G(t)$, and for all i, j,

$$\begin{cases} \partial_t u^{i*} = \nabla \cdot [D_u^i \nabla u^{i*} - u^{i*}\vec{P}^i] + F(t)u^{i*}, & \text{in } \Omega \times (0,\infty), \\ \partial_t v^{j*} = \nabla \cdot [D_v^j \nabla v^{j*} - v^{j*}\vec{Q}^j] + G(t)v^{j*}, & \text{in } \Omega \times (0,\infty), \\ [D_u^i \nabla u^{i*} - u^{i*}\vec{P}^i] \cdot \nu = [D_v^j \nabla v^{j*} - v^{j*}\vec{Q}^j] \cdot \nu = 0, & \text{on } \partial\Omega \times (0,\infty). \end{cases} \tag{16}$$

Define $M(t) = \int_\Omega \sum_{i=1}^n u^{i*}(x,t)dx$ and $N(t) = \int_\Omega \sum_{j=1}^m v^{j*}(x,t)dx$. Then $M(t), N(t) > 0$ are T-periodic. Summing (16) over i, j and integrating over Ω yields

$$\begin{cases} \frac{M'(t)}{M(t)} = F(t) = a - b\sum_{i=1}^n u^{i*} - c\sum_{j=1}^m v^{j*}, \\ \frac{N'(t)}{N(t)} = G(t) = -d + e\sum_{i=1}^n u^{i*} - f\sum_{j=1}^m v^{j*}. \end{cases} \tag{17}$$

Using the similar arguments for (10) and (11), we deduce that $(M(t), N(t))$ is a positive solution of (7).

Note that $K^{(1)}(x,t), K^{(2)}(x,t)$ defined by (13) satisfy

$$\begin{cases} a - bM(t)K^{(1)}(x,t) - cN(t)K^{(2)}(x,t) = \frac{M'(t)}{M(t)}, \\ -d + eM(t)K^{(1)}(x,t) - fN(t)K^{(2)}(x,t) = \frac{N'(t)}{N(t)}. \end{cases} \tag{18}$$

Subtracting (18) from (17) yields

$$\begin{cases} -b\left[\sum_{i=1}^n u^{i*} - M(t)K^{(1)}(x,t)\right] - c\left[\sum_{i=1}^m v^{i*} - N(t)K^{(2)}(x,t)\right] = 0, \\ e\left[\sum_{i=1}^n u^{i*} - M(t)K^{(1)}(x,t)\right] - f\left[\sum_{i=1}^m v^{i*} - N(t)K^{(2)}(x,t)\right] = 0. \end{cases}$$

This proves (15), which implies the pointwise positivity of $K^{(1)}(x,t), K^{(2)}(x,t)$.

We now prove "(ii)⇒(i)". Suppose that $(M(t), N(t))$ is a positive T-periodic solution of (7), and $K^{(1)}(x,t), K^{(2)}(x,t)$ defined in terms of $M(t), N(t)$ by (13) are positive. Then $M(t)K^{(1)}(x,t)$ and $N(t)K^{(2)}(x,t)$ are positive and T-periodic in t. By (18) and Definition 1, the distribution $(M(t)K^{(1)}(x,t), M(t)K^{(2)}(x,t))$ is an IFD.

It suffices to show $(M(t)K^{(1)}(x,t), M(t)K^{(2)}(x,t))$ is a solution to (1) with $n = m = 1$ by choosing suitable dispersal strategies $(D_u, \vec{P})$ and $(D_v, \vec{Q})$. For given $D_u(x,t)$ and $D_v(x,t)$, take

$$\begin{aligned} \vec{P}(x,t) &= \frac{1}{K^{(1)}(x,t)}\left[D_u \nabla K^{(1)}(x,t) - \nabla p(x,t)\right], \\ \vec{Q}(x,t) &= \frac{1}{K^{(2)}(x,t)}\left[D_v \nabla K^{(2)}(x,t) - \nabla q(x,t)\right], \end{aligned} \tag{19}$$

where $p(\cdot,t), q(\cdot,t)$, for each $t \in \mathbb{R}$, uniquely solve

$$\begin{aligned} &\Delta p = \partial_t K^{(1)} \text{ in } \Omega, \quad \nabla p \cdot \nu = 0 \text{ on } \partial\Omega, \\ &\Delta q = \partial_t K^{(2)} \text{ in } \Omega, \quad \nabla q \cdot \nu = 0 \text{ on } \partial\Omega. \end{aligned}$$

This and (19) imply that

$$\nabla \cdot (K^{(1)}\vec{P}) = \nabla \cdot [D_u \nabla K^{(1)} - \nabla p] = \nabla \cdot (D_u \nabla K^{(1)}) - \partial_t K^{(1)}.$$

Then for $u = MK^{(1)}$, a direct calculation yields

$$\begin{cases} \partial_t(MK^{(1)}) = M\partial_t K^{(1)} + K^{(1)}M' \\ \quad = M\left[\nabla\cdot(D_u\nabla K^{(1)}) - \nabla\cdot(K^{(1)}\vec{P})\right] + MK^{(1)}\left(a - bMK^{(1)} - cNK^{(2)}\right) \\ \quad = \nabla\cdot\left[D_u\nabla(MK^{(1)}) - (MK^{(1)})\vec{P}\right] + MK^{(1)}\left(a - bMK^{(1)} - cNK^{(2)}\right), & \text{in } \Omega\times(0,\infty), \\ \left[D_u\nabla(MK^{(1)}) - (MK^{(1)})\vec{P}\right]\cdot\nu = M\nabla p\cdot\nu = 0, & \text{on } \partial\Omega\times(0,\infty). \end{cases}$$

Similarly, $v = NK^{(2)}$ satisfies

$$\begin{cases} \partial_t(NK^{(2)}) = \nabla\cdot\left[D_v\nabla(NK^{(2)}) - (NK^{(2)})\vec{Q}\right] \\ \qquad\qquad +NK^{(2)}\left(-d + eMK^{(1)} - fNK^{(2)}\right), & \text{in } \Omega\times(0,\infty), \\ \left[D_v\nabla(NK^{(2)}) - (NK^{(2)})\vec{Q}\right]\cdot\nu = 0, & \text{on } \partial\Omega\times(0,\infty). \end{cases}$$

Therefore, $(M(t)K^{(1)}(x,t), N(t)K^{(2)}(x,t))$ is a solution of (1) with $m = n = 1$. □

Note that for general n and m, we can choose the dispersal strategies $(D_u^i, \vec{P}^i, D_v^j, \vec{Q}^j)$ in the form of (19), such that system (1) has a $\mathcal{S}$-$\mathcal{K}$ joint IFD $(\vec{u}^*, \vec{v}^*) = (\vec{C}_u M(t)K^{(1)}(x,t), \vec{C}_v N(t)K^{(2)}(x,t))$, where $\vec{C}_u = \{C_u^i\}_{i=1}^n$ and $\vec{C}_v = \{C_v^j\}_{j=1}^m$ are constants satisfying $\sum_{i=1}^n C_u^i = \sum_{j=1}^m C_v^j = 1$.

4 Evolutionary stability with predator self-limitation

In this section, we establish that, in the presence of predator self-limitation, the total population of the prey-predator species approaches an IFD as $t \to \infty$. In particular, any species that cannot participate in IFD is automatically excluded. Note that assertion (b) of the following implies Theorem 3.

Theorem 10 (With self-limitation) *Let D_u^i, P^i, D_v^j, Q^j and a, b, c, d, e, f satisfy* **(A)** *and* **(Ha')**. *Suppose system (1) has a $\mathcal{S}$-$\mathcal{K}$ joint IFD $(\vec{u}^*, \vec{v}^*)$. Then for any solution $(\vec{u}, \vec{v})$ to the initial value problem (1) with nontrivial nonnegative initial data, the following statements hold.*

(a) *(The total distribution of the prey-predator species community approaches IFD) As the integer $k \to +\infty$,*

$$\sum_{i=1}^n u^i(x,t+kT) \to \sum_{i=1}^n u^{i*}(x,t) \text{ and } \sum_{j=1}^m v^j(x,t+kT) \to \sum_{j=1}^m v^{j*}(x,t) \text{ in } C(\overline{\Omega}\times[0,T]).$$

(b) *(Only the unique combination of IFD species survives) In addition, suppose that for any nonempty sets $\mathcal{S}' \subseteq \{1,\cdots,n\}$ and $\mathcal{K}' \subseteq \{1,\cdots,m\}$, system (1) has a $\mathcal{S}'$-$\mathcal{K}'$ joint IFD only when $\mathcal{S}' = \mathcal{S}$ and $\mathcal{K}' = \mathcal{K}$. Then, as $t \to +\infty$,*

$$u^i(x,t) \to u^{i*}(x,t) \quad \text{and} \quad v^j(x,t) \to v^{j*}(x,t) \quad \text{in} \quad C_{loc}(\overline{\Omega}\times\mathbb{R}).$$

Remark 7 Conclusion (b) of the Theorem 10 can be rephrased as follows: there exist nonnegative constants p^i, q^j such that

$$\sum_{i=1}^{n} p^i \phi_1^i(x,t) = K_{MN}^{(1)}(x,t) \quad \text{and} \quad \sum_{j=1}^{m} q^j \phi_2^j(x,t) = K_{MN}^{(2)}(x,t),$$

if and only if $\{i:\ p^i > 0\} = \mathcal{S}$ and $\{j:\ q^j > 0\} = \mathcal{K}$, where $K_{MN}^{(1)}(x,t)$ and $K_{MN}^{(2)}(x,t)$ are given in (13), and $\phi_1^i(x,t)$ and $\phi_2^j(x,t)$ are given by Definition 3.

4.1 Proof of Theorems 10

Proof Throughout this proof, denote, for $1 \le i \le n$ and $1 \le j \le m$,

$$L^i\varphi = \nabla\cdot[D_u^i\nabla\varphi - \varphi\vec{P}^i], \quad \text{in } \Omega\times\mathbb{R}, \quad \mathcal{B}^i\varphi = [D_u^i\nabla\varphi - \varphi\vec{P}^i]\cdot\nu, \quad \text{on } \partial\Omega\times\mathbb{R},$$

$$A^j\varphi = \nabla\cdot[D_v^j\nabla\varphi - \varphi\vec{Q}^j], \quad \text{in } \Omega\times\mathbb{R}, \quad \tilde{\mathcal{B}}^j\varphi = [D_v^j\nabla\varphi - \varphi\vec{Q}^j]\cdot\nu, \quad \text{on } \partial\Omega\times\mathbb{R}.$$

By Theorem 9, we obtain the existence of positive T-periodic functions $M(t)$, $N(t)$, and that $K_{MN}^{(1)}(x,t)$, $K_{MN}^{(2)}(x,t)$ defined by (13) are positive. For convenience, we write $K^{(1)}(x,t)$, $K^{(2)}(x,t)$ in that which follows.

With the help of (17), $M(t)$, $N(t)$ and the $\mathcal{S}$-$\mathcal{K}$ joint IFD, $(\vec{u}^*, \vec{v}^*)$ satisfy

$$\begin{cases} \frac{M'(t)}{M(t)} = a - b\sum_{i=1}^n u^{i*} - c\sum_{j=1}^m v^{j*}, \\ \frac{N'(t)}{N(t)} = -d + e\sum_{i=1}^n u^{i*} - f\sum_{j=1}^m v^{j*}. \end{cases} \tag{20}$$

Hence, for all i, j,

$$\begin{cases} \partial_t u^{i*} = L^i u^{i*} + u^{i*}\frac{M'(t)}{M(t)}, & \text{in } \Omega\times(0,\infty), \\ \partial_t v^{j*} = A^j v^{j*} + v^{j*}\frac{N'(t)}{N(t)}, & \text{in } \Omega\times(0,\infty). \end{cases} \tag{21}$$

Step 1. Fix a solution $(\vec{u}(x,t), \vec{v}(x,t))$ of system (1) with $\{u^i\}_{i\in\mathcal{S}}$ and $\{v^j\}_{j\in\mathcal{K}}$ being componentwise positive, define

$$E(t) = \rho_1 E_1(t) + E_2(t) + \rho_1 E_3(t) + E_4(t), \tag{22}$$

where $\rho_1 > 0$ is given in **(Ha')** and

$$E_1 = \int_\Omega \sum_{i\in\mathcal{S}} \left[\frac{u^i}{M} - \frac{u^{i*}}{M}\log\left(\frac{u^i}{u^{i*}}\right)\right]dx, \quad E_3 = \int_\Omega \sum_{i\in\mathcal{S}^c}\frac{u^i}{M}dx,$$

$$E_2 = \int_\Omega \sum_{j\in\mathcal{K}} \left[\frac{v^j}{N} - \frac{v^{j*}}{N}\log\left(\frac{v^j}{v^{j*}}\right)\right]dx, \quad E_4 = \int_\Omega \sum_{j\in\mathcal{K}^c}\frac{v^j}{N}dx.$$

Thanks to the no-flux boundary conditions, we calculate that

$$\begin{aligned} \int_\Omega \left[\frac{u^{i*}}{u^i}L^i u^i + \log\left(\frac{u^i}{u^{i*}}\right)L^i u^{i*}\right]dx &= -\int_\Omega \left[\left(D_u^i\nabla u^i - \vec{P}^i u^i\right)\nabla\frac{u^{i*}}{u^i} + \left(D_u^i\nabla u^{i*} - \vec{P}^i u^{i*}\right)\nabla\log\left(\frac{u^i}{u^{i*}}\right)\right]dx \\ &= \int_\Omega D_u^i u^{i*}\left(\frac{\nabla u^i}{u^i} - \frac{\nabla u^{i*}}{u^{i*}}\right)^2 dx, \text{ for all } i\in\mathcal{S}, \\ \int_\Omega \left[\frac{v^{j*}}{v^j}A^j v^j + \log\left(\frac{v^j}{v^{j*}}\right)A^j v^{j*}\right]dx &= -\int_\Omega \left[\left(D_v^j\nabla v^j - \vec{Q}^j v^j\right)\nabla\frac{v^{j*}}{v^j} + \left(D_v^j\nabla v^{j*} - \vec{Q}^j v^{j*}\right)\nabla\log\left(\frac{v^j}{v^{j*}}\right)\right]dx \\ &= \int_\Omega D_v^j v^{j*}\left(\frac{\nabla v^j}{v^j} - \frac{\nabla v^{j*}}{v^{j*}}\right)^2 dx, \text{ for all } j\in\mathcal{K}. \end{aligned} \tag{23}$$

Moreover, we use (20) to deduce the following identities:

$$\begin{aligned}
&\int_\Omega (u^i - u^{i*}) \left(a - b\sum_{k=1}^n u^k - c\sum_{k=1}^m v^k - \frac{M'}{M} \right) dx \\
&\quad = \int_\Omega (u^i - u^{i*}) \left[b\left(\sum_{i=1}^n u^{k*} - \sum_{k=1}^n u^k \right) + c\left(\sum_{j=1}^m v^{j*} - \sum_{k=1}^m v^k \right) \right] dx, \\
&\int_\Omega (v^i - v^{i*}) \left(-d + e\sum_{k=1}^n u^k - f\sum_{k=1}^m v^k - \frac{N'}{N} \right) dx \\
&\quad = \int_\Omega (v^i - v^{i*}) \left[e\left(\sum_{k=1}^n u^k - \sum_{i=1}^n u^{k*} \right) - f\left(\sum_{k=1}^m v^k - \sum_{j=1}^m v^{j*} \right) \right] dx.
\end{aligned} \tag{24}$$

Now some calculations yield that

$$\begin{aligned}
\frac{dE_1}{dt} &= \frac{1}{M}\int_\Omega \sum_{i\in\mathcal{S}} \left[\partial_t u^i \left(1 - \frac{u^{i*}}{u^i} \right) - \left(\partial_t u^{i*} - u^{i*}\frac{M'}{M} \right) \log\left(\frac{u^i}{u^{i*}} \right) + \partial_t u^{i*} - u^i \frac{M'}{M} \right] dx \\
&= \frac{1}{M}\int_\Omega \sum_{i\in\mathcal{S}} \left[L^i u^i \left(1 - \frac{u^{i*}}{u^i} \right) + (u^i - u^{i*}) \left(a - b\sum_{k=1}^n u^k - c\sum_{k=1}^m v^k \right) \right. \\
&\quad \left. - L^i u^{i*} \log\left(\frac{u^i}{u^{i*}} \right) + L^i u^{i*} + u^{i*}\frac{M'}{M} - u^i \frac{M'}{M} \right] dx \\
&= -\frac{1}{M}\int_\Omega \sum_{i\in\mathcal{S}} \left[\frac{u^{i*}}{u^i} L^i u^i + \log\left(\frac{u^i}{u^{i*}} \right) L^i u^{i*} \right] \\
&\quad + \frac{1}{M}\int_\Omega \sum_{i\in\mathcal{S}} (u^i - u^{i*}) \left(a - b\sum_{k=1}^n u^k - c\sum_{k=1}^m v^k - \frac{M'}{M} \right) dx \\
&= -\frac{1}{M}\int_\Omega \sum_{i\in\mathcal{S}} D_u^i u^{i*} \left(\frac{\nabla u^i}{u^i} - \frac{\nabla u^{i*}}{u^{i*}} \right)^2 dx \\
&\quad + \frac{1}{M}\int_\Omega \left[b\left(\sum_{i=1}^n u^{i*} - \sum_{k=1}^n u^k \right) + c\left(\sum_{j=1}^m v^{j*} - \sum_{k=1}^m v^k \right) \right] \sum_{i\in\mathcal{S}} (u^i - u^{i*}) dx.
\end{aligned} \tag{25}$$

An analogous calculation gives

$$\begin{aligned}
\frac{dE_2}{dt} &= -\frac{1}{N}\int_\Omega \sum_{j\in\mathcal{K}} D_v^j v^{j*} \left(\frac{\nabla v^j}{v^j} - \frac{\nabla v^{j*}}{v^{j*}} \right)^2 dx \\
&\quad + \frac{1}{N}\int_\Omega \left[e\left(\sum_{k=1}^n u^k - \sum_{i=1}^n u^{i*} \right) - f\left(\sum_{k=1}^m v^k - \sum_{j=1}^m v^{j*} \right) \right] \sum_{j\in\mathcal{K}} (v^j - v^{j*}) dx.
\end{aligned} \tag{26}$$

Again apply the no-flux boundary conditions and (20) to obtain that

$$\begin{aligned}\frac{dE_3}{dt} &= \int_\Omega \sum_{i\in\mathcal{S}^c}\left(\frac{1}{M}\partial_t u^i - u^i\frac{M'}{M^2}\right)dx\\ &= \frac{1}{M}\int_\Omega \sum_{i\in\mathcal{S}^c} u^i\left(a - b\sum_{k=1}^n u^k - c\sum_{k=1}^m v^k - \frac{M'}{M}\right)dx,\\ &= \frac{1}{M}\int_\Omega \left[b\left(\sum_{i=1}^n u^{i*} - \sum_{k=1}^n u^k\right) + c\left(\sum_{j=1}^m v^{j*} - \sum_{k=1}^m v^k\right)\right]\sum_{i\in\mathcal{S}^c} u^i dx,\end{aligned} \tag{27}$$

and

$$\begin{aligned}\frac{dE_4}{dt} &= \int_\Omega \sum_{j\in\mathcal{K}^c}\left(\frac{1}{N}\partial_t v^j - v^j\frac{N'}{N^2}\right)dx\\ &= \frac{1}{N}\int_\Omega \sum_{j\in\mathcal{K}^c} v^j\left(-d + e\sum_{k=1}^n u^k - f\sum_{k=1}^m v^k - \frac{N'}{N}\right)dx\\ &= \frac{1}{N}\int_\Omega \left[e\left(\sum_{k=1}^n u^k - \sum_{i=1}^n u^{i*}\right) - f\left(\sum_{k=1}^m v^k - \sum_{j=1}^m v^{j*}\right)\right]\sum_{j\in\mathcal{K}^c} v^j dx.\end{aligned} \tag{28}$$

Substituting (25), (26), (27) and (28) into (22), we derive that

$$\begin{aligned}\frac{dE}{dt} =& -\frac{\rho_1}{M}\int_\Omega \sum_{i\in\mathcal{S}} D_u^i u^{i*}\left(\frac{\nabla u^i}{u^i} - \frac{\nabla u^{i*}}{u^{i*}}\right)^2 dx - \frac{1}{N}\int_\Omega \sum_{j\in\mathcal{K}} D_v^j v^{j*}\left(\frac{\nabla v^j}{v^j} - \frac{\nabla v^{j*}}{v^{j*}}\right)^2 dx\\ &- \int_\Omega\left[\frac{\rho_1 b}{M}\left(\sum_{i=1}^n u^{i*} - \sum_{k=1}^n u^k\right)^2 + \frac{f}{N}\left(\sum_{j=1}^m v^{j*} - \sum_{k=1}^m v^k\right)^2\right]dx\\ &+ \int_\Omega\left(\frac{\rho_1 c}{M} - \frac{e}{N}\right)\left(\sum_{j=1}^m v^{j*} - \sum_{k=1}^m v^k\right)\left(\sum_{k=1}^n u^k - \sum_{i=1}^n u^{i*}\right)dx\\ =& -\frac{\rho_1}{M}\int_\Omega \sum_{i\in\mathcal{S}} D_u^i u^{i*}\left(\frac{\nabla u^i}{u^i} - \frac{\nabla u^{i*}}{u^{i*}}\right)^2 dx - \frac{1}{N}\int_\Omega \sum_{j\in\mathcal{K}} D_v^j v^{j*}\left(\frac{\nabla v^j}{v^j} - \frac{\nabla v^{j*}}{v^{j*}}\right)^2 dx\\ &- \int_\Omega X^T\begin{pmatrix}\frac{\rho_1 b}{M} & \frac{1}{2}\left(\frac{\rho_1 c}{M} - \frac{e}{N}\right)\\ \frac{1}{2}\left(\frac{\rho_1 c}{M} - \frac{e}{N}\right) & \frac{f}{N}\end{pmatrix}X dx,\end{aligned} \tag{29}$$

where $X^T = \left(\sum_{i=1}^n u^{i*} - \sum_{k=1}^n u^k, \sum_{j=1}^m v^{j*} - \sum_{k=1}^m v^k\right)$.

Thanks to **(Ha')**, the matrix

$$B(x,t) = \begin{pmatrix}\frac{\rho_1 b}{M} & \frac{1}{2}\left(\frac{\rho_1 c}{M} - \frac{e}{N}\right)\\ \frac{1}{2}\left(\frac{\rho_1 c}{M} - \frac{e}{N}\right) & \frac{f}{N}\end{pmatrix}$$

is positive definite for any $(x,t)\in\overline{\Omega}\times\mathbb{R}$, and hence there exists constant $K>0$ such that for any $w^T(x,t) = (w_1(x,t), w_2(x,t)) \in [C^\infty_{per}(\overline{\Omega}\times\mathbb{R};\mathbb{R})]^2$,

$$w^T(x,t)B(x,t)w(x,t) \geq K\sum_{i=1}^2 w_i^2(x,t).$$

Therefore,

$$\frac{dE}{dt} \le -\frac{\rho_1}{M}\int_\Omega \sum_{i\in\mathcal{S}} D_u^i u^{i*}\left(\frac{\nabla u^i}{u^i}-\frac{\nabla u^{i*}}{u^{i*}}\right)^2 dx - \frac{1}{N}\int_\Omega \sum_{j\in\mathcal{K}} D_v^j v^{j*}\left(\frac{\nabla v^j}{v^j}-\frac{\nabla v^{j*}}{v^{j*}}\right)^2 dx$$
$$- K\int_\Omega \left[\left(\sum_{i=1}^n u^{i*}-\sum_{k=1}^n u^k\right)^2 + \left(\sum_{j=1}^m v^{j*}-\sum_{k=1}^m v^k\right)^2\right] dx. \tag{30}$$

Step 2. Denote

$$X = [C(\overline{\Omega})]^{n+m}, \quad X^+ = \{(\vec{u},\vec{v}) \in X : u^i, v^j \ge 0, i = 1,\cdots,n, j = 1,\cdots,m\},$$

We note that the solution semiflow of system (1) is compact for any $t > 0$ and it is point dissipative by Theorem 6. It then follows from Theorem 1.1.2 (Zhao 2017) that system (1) has a global compact attractor $\mathcal{A}$, which we understand here as a collection of entire solutions.

Define the ω-limit set of a positive orbit of system (1) to be the set of all subsequential limits as we let $t = nT \to \infty$. It is easy to see that every member $(\vec{u},\vec{v})$ of the ω-limit set is an entire solution of the system (1). By LaSalle's invariance principle (LaSalle 1967, Theorem 3), each such entire solution satisfies

$$\frac{d}{dt}E(t;\vec{u},\vec{v}) = 0 \text{ for all } t \in \mathbb{R}. \tag{31}$$

Thus, we define

$$\mathcal{M} = \{(\vec{u},\vec{v}) \in \mathcal{A} : \quad (31) \text{ holds}\}.$$

In view of (30), every $(\vec{u},\vec{v}) \in \mathcal{M}$ satisfies

$$\frac{\nabla u^i}{u^i}-\frac{\nabla u^{i*}}{u^{i*}} = 0, \quad \frac{\nabla v^j}{v^j}-\frac{\nabla v^{j*}}{v^{j*}} = 0 \text{ for } i \in \mathcal{S}, j \in \mathcal{K}, \tag{32}$$

and

$$\sum_{i=1}^n u^{i*}-\sum_{k=1}^n u^k = 0, \quad \sum_{j=1}^m v^{j*}-\sum_{k=1}^m v^k = 0. \tag{33}$$

Clearly, (33) implies statement (a).

Claim. The function pair $(M(t),N(t))$ such that $K_{MN}^{(1)}(x,t), K_{MN}^{(2)}(x,t) > 0$ is unique. This claim implies the uniqueness in Theorem 9. Otherwise, suppose that there exists another $(\tilde{M}(t),\tilde{N}(t))$ with $\tilde{K}_{MN}^{(1)}(x,t)$, $\tilde{K}_{MN}^{(2)}(x,t) > 0$. Without loss of generality, we consider the case $n = 2$, $m = 2$ and write

$$(u^1,u^2,v^1,v^2) = \left(MK_{MN}^{(1)},0,NK_{MN}^{(2)},0\right) \quad \text{and} \quad \left(0,\tilde{M}\tilde{K}_{MN}^{(1)},0,\tilde{N}\tilde{K}_{MN}^{(2)}\right),$$

where both are IFDs. Then using (33) and integrating over Ω implies $M(t) = \tilde{M}(t)$ and $N(t) = \tilde{N}(t)$.

Next, we assume there is a unique combination $\mathcal{S}$-$\mathcal{K}$ such that (1) achieves a $\mathcal{S}$-$\mathcal{K}$ joint IFD, and proceed to prove (b). By (33) and (20), the solution $(\vec{u},\vec{v})$ in $\mathcal{M}$ satisfies

$$\begin{cases} \partial_t u^i = L^i u^i + u^i\left(a - b\sum_{i=1}^n u^{i*} - c\sum_{j=1}^m v^{j*}\right) & \\ \quad = L^i u^i + u^i\frac{M'(t)}{M(t)}, & \text{in } \Omega\times\mathbb{R}, \\ \partial_t v^j = A^j v^j + v^j\left(-d + e\sum_{i=1}^n u^{i*} - f\sum_{j=1}^m v^{j*}\right) & \\ \quad = A^j v^j + v^j\frac{N'(t)}{N(t)}, & \text{in } \Omega\times\mathbb{R}, \\ \mathcal{B}^i u^i = \tilde{\mathcal{B}}^j v^j = 0, & \text{on } \partial\Omega\times\mathbb{R}, \end{cases} \tag{34}$$

for all $1 \le i \le n$, $1 \le j \le m$.

Step 3. We claim that $(\vec{u}, \vec{v})$ is T-periodic. By Lemma 8, there exist nonnegative constants $\{C_u^i\}_{i=1}^n$ and $\{C_v^j\}_{j=1}^m$ such that $u^i = C_u^i M(t)\phi_1^i$ and $v^j = C_v^j N(t)\phi_2^i$, $\sum_{i=1}^n C_u^i = \sum_{i=1}^m C_v^j = 1$, where ϕ_1^i and ϕ_2^j are given in Definition 3. Thus, $(\vec{u}, \vec{v})$ is T-periodic.

Step 4. We claim that, for every $i \in \mathcal{S}$ (resp. $j \in \mathcal{K}$), there exists a nonnegative constant S_u^i (resp. K_v^j) such that $u^i = S_u^i u^{i*}$ (resp. $v^j = K_v^j v^{j*}$). Upon combining with (33), we have

$$\frac{1}{|\mathcal{S}|}\sum_{i\in\mathcal{S}} S_u^i = 1 \quad \text{and} \quad \frac{1}{|\mathcal{K}|}\sum_{j\in\mathcal{K}} K_v^j = 1. \tag{35}$$

Indeed, (32) implies $u^i = S_u^i(t)u^{i*}$ for each $i \in \mathcal{S}$. Moreover, $S_u^i(t)$ is C^1 (since u^i and u^{i*} are both C^1 in t). Substituting $u^i = S_u^i(t)u^{i*}$ into u^i-equation of (34) leads to $(S_u^i(t))' = 0$. Thus, $S_u^i \ge 0$ is a constant. Similarly, we have $\{v^j\}_{j\in\mathcal{K}} = \{K_v^j v^{j*}\}_{j\in\mathcal{K}}$ for some constants $K_v^j \ge 0$, $j \in \mathcal{K}$. It suffices to prove the following claim, so that the set $\mathcal{M}$ consists of a single entire solution.

Step 5. We claim that $S_u^i = 1$ for all $i \in \mathcal{S}$ and $K_v^j = 1$ for all $j \in \mathcal{K}$.

Suppose, on the contrary, that $S_u^i \ne 1$ for some $i \in \mathcal{S}$. (The case $K_v^j \ne 1$ for some $j \in \mathcal{K}$ can be treated in a similar manner.) Then by (35), there exists $i_0 \in \mathcal{S}$ such that $S_u^{i_0} = \max_{i\in\mathcal{S}} S_u^i > 1$. Now, if we set $b^i = \frac{S_u^{i_0} - S_u^i}{S_u^{i_0} - 1}$ for $i \in \mathcal{S}$ and $b^i = 0$ for $i \in \mathcal{S}^c$, then clearly $\sum_{i\in\mathcal{S}} b^i = \sum_{i=1}^n b^i = 1$. Define

$$\tilde{u}^i = b^i u^{i^*} \quad \text{for } i \in \mathcal{S} \quad \text{and} \quad \tilde{u}^i = 0 \quad \text{for } i \in \mathcal{S}^c.$$

Then it is clear that $\sum_{i=1}^n \tilde{u}^i = \sum_{i=1}^n u^{i*}$ and that $(\vec{\tilde{u}}, \vec{v}^*)$ gives a $\mathcal{S}'-\mathcal{K}$ joint IFD where $\mathcal{S}'$ is a proper subset of $\mathcal{S}$. This is a contradiction, so $S_u^i \equiv 1$ for all $i \in \mathcal{S}$. A similar contradiction can be reached in $K_v^j \ne 1$ for some $j \in \mathcal{K}$. □

5 Evolutionary stability without predator self-limitation

Now we consider the evolutionary stability of ideal dispersal strategies in the more delicate case where there is no self-limitation of the predator species. Theorem 5 is stated as assertion (b) in the following theorem.

Theorem 11 (Without self-limitation) *Suppose D_u^i, P^i, D_v^j, Q^j and a, b, c, d, e, f satisfy* **(A)** *and* **(Hb')**. *Then suppose that the system (1) has a $\mathcal{S}$-$\mathcal{K}$ joint IFD $(\vec{u}^*, \vec{v}^*)$. Then for each solution $(\vec{U}, \vec{V})$ initiating from any nontrivial and nonnegative data $(\vec{U}_{in}, \vec{V}_{in})$, the orbit*

$$\left\{(\vec{U}_k(x,t), \vec{V}_k(x,t))\right\}_{k=1}^{\infty} := \left\{(\vec{U}(x,t+kT), \vec{V}(x,t+kT)\right\}_{k=1}^{\infty}$$

has compact closure in $C_{loc}(\overline{\Omega}\times\mathbb{R})$, which we denote by $\omega(\vec{U}_{in}, \vec{V}_{in})$.[1]

(a) *Any entire solution $(\vec{u}, \vec{v}) \in \omega(\vec{U}_{in}, \vec{V}_{in})$ (which is defined in $\Omega\times\mathbb{R}$) satisfies*

$$\sum_{i=1}^n u^i = \sum_{i=1}^n u^{i*} = \frac{1}{e}\left(d + \frac{N'(t)}{N(t)}\right) \quad \text{in} \quad \Omega\times\mathbb{R}. \tag{36}$$

Moreover, exactly one of the following holds:

[1] Note that for any compact set $\Lambda_1 \subseteq \overline{\Omega}\times\mathbb{R}$, $(\vec{U}_k, \vec{V}_k)$ is well-defined on Λ_1 for all $k \gg 1$. Hence it makes sense to speak of precompactness of $(\vec{U}_k, \vec{V}_k)$ in $C_{loc}(\overline{\Omega}\times\mathbb{R})$.

(i) *The total distribution of* $\{v^j\}_{j=1}^m$ *is IFD, i.e.*

$$\sum_{j=1}^{m} v^j = \sum_{j=1}^{m} v^{j*} = \frac{1}{c}\left[a - \frac{b}{e}\left(d + \frac{N'(t)}{N(t)}\right) - \frac{M'(t)}{M(t)}\right] \quad \text{in} \quad \Omega \times \mathbb{R}.$$

(ii) $n > 1$ *and* $m > 1$ *and none of the species* $\{u^i\}_{i\in\mathcal{S}}$ *persists, i.e.*

$$u^i \equiv 0 \quad \text{for all } i \in \mathcal{S}, \quad \text{and} \quad \sum_{i\in\mathcal{S}^c}^{n} u^i = \sum_{i=1}^{n} u^{i*} = \frac{1}{e}\left(d + \frac{N'(t)}{N(t)}\right) \text{ in } \Omega \times \mathbb{R}. \tag{37}$$

Moreover, there exist nonnegative constants $\{K_v^j\}_{j=1}^m$ *such that*

$$\begin{cases} v^j(x,t) = K_v^j N(t)\phi_2^j(x,t), \\ \partial_t u^i - L^i u^i = u^i\left(a - b\sum_{i=1}^n u^{i*} - c\sum_{j=1}^m v^j\right). \end{cases} \tag{38}$$

(b) *Suppose* $\mathcal{S} - \mathcal{K}$ *is the unique combination that supports a joint IFD, and at least one of the following conditions holds:*

(i) $n = 1$*;*
(ii) $m = 1$*;*
(iii) $n > 1$*,* $m > 1$*, and no subsets* $\mathcal{S}' \subseteq \mathcal{S}^c$ *and* $\mathcal{K}' \subseteq \{1, \cdots, m\}$ *can support a positive periodic solution* $(\vec{u}, \vec{v})$ *such that* $\sum_{i=1}^n u^i = \frac{1}{e}\left(d + \frac{N'(t)}{N(t)}\right)$.

Then the following convergence holds uniformly in $x \in \Omega$*:*

$$\lim_{t\to\infty} u^i(x,t) = u^{i*}(x,t), \quad \lim_{t\to\infty} v^j(x,t) = v^{j*}(x,t).$$

As an application, we derive the following exclusion principle when a single prey-predator pair forms an IFD.

Corollary 12 Let D_u^i, P^i, D_v^j, Q^j and a, b, c, d, e, f satisfy **(A)** and **(Hb')**. Suppose the following two conditions hold simultaneously:

(i) $n = 1$ or $m = 1$;
(ii) $\mathcal{S} = \{1\}$ and $\mathcal{K} = \{1\}$ are the unique subsets of prey-predator species that jointly support an IFD.

Then the following convergences hold uniformly in $x \in \Omega$:

$$\begin{cases} \lim_{t\to\infty} u^1(x,t) = u^{1*}(x,t), & \lim_{t\to\infty} u^i(x,t) = 0 \quad \text{for } i = 2, \cdots, n, \\ \lim_{t\to\infty} v^1(x,t) = v^{1*}(x,t), & \lim_{t\to\infty} v^j(x,t) = 0 \quad \text{for } j = 2, \cdots, m. \end{cases}$$

Remark 8 Conditions (ii) of the above corollary can be rephrased as follows: suppose there exist nonnegative constants p^i, q^j such that

$$\sum_{i=1}^{n} p^i M(t)\phi_1^i(x,t) = \frac{1}{e}\left(d + \frac{N'(t)}{N(t)}\right) \text{ and } \sum_{j=1}^{m} q^i N(t)\phi_2^i(x,t) = \frac{1}{c}\left[a - \frac{b}{e}\left(d + \frac{N'(t)}{N(t)}\right) - \frac{M'(t)}{M(t)}\right],$$

then $\{i:\ p^i > 0\} = \{1\}$ and $\{j:\ q^j > 0\} = \{1\}$, where ϕ_1^i and ϕ_2^j are given in Definition 3.

5.1 Proof of Theorem 11

Proof By Theorem 9 and its proof, there exist positive T-periodic functions $M(t)$, $N(t)$ such that $K^{(1)}(x,t)$, $K^{(2)}(x,t)$ defined by (13) are positive, and the $\mathcal{S}$-$\mathcal{K}$ joint IFD $(\vec{u}^*, \vec{v}^*)$ satisfies

$$a - b\sum u^{i*} - c\sum v^{j*} = \frac{M'(t)}{M(t)} \quad \text{and} \quad -d + e\sum u^{i*} = \frac{N'(t)}{N(t)}, \tag{39}$$

which implies that

$$\sum u^{i*} = \frac{1}{e}\left(d + \frac{N'(t)}{N(t)}\right) \quad \text{and} \quad \sum v^{j*} = \frac{1}{c}\left[a - \frac{b}{e}\left(d + \frac{N'(t)}{N(t)}\right) - \frac{M'(t)}{M(t)}\right].$$

When **(Hb')** is satisfied, set $f(x,t) \equiv 0$ and substitute ρ_2 for ρ_1 in (29) to derive

$$\frac{dE}{dt} = -\frac{\rho_2}{M}\int_\Omega \sum_{i\in\mathcal{S}} D_u^i u^{i*}\left(\frac{\nabla u^i}{u^i} - \frac{\nabla u^{i*}}{u^{i*}}\right)^2 dx - \frac{1}{N}\int_\Omega \sum_{j\in\mathcal{K}} D_v^j v^{j*}\left(\frac{\nabla v^j}{v^j} - \frac{\nabla v^{j*}}{v^{j*}}\right)^2 dx$$
$$- \int_\Omega \frac{\rho_2 b}{M}\left(\sum_{i=1}^{n} u^{i*} - \sum_{k=1}^{n} u^k\right)^2 dx.$$

It follows that

$$\mathcal{M} = \{(\vec{u},\vec{v}) \in \mathcal{A}:\ (40) \text{ and } (41) \text{ hold}\},$$

where $\mathcal{A}$ is the global attractor which is a collection of entire solutions, and

$$\frac{\nabla u^i}{u^i} - \frac{\nabla u^{i*}}{u^{i*}} = 0, \quad \frac{\nabla v^j}{v^j} - \frac{\nabla v^{j*}}{v^{j*}} = 0 \quad \text{for } i \in \mathcal{S}, j \in \mathcal{K}, \tag{40}$$

$$\sum_{i=1}^{n} u^{i*} - \sum_{k=1}^{n} u^k = 0. \tag{41}$$

This establishes (36).

Suppose there exist alternative $\tilde{M}(t)$, $\tilde{N}(t)$, $\tilde{K}^{(1)}(x,t)$ and $\tilde{K}^{(2)}(x,t)$. Let

$$(M(t)K^{(1)}(x,t), \cdots, 0, N(t)K^{(2)}(x,t), \cdots, 0),$$
$$(\tilde{M}(t)\tilde{K}^{(1)}(x,t), 0\cdots, 0, \tilde{N}(t)\tilde{K}^{(2)}(x,t), 0\cdots, 0)$$

be two solutions of (1), then we will see that $M(t) = \tilde{M}(t)$ by integrating (41) over Ω, whereas the uniqueness of $N(t)$ follows from the first equation of (7). This proves the uniqueness of $(M(t), N(t))$ in Theorem 9.

We further get from (41) that the solution $(\vec{u},\vec{v}) \in \mathcal{M}$ satisfies that

$$\begin{cases} \partial_t u^i = L^i u^i + u^i\left(a - b\sum_{i=1}^n u^{i*} - c\sum_{j=1}^m v^j\right), & \text{in } \Omega\times\mathbb{R}, \\ \partial_t v^j = A^j v^j + v^j\left(-d + e\sum_{i=1}^n u^{i*}\right) = A^j v^j + v^j\frac{N'(t)}{N(t)}, & \text{in } \Omega\times\mathbb{R}, \\ \mathcal{B}^i u^i = \tilde{\mathcal{B}}^j v^j = 0, & \text{on } \partial\Omega\times\mathbb{R}, \end{cases} \tag{42}$$

where $1 \le i \le n, 1 \le j \le m$.

Claim. The solution $(\vec{u}, \vec{v})$ of (42) is T-periodic. Combining the v^j-equation in (42) and Lemma 8, we conclude that there exist nonnegative constants $\{C_v^j\}_{j=1}^m$ such that $v^j = C_v^j N(t)\phi_2^i$, where $\sum_{i=1}^m C_v^j = 1$ and ϕ_2^j is given in Definition 3. Thus, $\vec{v}$ is T-periodic. Substituting $v^j = C_v^j N(t)\phi_2^i$ into u^i-equation, and again using Lemma 8 to see u^i is T-periodic.

Next, we establish the dichotomy in assertion (a). We divide the proof into the following cases: (I) $u^i \not\equiv 0$ for some $i \in \mathcal{S}$; (II) $n = 1$ (there is only one prey species); (III) $m = 1$ (there is only one predator species); (IV) $u^i \equiv 0$ for all $i \in \mathcal{S}$. We will show that in cases (I), (II) and (III), the alternative (i) holds, and that (ii) holds in case (IV).

Case (I). Suppose $u^i \not\equiv 0$ for some $i \in \mathcal{S}$, then (40) implies that

$$u^i = p(t)u^{i*} = S_u^i p(t) M(t)\phi_1^i(x,t) \quad \text{with some positive } T\text{-periodic function } p(t) \text{ and constant } S_u^i \ge 0.$$

Substituting into the i-th equation in (42), we see if $S_u^i \neq 0$ (i.e., $u^i \neq 0$), then

$$(p(t)M(t)'\phi_1^i + p(t)M(t)\partial_t\phi_1^i = p(t)M(t)\left[L^i\phi_1^i + \phi_1^i\left(a - b\sum_{i=1}^n u^{i*} - c\sum_{j=1}^m v^j\right)\right].$$

By Definition 3 and $p(t) > 0$, we deduce that $H(t) := a - b\sum_{i=1}^n u^{i*} - c\sum_{j=1}^m v^j$ is independent of x.

We claim that $H(t) = \frac{M'(t)}{M(t)}$. Indeed, integrating the equation of u^i in (42) in Ω and summing over $1 \le i \le n$, we have

$$\frac{d}{dt}\int_\Omega \sum_{i=1}^n u^i\,dx = \int_\Omega \sum_{i=1}^n u^i(x,t)H(t)\,dx,$$

and we conclude the claim by (41) and $\int_\Omega \sum_{i=1}^n u^i\,dx = \int_\Omega \sum_{i=1}^n u^{i*}\,dx = M(t)$. This, in turn, determines the sum $\sum_{j=1}^m v^j$ uniquely:

$$\sum_{j=1}^m v^j = \frac{1}{c}\left(a - b\sum_{i=1}^n u^{i*} - H(t)\right) = \frac{1}{c}\left(a - b\sum_{i=1}^n u^{i*} - \frac{M'(t)}{M(t)}\right) = \sum_{j=1}^m v^{j*}.$$

Hence, we showed that (i) holds if $u^i \not\equiv 0$ for some $i \in \mathcal{S}$.

Case (II). If $n = 1$, then we must have $\mathcal{S} = \{1\}$ and $u^1 \not\equiv 0$ thanks to (41). Hence $n = 1$ implies alterative (i) holds.

Case (III). Assume $m = 1$. In this case, we must have $\mathcal{K} = \{1\}$, so that $\sum_{j=1}^m v^{j*} = v^{1*}$ and $\sum_{j=1}^m v^j = v^1$. Integrating the equations of u^{i*} in Ω and adding over $1 \le i \le n$, we derive that

$$\frac{d}{dt}\int_\Omega \sum_{i=1}^n u^{i*}dx = \int_\Omega \sum_{i=1}^n u^{i*}\left(a - b\sum_{i=1}^n u^{i*} - cv^{1*}\right)dx. \tag{43}$$

By the equation of v^1 in (42) and that of v^{1*}, we see that $v^1 = qv^{1*}$ for some constant $q > 0$. Now, we integrate the equations of u^i in Ω and add over $1 \le i \le n$, and obtain

$$\frac{d}{dt}\int_\Omega \sum_{i=1}^n u^i\,dx = \int_\Omega \sum_{i=1}^n u^i\left(a - b\sum_{i=1}^n u^{i*} - c\sum_{j=1}^m v^j\right)dx.$$

Using $\sum_{i=1}^n u^i = \sum_{i=1}^n u^{i*}$ by (41) and $\sum_{j=1}^m v^j = v^1 = qv^{1*}$, we have

$$\frac{d}{dt}\int_\Omega \sum_{i=1}^n u^{i*}dx = \int_\Omega \sum_{i=1}^n u^{i*}\left(a - b\sum_{i=1}^n u^{i*} - cqv^{1*}\right)dx.$$

Subtract this from (43) to show $(q-1)\int_\Omega cv^{1*}\sum_{i=1}^n u^{i*}dx = 0$, which implies that $q=1$, and hence (i) holds.

Case (IV). Finally, we assume that $u^i \equiv 0$ for all $i \in \mathcal{S}$ (which implies $m>1$ and $n>1$). We need to deduce (ii). Substituting $u^i \equiv 0$ into (41), we deduce (37). Since v^j is a positive solution to a linear equation in (42), it follows by the Lemma 8 that $v^j = K_v^j N(t)\phi_2^j(x,t)$ for some constant $K_v^j \geq 0$ and is therefore T-periodic, where ϕ_2^j, $1 \leq j \leq m$, are given in Definition 3. Substituting back to (42) proves the conclusion of (ii). This finishes the proof of assertion (a).

Next, we prove assertion (b). Under the additional assumption, we conclude from part (a) that

$$\left(\sum_{i=1}^n u^i, \sum_{j=1}^m v^j\right) = \left(\sum_{i=1}^n u^{i*}, \sum_{j=1}^m v^{j*}\right) \quad \text{and} \quad u^i \not\equiv 0 \quad \text{for some } i \in \mathcal{S}.$$

Now, $(\vec{u},\vec{v})$ is a positive entire solution satisfying the system (34) with $f \equiv 0$. From this point, we can repeat Step 3, Step 4, and Step 5 in the proof of Theorem 10. This concludes the proof. □

6 Proof of Theorem 2

The proof of Theorem 2 The eigenvalue problem corresponding to the linearized system of (1) with $m=n=2$ at $(u^{1*},0,v^{1*},0)$ is

$$\begin{cases}
\partial_t\varphi^1 = \nabla\cdot[D_u^1\nabla\varphi^1 - \varphi^1\vec{P}^1] + \varphi^1\left(a - 2bu^{1*} - cv^{1*}\right) & \\
\qquad -bu^{1*}\varphi^2 - cu^{1*}\varphi^3 - cu^{1*}\varphi^4 + \lambda\varphi^1, & \text{in } \Omega\times\mathbb{R},\\
\partial_t\varphi^2 = \nabla\cdot[D_u^2\nabla\varphi^2 - \varphi^2\vec{P}^2] + \varphi^2\left(a - bu^{1*} - cv^{1*}\right) + \lambda\varphi^2, & \text{in } \Omega\times\mathbb{R},\\
\partial_t\varphi^3 = \nabla\cdot[D_v^1\nabla\varphi^3 - \varphi^3\vec{Q}^1] + \varphi^3\left(-d + eu^{1*} - 2fv^{1*}\right) & \\
\qquad +ev^{1*}\varphi^1 + ev^{1*}\varphi^2 - fv^{1*}\varphi^4 + \lambda\varphi^3, & \text{in } \Omega\times\mathbb{R},\\
\partial_t\varphi^4 = \nabla\cdot[D_v^2\nabla\varphi^4 - \varphi^4\vec{Q}^2] + \varphi^4\left(-d + eu^{1*} - fv^{1*}\right) + \lambda\varphi^4, & \text{in } \Omega\times\mathbb{R},\\
[D_u^1\nabla\varphi^1 - \varphi^1\vec{P}^1]\cdot\nu = [D_u^2\nabla\varphi^2 - \varphi^2\vec{P}^2]\cdot\nu = 0, & \text{on } \partial\Omega\times\mathbb{R},\\
[D_v^1\nabla\varphi^3 - \varphi^3\vec{Q}^1]\cdot\nu = [D_v^2\nabla\varphi^4 - \varphi^4\vec{Q}^2]\cdot\nu = 0, & \text{on } \partial\Omega\times\mathbb{R}.
\end{cases} \tag{44}$$

It suffices to prove that problem (44) has at least one eigenvalue with negative real part when (u^{1*},v^{1*}) is not an IFD, where (u^{1*},v^{1*}) satisfies

$$\begin{cases}
\partial_t u^{1*} = \nabla\cdot[D_u^1\nabla u^{1*} - u^{1*}\vec{P}^1] + u^{1*}\left(a - bu^{1*} - cv^{1*}\right), & \text{in } \Omega\times\mathbb{R},\\
\partial_t v^{1*} = \nabla\cdot[D_v^1\nabla v^{1*} - v^{1*}\vec{Q}^1] + v^{1*}\left(-d + eu^{1*} - fv^{1*}\right), & \text{in } \Omega\times\mathbb{R},\\
[D_u^1\nabla u^{1*} - u^{1*}\vec{P}^1]\cdot\nu = [D_v^1\nabla v^{1*} - v^{1*}\vec{Q}^1]\cdot\nu = 0, & \text{on } \partial\Omega\times\mathbb{R}.
\end{cases} \tag{45}$$

Case (a). The following problem (46) has at least one eigenvalue with negative real part:

$$\begin{cases}
\partial_t\varphi^1 = \nabla\cdot[D_u^1\nabla\varphi^1 - \varphi^1\vec{P}^1] + \varphi^1\left(a - 2bu^{1*} - cv^{1*}\right) - cu^{1*}\varphi^3 + \lambda\varphi^1, & \text{in } \Omega\times\mathbb{R},\\
\partial_t\varphi^3 = \nabla\cdot[D_v^1\nabla\varphi^3 - \varphi^3\vec{Q}^1] + \varphi^3\left(-d + eu^{1*} - 2fv^{1*}\right) + ev^{1*}\varphi^1 + \lambda\varphi^3, & \text{in } \Omega\times\mathbb{R},\\
[D_u^1\nabla\varphi^1 - \varphi^1\vec{P}^1]\cdot\nu = [D_v^1\nabla\varphi^3 - \varphi^3\vec{Q}^1]\cdot\nu = 0, & \text{on } \partial\Omega\times\mathbb{R}.
\end{cases} \tag{46}$$

We prove the conclusion by choosing eigenfunction as $(\varphi^1,0,\varphi^3,0)$, where (φ^1,φ^3) are the eigenfunction of (46) corresponding to the eigenvalue with negative real part.

Case (b). All eigenvalues of problem (46) have nonnegative real parts. Since (u^{1*}, v^{1*}) is not an IFD of (45), we have

$$\partial_x(a - bu^{1*} - cv^{1*}) \neq 0 \quad \text{or} \quad \partial_x(-d + eu^{1*} - fv^{1*}) \neq 0 \quad \text{in } \Omega \times \mathbb{R}.$$

Case (i). If $\partial_x(a - bu^{1*} - cv^{1*}) \neq 0$, integrate the first equation of (45) over Ω, then

$$\frac{d}{dt}\int_\Omega u^{1*}dx < \sup_{x\in\Omega}\left(a - bu^{1*} - cv^{1*}\right)\int_\Omega u^{1*}dx,$$

which implies that

$$0 = \int_0^T \frac{d}{dt}\log\left(\int_\Omega u^{1*}dx\right)dt < \int_0^T \sup_{x\in\Omega}\left(a - bu^{1*} - cv^{1*}\right)dt. \tag{47}$$

By (47) and Lemma B.1 (Cantrell et al. 2021) (i.e, $\sup_{\gamma\in C^\infty_{per}(\mathbb{R};\mathrm{Int}\Omega)}\int_0^T F(\gamma(t),t)dt = \int_0^T \sup_{x\in\Omega} F(x,t)dt$ for all $F(x,t) \in C(\overline{\Omega}\times[0,T])$), there exists $\gamma_1 \in C^\infty_{per}(\mathbb{R};\mathrm{Int}\Omega)$ such that

$$\int_0^T \left[a(x,t) - b(x,t)u^{1*}(x,t) - c(x,t)v^{1*}(x,t)\right]\Big|_{x=\gamma_1(t)}dt > 0.$$

Thus, using the arguments in Theorem 4.2 (Cantrell et al. 2021), for given $D_u^2(x,t)$ satisfying **(A)**, we can choose

$$\vec{P}_\tau^2(x,t) = \tau(\gamma_1(t) - x),$$

then $\limsup_{\tau\to\infty}\lambda_1 < 0$, where λ_1 is the principal eigenvalue of the following problem

$$\begin{cases} \partial_t\varphi^2 = \nabla\cdot[D_u^2\nabla\varphi^2 - \varphi^2\vec{P}_\tau^2] + \varphi^2\left(a - bu^{1*} - cv^{1*}\right) + \lambda\varphi^2, & \text{in } \Omega\times\mathbb{R}, \\ [D_u^2\nabla\varphi^2 - \varphi^2\vec{P}_\tau^2]\cdot\nu = 0, & \text{on } \partial\Omega\times\mathbb{R}. \end{cases}$$

Denote the corresponding eigenfunction to λ_1 as φ^{2*}, and choose $\varphi^{4*} = 0$. Then substitute $(\lambda_1, \varphi^{2*}, \varphi^{4*})$ into the first and third equations of (44) and obtain

$$\begin{cases} \partial_t\varphi^1 = \nabla\cdot[D_u^1\nabla\varphi^1 - \varphi^1\vec{P}^1] + \varphi^1\left(a - 2bu^{1*} - cv^{1*} + \lambda_1\right) - cu^{1*}\varphi^3 - bu^{1*}\varphi^{2*}, & \text{in } \Omega\times\mathbb{R}, \\ \partial_t\varphi^3 = \nabla\cdot[D_v^1\nabla\varphi^3 - \varphi^3\vec{Q}^1] + \varphi^3\left(-d + eu^{1*} - 2fv^{1*} + \lambda_1\right) + ev^{1*}\varphi^1 + ev^{1*}\varphi^{2*}, & \text{in } \Omega\times\mathbb{R}, \\ [D_u^1\nabla\varphi^1 - \varphi^1\vec{P}^1]\cdot\nu = [D_v^1\nabla\varphi^3 - \varphi^3\vec{Q}^1]\cdot\nu = 0, & \text{on } \partial\Omega\times\mathbb{R}. \end{cases}$$

Observe that $\lambda_1 < 0$ is not an eigenvalue of (46), so that the above system has a unique solution $(\varphi^{1*}, \varphi^{3*})$.

Case (ii). If $\partial_x(a - bu^{1*} - cv^{1*}) \equiv 0$ and $\partial_x(-d + eu^{1*} - fv^{1*}) \neq 0$, then we get

$$\int_0^T \left[-d(x,t) + e(x,t)u^{1*}(x,t) - f(x,t)v^{1*}(x,t)\right]\Big|_{x=\gamma_2(t)}dt > 0$$

holds for some $\gamma_2 \in C^\infty_{per}(\mathbb{R};\mathrm{Int}\Omega)$. Moreover, fix $D_v^2(x,t)$ satisfying **(A)**, choose

$$\vec{Q}_\tau^2(x,t) = \tau(\gamma_2(t) - x),$$

then $\limsup_{\tau\to\infty}\lambda_1 < 0$, where λ_1 is the principal eigenvalue of the following problem

$$\begin{cases} \partial_t\varphi^4 = \nabla\cdot[D_v^2\nabla\varphi^4 - \varphi^4\vec{Q}_\tau^2] + \varphi^4\left(-d + eu^{1*} - fv^{1*}\right) + \lambda\varphi^4, & \text{in } \Omega\times\mathbb{R}, \\ [D_v^2\nabla\varphi^4 - \varphi^4\vec{Q}_\tau^2]\cdot\nu = 0, & \text{on } \partial\Omega\times\mathbb{R}, \end{cases}$$

and the associated eigenfunction is φ^{4*}. In a similar manner to **Case (i)** , we can prove that (44) has an eigenvalue λ_1 with $\limsup_{\tau\to\infty}\lambda_1 < 0$ and the associated eigenfunction is $(\varphi^{1*}, 0, \varphi^{3*}, \varphi^{4*})$. □

7 Convergence stability of approximate IFD

We now conduct numerical simulations to show that in lieu perfectly achieving IFD, being able to approximate the conditions for IFD is utilitarian. This corresponds to the concept of convergence stability (Christiansen 1991; Eshel et al. 1997), which means that the closer a (collection of) species is to IFD, then it has more competitive advantage against (another collection of) species that are further away from IFD. In particular, this suggest competitive advantage when IFD is approximately achieved. According to the basic timescale separation assumption of adaptive dynamics, upon repeated introduction of mutant prey/predator species, the total population evolves closer and closer towards achieving an IFD.

To study convergence stability, it is necessary to introduce a *metric* to measure the deviation of a given distribution (in space-time coordinates) from IFD. Let $\Lambda := \{(\mathcal{S}', \mathcal{K}') : \emptyset \neq \mathcal{S}' \subseteq \{1, \cdots, n\}, \emptyset \neq \mathcal{K}' \subseteq \{1, \cdots, m\}\}$. Then Λ is the collection of subsets of $\{\{1, 2, .., n\}, \{1, 2, ..m\}\}$, for which $\phi_1^i(x,t), \phi_2^j(x,t)$ are unique positive solutions to (14) for appropriate dispersal functions $(D_u^i, \vec{P}^i; D_v^j, \vec{Q}^j)$. We fix our discussion by defining a function G on the set Λ as

$$G(\Lambda) = \inf_{\substack{r_i, p_j > 0, \\ (i,j) \in \Lambda}} \left\{ \left\| a(x,t) - b(x,t) \sum_{i \in \mathcal{S}'} r_i M(t) \phi_1^i(x,t) - c(x,t) \sum_{j \in \mathcal{K}'} p_j N(t) \phi_2^j(x,t) - \frac{M'(t)}{M(t)} \right\| \right.$$
$$\left. + \left\| -d(x,t) + e(x,t) \sum_{i \in \mathcal{S}'} r_i M(t) \phi_1^i(x,t) - f(x,t) \sum_{j \in \mathcal{K}'} p_j N(t) \phi_2^j(x,t) - \frac{N'(t)}{N(t)} \right\| \right\}.$$

Here $(M(t), N(t))$ is a positive T-periodic solution of system (7), and $\|h\| = \sup_{(x,t) \in \overline{\Omega} \times [0,T]} |h(x,t)|$. The above norm is well-defined since all functions involved are continuous and T-periodic in time.

By (17), if $(\vec{u}^*, \vec{v}^*) = (u^{1*}, \cdots, u^{n*}, v^{1*}, \cdots, v^{n*})$ forms a $\mathcal{S}' - \mathcal{K}'$ joint IFD, then

$$\begin{cases} \frac{M'(t)}{M(t)} = a(x,t) - b(x,t) \sum_{i \in \mathcal{S}'} u^{i*} - c(x,t) \sum_{j \in \mathcal{K}'} v^{j*}, \\ \frac{N'(t)}{N(t)} = -d(x,t) + e(x,t) \sum_{i \in \mathcal{S}'} u^{i*} - f(x,t) \sum_{j \in \mathcal{K}'} v^{j*}. \end{cases} \tag{48}$$

Substituting this into system (1), and comparing the result with Definition 3, we see that

$$u^{i*}(x,t) = r_i M(t) \phi_1^i(x,t), \quad v^{j*}(x,t) = p_j N(t) \phi_2^j(x,t), \tag{49}$$

for some positive constants r_i, p_j, $i \in \mathcal{S}'$ and $j \in \mathcal{K}'$. Consequently, under an IFD, r_i, p_j such that the prey and predator fitness functions are spatially equilibrated, i.e.,

$$\begin{cases} a(x,t) - b(x,t) \sum_{i \in \mathcal{S}'} r_i M(t) \phi_1^i(x,t) - c(x,t) \sum_{j \in \mathcal{K}'} p_j M(t) \phi_2^j(x,t) - \frac{M'(t)}{M(t)} = 0, \\ -d(x,t) + e(x,t) \sum_{i \in \mathcal{S}'} r_i M(t) \phi_1^i(x,t) - f(x,t) \sum_{j \in \mathcal{K}'} p_j M(t) \phi_2^j(x,t) - \frac{N'(t)}{N(t)} = 0. \end{cases}$$

Therefore, the two terms appearing in the definition of $G(\Lambda)$ measure the deviation of the distribution of species from the IFD. In particular, $G(\mathcal{S}', \mathcal{K}') \geq 0$ and $G(\mathcal{S}', \mathcal{K}') = 0$ if and only if the system at hand admits a $\mathcal{S}' - \mathcal{K}'$ joint IFD.

For each species subset in $\Lambda = (\mathcal{S}', \mathcal{K}')$, we let the species reach a terminal stable time-periodic state, then we compute the approximate value of $G(\Lambda)$ by considering the deviation from IFD. The latter is computed using the $M(t)$ and $N(t)$ defined in Subsection 2.2. To show convergence stability, we demonstrate with our numerical example that species subsets while distribution is closest to an IFD, i.e. that generates a smaller value of $G(\Lambda)$, will have a competitive advantage.

With self-limitation

Consider $n = 2$, $m = 2$, $\Omega = (0, 3\pi)$ and $T = 24$. In the case of $f(x,t) > 0$ for all $(x,t) \in [0, 3\pi] \times \mathbb{R}$, take the following parameters:

$$D_u^1(x,t) = (0.4x + 1)\left(1 + 0.5\sin\left(\frac{2\pi t}{T} + 0.5\right)\right),$$

$$D_u^2(x,t) = (0.3x + 0.3)\left(1 + 0.3\sin\left(\frac{2\pi t}{T} + 0.5\right)\right),$$

$$\vec{P}^1(x,t) = (0.7x + 0.3)\left(0.6 + 0.4\sin\left(\frac{2\pi t}{T} + 0.5\right)\right),$$

$$\vec{P}^2(x,t) = 0.3x\left(0.2 + 0.3\sin\left(\frac{2\pi t}{T} + 0.5\right)\right),$$

$$D_v^1(x,t) = (0.8x + 0.6)\left(0.8 + 0.3\sin\left(\frac{2\pi t}{T} + 0.5\right)\right),$$

$$D_v^2(x,t) = (0.7x + 0.7)\left(1 + 0.5\sin\left(\frac{2\pi t}{T} + 0.5\right)\right),$$

$$\vec{Q}^1(x,t) = (0.7x + 0.5)\left(0.3 + 0.1\sin\left(\frac{2\pi t}{T} + 0.5\right)\right),$$

$$\vec{Q}^2(x,t) = (x + 0.7)\left(0.8 + 0.2\sin\left(\frac{2\pi t}{T} + 0.5\right)\right),$$

$$a(x,t) = 8x + 0.4 + 0.1\sin\left(\frac{2\pi t}{T} + 0.5\right),$$

$$b(x,t) = 4x + 0.6 + 0.2\sin\left(\frac{2\pi t}{T} + 0.5\right),$$

$$c(x,t) = 5x + 0.3 + 0.2\sin\left(\frac{2\pi t}{T} + 0.5\right),$$

$$d(x,t) = 2x + 0.25 + 0.1\sin\left(\frac{2\pi t}{T} + 0.5\right),$$

$$e(x,t) = 0.7c(x,t), \quad f(x,t) = 0.6x + 0.2 + 0.15\sin\left(\frac{2\pi t}{T} + 0.5\right).$$

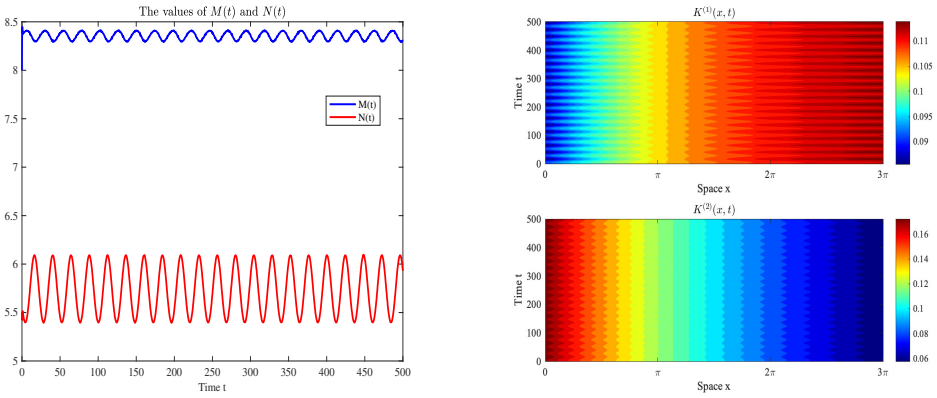

Fig. 1 The graphs of $M(t), N(t)$ and $K^{(1)}(x,t)$, $K^{(2)}(x,t)$.

Under our choice o parameters, system (7) admits a positive solution $(M(t), N(t))$ and the corresponding $K^{(1)}(x,t) > 0$, $K^{(2)}(x,t) > 0$ (Fig. 1). By Theorem 9, system (1) with $n = m = 2$ has an $\mathcal{S}$-$\mathcal{K}$ joint IFD. The values of $G(\Lambda)$ are computed as follows:

$$G((\{1\},\{1\})) \approx 5.718125,\ G((\{1\},\{2\})) \approx 8.380197,\ G((\{2\},\{1\})) \approx 4.645075,$$
$$G((\{2\},\{2\})) \approx 7.208275,\ G((\{1,2\},\{1\})) \approx 4.720949,\ G((\{1,2\},\{2\})) \approx 7.227819,$$
$$G((\{1\},\{1,2\})) \approx 5.717357,\ G((\{2\},\{1,2\})) \approx 4.674425,\ G((\{1,2\},\{1,2\})) \approx 4.744849.$$

Obviously, the function G attains its unique minimum at $(\{2\},\{1\})$. This implies that the species combination of the second prey and the first predator is closest to one IFD, and is more likely to be selected, which is confirmed by Fig. 2.

We perturb the dispersal strategy of the second prey species by modifying its directed movement as

$$\vec{P}^2(x,t) = 0.8x\left(0.3 + 0.2\sin\left(\frac{2\pi t}{T} + 0.5\right)\right). \tag{50}$$

Despite this perturbation, the functional G maintains its unique minimum at $(\{2\},\{1\})$, and numerical simulation also shows the coexistence of the second prey and first predator species (Fig. 3). This demonstrates that dispersal strategies that generate an approximation of IFD confer a competition advantage and it is not easily invaded.

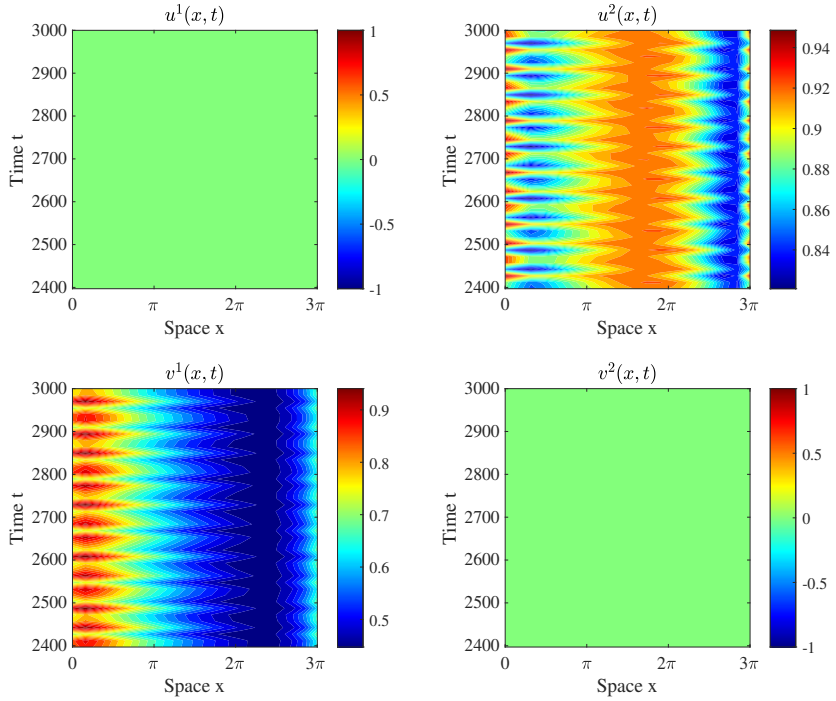

Fig. 2 The solution of (1) with two prey species and two predator species, where parameters are given at the beginning of the section.

Without self-limitation

We now turn to the case of $f(x,t) \equiv 0$ for all $(x,t) \in [0,3\pi] \times \mathbb{R}$. Take the following parameters:

$$
\begin{aligned}
D_u^1(x,t) &= (0.7x+0.4)\left(1+0.5\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
D_u^2(x,t) &= (x+0.7)\left(1+0.8\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
P^1(x,t) &= (0.5x+1)\left(0.3+0.2\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
P^2(x,t) &= (0.7x+1)\left(0.7+0.6\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
D_v^1(x,t) &= (0.5x+0.4)\left(0.8+0.3\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
D_v^2(x,t) &= (0.7x+0.7)\left(1.2+0.5\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
Q^1(x,t) &= (0.3x+0.6)\left(0.5+0.1\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
Q^2(x,t) &= (x+0.9)\left(0.8+0.4\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
a(x,t) &= 8x+0.4+0.1\sin\left(\frac{2\pi t}{T}+0.5\right),\\
b(x,t) &= 5.6x+0.6+0.25\sin\left(\frac{2\pi t}{T}+0.5\right),\\
c(x,t) &= 6x+0.3+0.15\sin\left(\frac{2\pi t}{T}+0.5\right),\\
d(x,t) &= 2x+0.25+0.1\sin\left(\frac{2\pi t}{T}+0.5\right),\\
e(x,t) &= 0.7c(x,t).
\end{aligned}
\tag{51}
$$

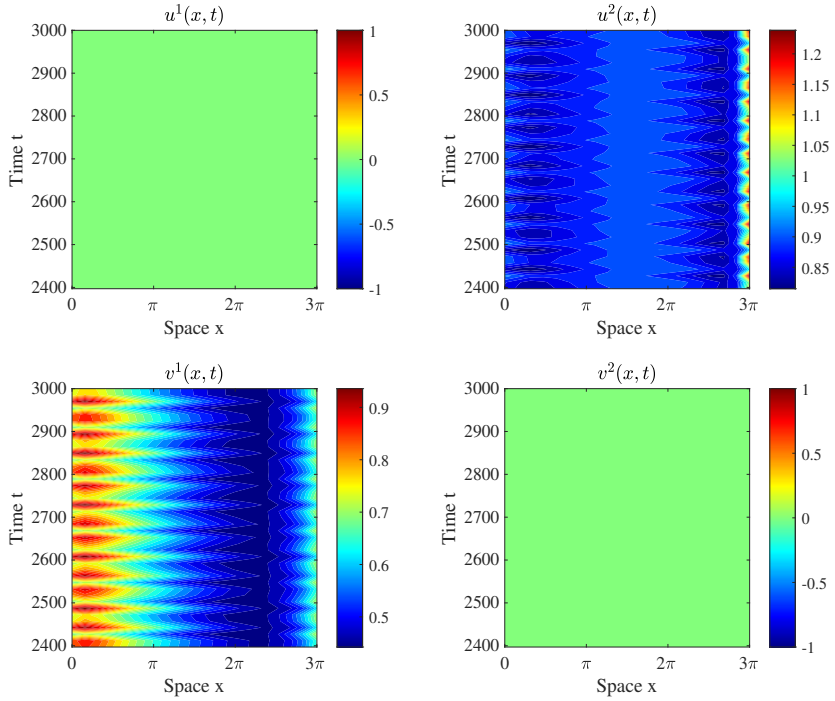

Fig. 3 The solution of (1) with two prey species and two predator species, where parameters are given in the beginning of Section 7 except for $\vec{P}^2(x,t)$.

It can be verified that $M(t) > 0, N(t) > 0, K^{(1)}(x,t) > 0,\ K^{(2)}(x,t) > 0$ through numerical analysis, see Fig. 4. It follows from Theorem 9 that system (1) with $n =$

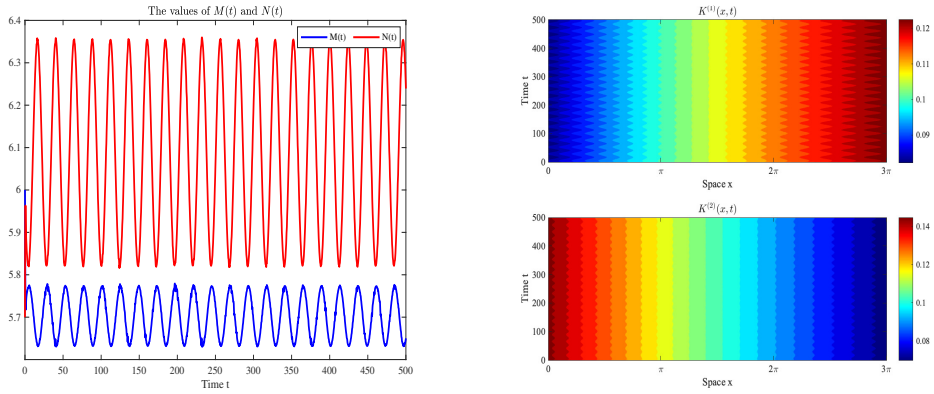

Fig. 4 The graphs of $M(t), N(t)$ and $K^{(1)}(x,t),\ K^{(2)}(x,t)$.

$m = 2$ admits IFD. Further computations yield

$$G(\{\{1\},\{1\}\}) \approx 6.602968,\ G(\{\{1\},\{2\}\}) \approx 7.431340,\ G(\{\{2\},\{1\}\}) \approx 6.924499,$$
$$G(\{\{2\},\{2\}\}) \approx 8.162841,\ G(\{\{1,2\},\{1\}\}) \approx 6.718484,\ G(\{\{1,2\},\{2\}\}) \approx 7.501167,$$
$$G(\{\{1\},\{1,2\}\}) \approx 6.661607,\ G(\{\{2\},\{1,2\}\}) \approx 6.907674,\ G(\{\{1,2\},\{1,2\}\}) \approx 6.669602,$$

and hence $G(\{\{1\},\{1\}\}) = \min_{(\mathcal{S}',\mathcal{K}')\in\Lambda} G((\mathcal{S}',\mathcal{K}')) \approx 6.602968$. Meanwhile, Fig. 5 shows that the first prey and the first predator species prevail in the predation-competition interactions, which is consistent with that the combination with smallest G wins.

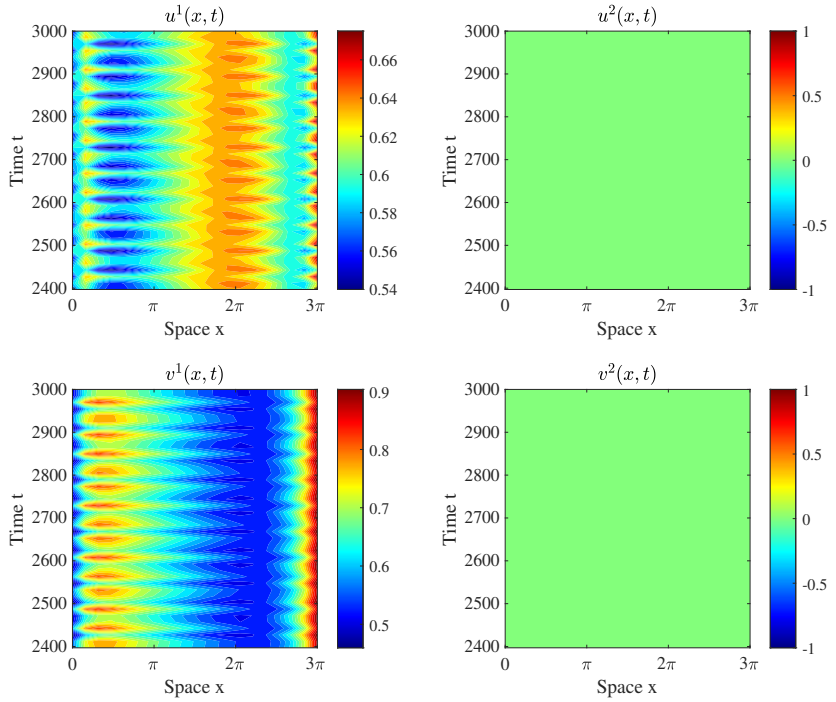

Fig. 5 The solution of (1) with two prey species and two predator species, where parameters are given in (51).

Invasion of non-ideal free dispersal strategies

In what follows, we show that the prey and predator species not jointly forming IFD will be invaded. Take the following parameters for system (45):

$$
\begin{aligned}
D_u^1(x,t) &= (0.6x+0.5)\left(1+0.5\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
\vec{P}^1(x,t) &= (0.7x+0.3)\left(0.6+0.4\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
D_v^1(x,t) &= (x+2)\left(1.5+0.3\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
\vec{Q}^1(x,t) &= (0.8x+0.9)\left(0.8+0.6\sin\left(\frac{2\pi t}{T}+0.5\right)\right),\\
a(x,t) &= 3x+0.3+0.1\sin\left(\frac{2\pi t}{T}+0.5\right),\\
b(x,t) &= 4x+0.6+0.2\sin\left(\frac{2\pi t}{T}+0.5\right),\\
c(x,t) &= 9x+0.3+0.2\sin\left(\frac{2\pi t}{T}+0.5\right),\\
d(x,t) &= 3.3x+0.25+0.1\sin\left(\frac{2\pi t}{T}+0.5\right),\\
e(x,t) &= 0.7c(x,t), \quad f(x,t) = 0.6x+0.2+0.15\sin\left(\frac{2\pi t}{T}+0.5\right).
\end{aligned}
\tag{52}
$$

Then system (45) has a stable positive periodic solution (u^{1*}, v^{1*}) (Fig. 6 (the left two panels)). Since $K^{(2)}(x,t) < 0$ for some $(x,t) \in [0,3\pi] \times [0,500]$ (Fig. 6 (the right two panels)), we see from Theorem 9 that (u^{1*}, v^{1*}) is not an IFD of (45). Introduce a

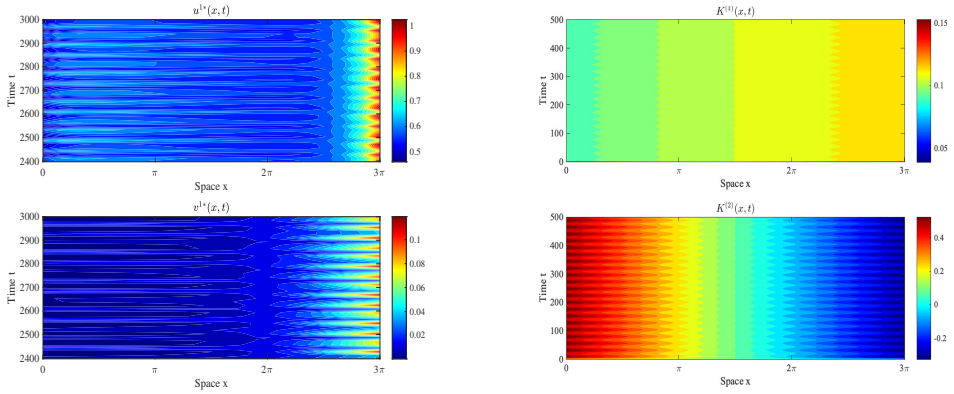

Fig. 6 The graphs of $(u^{1*}(x,t), v^{1*}(x,t))$ and $K^{(1)}(x,t)$, $K^{(2)}(x,t)$.

second prey-predator pair (u^2, v^2) to system (45) with dispersal strategies:

$$\begin{aligned} D_u^2(x,t) &= (0.2x+0.2)\left(1+0.2\sin\left(\frac{2\pi t}{T}+0.5\right)\right), \\ \vec{P}^2(x,t) &= (0.1x+0.2)\left(0.4+0.1\sin\left(\frac{2\pi t}{T}+0.5\right)\right), \\ D_v^2(x,t) &= (0.7x+1)\left(1.4+0.3\sin\left(\frac{2\pi t}{T}+0.5\right)\right), \\ \vec{Q}^2(x,t) &= (0.7x+0.6)\left(0.5+0.4\sin\left(\frac{2\pi t}{T}+0.5\right)\right). \end{aligned} \tag{53}$$

Numerical simulation demonstrates that species (u^2, v^2) drive (u^1, v^1) to extinction (see Fig. 7).

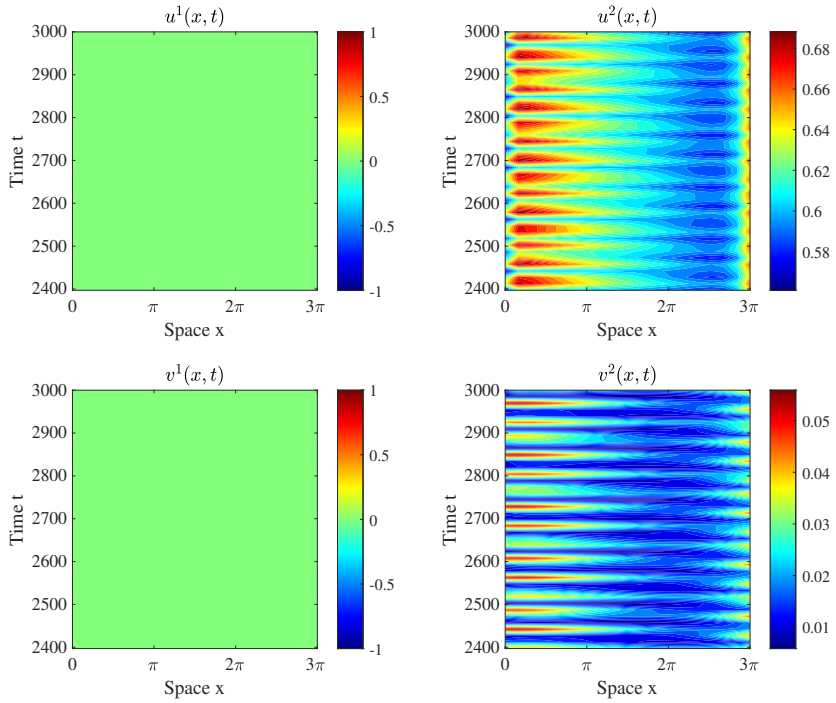

Fig. 7 The solution of (1) with parameters given in (52) and (53).

The minimum value of G also occurs at $(\{2\},\{2\})$, as computed that

$$G((\{1\},\{1\})) \approx 5.857280,\ G((\{1\},\{2\})) \approx 5.612749,\ G((\{2\},\{1\})) \approx 5.136587,$$
$$G((\{2\},\{2\})) \approx 5.030789,\ G((\{1,2\},\{1\})) \approx 5.216290,\ G((\{1,2\},\{2\})) \approx 5.092962,$$
$$G((\{1\},\{1,2\})) \approx 5.636194,\ G((\{2\},\{1,2\})) \approx 5.074812,\ G((\{1,2\},\{1,2\})) \approx 5.165150,$$

Thus, the combination closest to that at which G attains its minimum has competition advantages.

8 Discussion: The concept of IFD in a time-periodic environment

In temporally constant environments, a population is said to achieve an ideal free distribution (IFD) if the fitness (as a function of x only) is equilibrated. The evolutionary stability of IFD for a single population has been established across many modeling contexts, see Cantrell et al. (2017, 2012, 2022); Maciel et al. (2020); Cantrell et al. (2007) and references therein, where it is proved that when a single species population achieves IFD, then mutant phenotypes cannot invade when rare.

When considering a community of ecologically identical species, then the fitness of each resident species depends both on the abiotic environment and the other resident species it is interacting directly or indirectly with, and a community of species is said to achieve IFD if the fitness of every species is equilibrated in space. The evolutionary stability of IFD is proved in Cantrell et al. (2007) in the setting of discrete-patch models, where a community of interacting species achieving IFD is shown to resist invasion by rare mutant phenotypes. Hence, an ecological community forms an evolutionary endpoint if the community as a whole achieves IFD.

In this paper, we establish the evolutionary stability of IFD in the context of a system of reaction-diffusion equations modeling a community of multiple prey and predator species. Our results can be generalized to ecological communities where multiple prey and predator species exhibit distinct intraspecific and interspecific interactions:

8.1 Generalization

Consider the following system

$$\begin{cases} \partial_t U^i = \nabla\cdot[D_u^i\nabla U^i - U^i\vec{P}^i] + U^i\left(a - b\sum_{k=1}^n g_k U^k - c\sum_{k=1}^m h_k V^k\right), & \text{in } \Omega\times(0,\infty),\\ \partial_t V^j = \nabla\cdot[D_v^j\nabla V^j - V^j\vec{Q}^j] + V^j\left(-d + e\sum_{k=1}^n g_k U^k - f\sum_{k=1}^m h_k V^k\right), & \text{in } \Omega\times(0,\infty),\\ [D_u^i\nabla U^i - \vec{P}^i U^i]\cdot\nu = [D_v^j\nabla V^j - \vec{Q}^j V^j]\cdot\nu = 0, & \text{on } \partial\Omega\times(0,\infty), \end{cases} \tag{54}$$

where $D_u^i, D_v^j,\ \vec{P}^i, \vec{Q}^j,\ a,b,c,d,e,f$, satisfy assumption **(A)**, and g_i, h_j are positive constants for all $i = 1,\cdots,n,\ j = 1,\cdots,m$. Actually, set

$$u^i = g_i U^i \quad \text{and} \quad v^j = h_j V^j,$$

then we observe that $(\vec{u}, \vec{v})$ satisfies system (1), so that previous results apply. We may then define the joint IFD for system (54) in a similar fashion (see Definition 2):

Definition 4 Let $\mathcal{S}$ be a nonempty subset of $\{1, \cdots, n\}$ and $\mathcal{K}$ be a nonempty subset of $\{1, \cdots, m\}$. We say that system (54) has a $\mathcal{S}$-$\mathcal{K}$ joint IFD $(\vec{U}^*, \vec{V}^*) = (U^{1*}, \cdots, U^{n*}, V^{1*}, \cdots, V^{m*})$ if $(\vec{U}^*, \vec{V}^*)$ is a T-periodic solution of (54) satisfying

$$U^{i*} > 0 \text{ for } i \in \mathcal{S}, \quad U^{i*} \equiv 0 \text{ for } i \in \mathcal{S}^c, \quad V^{j*} > 0 \text{ for } j \in \mathcal{K}, \quad V^{j*} \equiv 0 \text{ for } j \in \mathcal{K}^c,$$

and

$$a - b\sum_{i=1}^{n} g_i U^{i*} - c\sum_{j=1}^{m} h_j V^{j*} \text{ and } -d + e\sum_{i=1}^{n} g_i U^{i*} - f\sum_{j=1}^{m} h_j V^{j*} \text{ are independent of } x.$$

Species, or groups of species achieving such IFD will have evolutionary stability under assumptions **(Ha')** or **(Hb')**. Indeed, denote

$$(\tilde{M}(t), \tilde{N}(t)) = \left(\int_\Omega \sum_{i=1}^{n} g_i U^{i*}(x,t)dx, \int_\Omega \sum_{j=1}^{m} h_j V^{j*}(x,t)dx \right),$$

and define $\left(K^{(1)}_{\tilde{M}\tilde{N}}, K^{(2)}_{\tilde{M}\tilde{N}}\right)$ as (13). Following analogous arguments to those in Theorem 9, we conclude that

- System (54) admits a $\mathcal{S} - \mathcal{K}$ joint IFD $(\vec{U}^*, \vec{V}^*)$ if and only if system (7) has a positive solution $(\tilde{M}(t), \tilde{N}(t))$ and the corresponding $K^{(1)}_{\tilde{M}\tilde{N}}(x,t)$ and $K^{(2)}_{\tilde{M}\tilde{N}}(x,t)$ are positive. Moreover,

$$\left(\sum_{i=1}^{n} g_i U^{i*}, \sum_{j=1}^{n} h_j V^{j*} \right) = \left(\tilde{M}(t) K^{(1)}_{\tilde{M}\tilde{N}}, \tilde{N}(t) K^{(2)}_{\tilde{M}\tilde{N}} \right).$$

Consider a solution $(\vec{U}(x,t), \vec{V}(x,t))$ of the system (54) with $\{U^i\}_{i\in\mathcal{S}}$ and $\{V^j\}_{j\in\mathcal{K}}$ being componentwise positive. We use the Lyapunov functional

$$W(t) = \rho W_1(t) + W_2(t) + \rho W_3(t) + W_4(t), \tag{55}$$

where $\rho > 0$ is a constant that remains to be specified and

$$W_1 = \int_\Omega \sum_{i\in\mathcal{S}} \left[\frac{g_i U^i}{M} - \frac{g_i U^{i*}}{M} \log\left(\frac{U^i}{U^{i*}}\right) \right] dx, \quad W_3 = \int_\Omega \sum_{i\in\mathcal{S}^c} \frac{g_i U^i}{M} dx,$$
$$W_2 = \int_\Omega \sum_{j\in\mathcal{K}} \left[\frac{h_j V^j}{N} - \frac{h_j V^{j*}}{N} \log\left(\frac{V^j}{V^{j*}}\right) \right] dx, \quad W_4 = \int_\Omega \sum_{j\in\mathcal{K}^c} \frac{h_j V^j}{N} dx.$$

Under the assumption **(Ha')**, choosing $\rho = \rho_1$ in (55), we can prove that the IFD of system (54) is evolutionarily stable, analogous to Theorem 10. When $\rho = \rho_2$ is given

by the assumption **(Hb')**, we can derive a similar result to Theorem 11 for system (54). By virtue of the arguments in Section 6, we can prove Theorem 2 for system (54). Here, we omit the proofs for simplicity.

8.2 Biological implications

Our analysis reveals the following biological insights:

IFD in time-periodic environments

Local ecological conditions are not always temporally constant. For temporally periodic environments, the fitness of a given population is generally a function of x and t, and it is demonstrated that the appropriate notion of IFD is for the fitness to equilibrate in x, but not necessarily in t. Inspired by our previous work in competition systems in the reaction-diffusion-advection model setting (Cantrell et al. 2021) and in patch model setting (Lam and Zhang 2025), we show here that an appropriate notion of IFD is introduced where we require that fitness be equilibrated in space alone, but not necessarily in time (see Definitions 1 and 2). Using this definition as an ansatz, we determine analytically the IFD based on environmental parameters. These conditions depend on the positive solutions of a non-autonomous predator-prey ODE system, which reflects the fact that anticipation, based on nonlocal information, is needed for a population to achieve IFD in an environment that is varying both spatially and temporally. Such nonlocal information can be obtained based on, e.g., a trial-and-error manner or via memory-based dispersal (Shi et al. 2021). For instance, empirical evidence shows that some whales can accurately track the places and times where resources will be most reliably abundant over periods of years, using memory and resource tracking to effectively average out yearly variations (Abrahms et al. 2019). Interestingly, species can still over-match or under-match resources when considering the time-periodic environments. We also discuss the necessary and sufficient conditions for a joint IFD to be feasible (see Theorem 9). It turns out that there exist time-periodic environments in which IFD is impossible no matter what dispersal strategies are adopted. This is due to the presence of "generalized sinks" where the species is too constrained by its birth and death rates and cannot be abundant enough to equilibrate fitness.

IFDs can be evolutionary endpoints for communities

We show that joint IFD consisting of a large number of species can be evolutionarily stable (see Theorems 10 and 11, generalizing previous results to the reaction-diffusion-advection context). This offers a plausible mechanism for the maintenance of food webs in nature, consisting of a large number of interacting species, and a mechanism for the evolution of partial migration (Chapman et al. 2011). However, when two different coalitions of species can form IFD, we cannot determine which subset can dominate. We conjecture that, under more realistic stochastic conditions, the two subcommunities of species form neutral populations, which remain stable while, over

time, individual subcommunities will drift according to random walk within this constraint of global IFD, and the number of such neutral groups will typically decrease over time until one neutral group remains (Chesson and Huntly 1997; Hubbell 2011).

IFDs are neighborhood invader strategies

Going a step beyond the local stability analysis performed in Cantrell et al. (2007), our argument shows the global stability of the joint IFD formed in a community. Namely, if a subset of species can achieve IFD, then the whole community must approach an IFD, even if the initial data is a large perturbation of IFD. Roughly speaking, our results show that a new species can invade a community and establish a viable population if it complements the existing population so that, as a whole, the community, after the inclusion of the new species, can achieve IFD.

Non-IFD is selected against

When the community does not form a joint IFD, it can be invaded by mutant species, provided it employs the appropriate dispersal strategy (see Theorem 2). This shows that IFD is a necessary condition for a community to be evolutionarily stable.

Selection advantage of approximate IFD

Extending and going beyond our analytical results, we also investigated the situation when IFD is not achieved by any subset of a community. For this purpose, we introduced in Section 7 a measure of how "close" a community is to achieving an IFD. Our numerical results show that a new species is more likely to invade and establish a viable population within an existing community if its presence can bring the community closer to achieving IFD. Interpreted in the framework of adaptive dynamics, it follows that by the repeated introduction of mutant phenotypes (either by immigration or by genetic diversification), natural selection tends to shape the community of species towards IFD. In the framework of adaptive dynamics, this suggests that the IFD is convergence stable as well as evolutionarily stable.

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Declarations

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- **Conflict of interest** The authors declare that they have no conflict of interest.

- **Ethical Approval** This declaration is not applicable.
- **Data Availability** All data generated or analyzed during this study is included in this article.

Appendix A The proof of Lemma 7

The proof of Lemma 7 Let A_i and B_{ij}, $i = 1, 2, j = 1, 2$, be defined as (8). We first prove statement (i). Since $a, b, c, d, e, f > 0$ are independent of t, it follows from (8) that A_i and $B_{ij} > 0$ are constants. We then have

$$\begin{aligned} M^* &= \frac{\int_\Omega \frac{af+dc}{bf+ce}dx}{B_{11}B_{22}+B_{12}B_{21}}\left(\int_\Omega \frac{b}{bf+ce}dx\int_\Omega \frac{f}{bf+ce}dx+\int_\Omega \frac{e}{bf+ce}dx\int_\Omega \frac{c}{bf+ce}dx\right),\\ N^* &= \frac{\int_\Omega \frac{ae-bd}{bf+ce}dx}{B_{11}B_{22}+B_{12}B_{21}}\left(\int_\Omega \frac{b}{bf+ce}dx\int_\Omega \frac{f}{bf+ce}dx+\int_\Omega \frac{e}{bf+ce}dx\int_\Omega \frac{c}{bf+ce}dx\right). \end{aligned} \tag{A1}$$

Therefore, M^*, N^* are positive constants provided $\frac{d}{a} < \frac{e}{b}$.

To prove (ii), define $\tilde{A}_i$ and $\tilde{B}_{ij}$ by replacing a, b, c, d, e, f with $\tilde{a}$, $\tilde{b}$, $\tilde{c}$, $\tilde{d}$, $\tilde{e}$, $\tilde{f}$ in A_i and B_{ij}, respectively. Then (7) becomes a fast-slow time-periodic system:

$$\begin{cases} M'(t) = \frac{M(t)}{\tilde{D}(\frac{t}{T})}\left[\tilde{A}_1(\frac{t}{T}) - M(t)\tilde{B}_{11}(\frac{t}{T}) - N(t)\tilde{B}_{12}(\frac{t}{T})\right],\\ N'(t) = \frac{N(t)}{\tilde{D}(\frac{t}{T})}\left[\tilde{A}_2(\frac{t}{T}) + M(t)\tilde{B}_{21}(\frac{t}{T}) - N(t)\tilde{B}_{22}(\frac{t}{T})\right]. \end{cases} \tag{A2}$$

Set $s = \frac{t}{T}$, $M(t) = M(sT) = \tilde{M}(s)$ and $N(t) = N(sT) = \tilde{M}(s)$. This yields

$$\begin{cases} \frac{d\tilde{M}(s)}{ds} = T\frac{\tilde{M}(s)}{\tilde{D}(s)}\left[\tilde{A}_1(s) - \tilde{M}(s)\tilde{B}_{11}(s) - \tilde{N}(s)\tilde{B}_{12}(s)\right],\\ \frac{d\tilde{N}(s)}{ds} = T\frac{\tilde{N}(s)}{\tilde{D}(s)}\left[\tilde{A}_2(s) + \tilde{M}(s)\tilde{B}_{21}(s) - \tilde{N}(s)\tilde{B}_{22}(s)\right]. \end{cases} \tag{A3}$$

Let

$$\tilde{M}(s) = \tilde{M}^*(s) + \frac{1}{T}\tilde{M}_1(s) + O(\frac{1}{T^2}), \quad \tilde{N}(s) = \tilde{N}^*(s) + \frac{1}{T}\tilde{N}_1(s) + O(\frac{1}{T^2}),$$

where $\tilde{M}_1(s)$ and $\tilde{N}_1(s)$ solve (A5). Substituting this into (A3) and comparing coefficients of like powers of $\frac{1}{T}$, we obtain

$$\begin{cases} 0 = \frac{\tilde{M}^*(s)}{\tilde{D}(s)}\left[\tilde{A}_1(s) - \tilde{M}^*(s)\tilde{B}_{11}(s) - \tilde{N}^*(s)\tilde{B}_{12}(s)\right],\\ 0 = \frac{\tilde{N}^*(s)}{\tilde{D}(s)}\left[\tilde{A}_2(s) + \tilde{M}^*(s)\tilde{B}_{21}(s) - \tilde{N}^*(s)\tilde{B}_{22}(s)\right], \end{cases} \tag{A4}$$

and

$$\begin{cases} \frac{d\tilde{M}^*(s)}{ds} = \frac{\tilde{M}^*(s)}{\tilde{D}(s)}\left[-\tilde{M}_1(s)\tilde{B}_{11}(s) - \tilde{N}_1(s)\tilde{B}_{12}(s)\right],\\ \frac{d\tilde{N}^*(s)}{ds} = \frac{\tilde{N}^*(s)}{\tilde{D}(s)}\left[\tilde{M}_1(s)\tilde{B}_{21}(s) - \tilde{N}_1(s)\tilde{B}_{22}(s)\right]. \end{cases} \tag{A5}$$

Clearly, if $\frac{\tilde{d}}{\tilde{a}} < \frac{\tilde{e}}{\tilde{b}}$, then (A4) has a unique 1-periodic solution $(\tilde{M}^*(s), \tilde{N}^*(s))$ given by (A1) with B_{ij} and a, b, c, d, e, f replaced by $\tilde{B}_{ij}$ and $\tilde{a}, \tilde{b}, \tilde{c}, \tilde{d}, \tilde{e}, \tilde{f}$, respectively. From (A5), $\tilde{M}_1(s)$ and $\tilde{N}_1(s)$ are uniformly bounded in s. Hence $\tilde{M}(s) \to \tilde{M}^*(s)$ and $\tilde{N}(s) \to \tilde{N}^*(s)$ as $T \to \infty$. Consequently, (7) has a positive T-periodic solution $(M(t), N(t))$ as $T \gg 1$.

In the case of (iii), $(M(t), N(t))$ satisfies

$$\begin{cases} M'(t) = M(t)\left[\int_\Omega a(x,t)dx - b(t)M(t) - c(t)N(t)\right],\\ N'(t) = N(t)\left[-\int_\Omega d(x,t)dx + e(t)M(t) - f(t)N(t)\right], \end{cases} \tag{A6}$$

It suffices to prove that condition

$$\frac{\int_0^T \int_\Omega d(x,t)dxdt}{\int_0^T \int_\Omega a(x,t)dxdt} < \min_{t\in[0,T]} \frac{e(t)}{b(t)} \tag{A7}$$

implies $-\int_0^T \int_\Omega d(x,t)dxdt + \int_0^T ew(t)dt > 0$, where $w(t)$ is the unique positive T-periodic solution to $w'(t) = w(t)\left[\int_\Omega a(x,t)dx - b(t)w(t)\right]$. If this holds, the existence of a positive T-periodic solution $(M(t), N(t))$ follows directly from Corollary 3 (Ding et al. 1995).

Observe that $\int_0^T \int_\Omega a(x,t)dxdt = \int_0^T b(t)w(t)dt$. Then (A7) implies that

$$\begin{aligned}\int_0^T \int_\Omega d(x,t)dxdt &< \min_{[0,T]} \frac{e(t)}{b(t)} \int_0^T \int_\Omega a(x,t)dxdt \\ &= \min_{[0,T]} \frac{e(t)}{b(t)} \int_0^T b(t)w(t)dt \le \int_0^T \frac{e(t)}{b(t)} b(t)w(t)dt \\ &= \int_0^T e(t)w(t)dt.\end{aligned}$$

This completes the proof. □

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