Ideal free distribution of multiple species in a time-periodic and patchy habitat *

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Abstract

Dispersal strategies that lead to the ideal free distribution (IFD) were shown to be evolutionarily stable in various ecological models. In this paper, we investigate this phenomenon in time-periodic environments where N species — identical except for dispersal strategies — compete. We extend the notions of IFD and joint IFD, previously established in spatially continuous models, to time-periodic and spatially discrete models and derive sufficient and necessary conditions for IFD to be feasible. Under these conditions, we demonstrate two competitive advantages of ideal free dispersal: if there exists a subset of species that can achieve a joint IFD, then for large time, the persisting collection of species must converge to an IFD for large time; if a unique subset of species achieves a joint IFD, then that group will dominate and competitively exclude all the other species. Furthermore, we show that ideal free dispersal strategies are the only evolutionarily stable strategies. Our results generalize previous work by construction of Lyapunov functions in multi-species, time-periodic setting.

Keywords: ideal free distribution; evolutionarily stable; time-periodic patch model; multiple-species model

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1 Introduction

The ideal free distribution (IFD) predicts how organisms distribute themselves in heterogeneous environments to optimize individual fitness [17]. It is based on two key

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assumptions: individuals possess complete knowledge of habitat quality, and they are free to move. The concept of IFD originated from observations of territorial patterns in birds [45] and has been central to understanding the evolution of dispersal [26].

An IFD is achieved when every individual has the same fitness across the habitat; otherwise, some individuals could improve their fitness by adopting a different dispersal strategy. In spatially heterogeneous but temporally constant environments, a species achieves IFD when its distribution of individuals perfectly matches resource availability, ensuring fitness to equilibrate throughout the habitat [4, 37]. In such a context, it is demonstrated across various modeling frameworks that dispersal strategies leading to IFD are evolutionarily stable strategies (ESS), see [6] for reaction-diffusion-advection models, [25] for patch models, [8, 13] for nonlocal diffusion models, and [9] for integrodifference models. These studies further demonstrated that dispersal strategies that can produce IFD qualify as ESS in temporally constant environments. The concept of ESS is central in evolutionary biology [15, 43], and has strong implications in the study of biological invasion, habitat selection and population distribution. However, ESS depends on the class of admissible strategies and does not always lead to IFD [10, 19, 27, 30, 34, 39].

Most natural environments exhibit diurnal or seasonal variations. Incorporating time-periodicity in the modeling, however, often leads to considerable mathematical difficulties. For instance, the characterization of IFD is no longer a static location selection as in temporally static environments, since the locations that maximize individual fitness may change over time. Temporal periodicity significantly alters the evolutionary dynamics of dispersal. It is for instance a driver of the diel migration in copepods [44]. It is demonstrated in [2, 22] that for reaction–diffusion models of two competing species with strictly unconditional dispersal, if the environment is time-periodic, then either fast or slow diffusion rate can be selected, or they could coexist. This stands in contrast with the seminal work of [1, 16, 20] establishing the selection of only slow diffusion rate in static environments. It is natural to ask the following questions: (1) How do we define IFD in time-periodic environments? (2) Are ideal free dispersal strategies ESS in time-periodic environments? These questions were addressed by Cantrell et al. [3, 5] by introducing a notion of generalized IFD via pathwise fitness of a typical individual within a population in the context of time-periodic reaction-diffusion-advection models. But [3, 5], as with most previous work, apply only in the restrictive context of two competing species due to the reliance on monotone dynamical system theory. For three or more competing species, most existing studies focus on the permanence or the existence of equilibrium solutions, and there is a gap in the understanding of long-term dynamical and evolutionary aspects [7, 14, 29, 36].

We will study the evolutionary stability of IFD for multiple competing species in adaptive dynamics framework. The motivation lies in the fact that multiple species can achieve IFD even though each individual single species cannot do so, forming the so-called joint IFD [18]. The evolutionary stability of such situations is interesting and cannot be captured by models of two competing species. For competition systems of multiple species in temporally constant environments, the joint IFD was defined to describe a combination of distribution for multiple species that exactly matched the resource [4, 7, 36]. In that case, dispersal strategies leading to IFD were proven to be ESS in the sense that when only one species had an IFD, the species won the competition; when two out of three species formed a unique joint IFD, the particular combination of species competitively excluded the third species. See also the recent work by Cantrell and Cosner. We will extend these results to multiple competing species in time-periodic, patchy environments with an appropriate generalized notion of IFD [5].

Patch models have been widely used to understand the mechanisms for the evolution of dispersal. For example, Chen et al. [11] gave a comprehensive classification of global dynamics between two weakly competing species based on inter-specific competition and the specific dispersal rates. Jiang et al. proposed a class of three-patch models and investigated the effect of different river network topologies [23, 24]. Extending this framework, the evolutionary impacts of drift, spatial heterogeneity, and inflow/outflow rates on competitive interactions of riverine species were studied in [10, 12, 32, 33]. Particularly, very fast dispersal strategy emerged as the unique ESS under suitable conditions [33]. In spatially and temporally varying environments, Schreiber and Li [42] derived invasion criteria for multiple dispersal phenotypes through eigenvalue analysis of nonnegative matrices, where the dispersal resulting in a balanced patch was selected. In a more recent work, it is demonstrated that IFD can arise in a partially migrating population [40].

In this paper, we will explore the competition dynamics between *coalition of IFD species* and other non-IFD species, and consider the adaptive dynamics and particularly the existence of ESS in the class of dispersal strategies that vary periodically in time, a class which is larger than static dispersal strategies that are frequently studied in the aforementioned literature. To mathematically characterize the long-term dynamics of positive solutions when one or multiple species adopt ideal free dispersal strategies, we will construct Lyapunov functions based on the generalized relative entropy inequality (see [38] or [28, Ch. 4]). While the generalized relative entropy inequality has extensive applications in measuring the convergence of solutions to steady states/periodic solutions for linear models, we will employ this method for nonlinear time-periodic model with multiple competing species. Although we state and prove our results for patch models, note that our arguments may also be applied to extend the results in [5] (for reaction-diffusion models) to N-species case with $N \geq 3$.

Specifically, we consider the following competition model

$$\begin{cases} \dfrac{du_i^k}{dt} = \displaystyle\sum_{j\in\Omega} \ell_{ij}^k(t) u_j^k + u_i^k \tilde{F}_i\left(t,\ \sum_{h=1}^{N} u_i^h\right), & i \in \Omega, k = 1, \cdots, N,\ t > 0, \\ u_i^k(0) = u_{i0}^k, & i \in \Omega, k = 1, \cdots, N. \end{cases} \tag{1.1}$$

Here, $\Omega = \{1, \cdots, n\}$, $n \geq 2$, is the total number of patches. The function $u_i^k(t)$ denotes the population density of species k in patch i. There are a total of N species, which are identical except possibly for their dispersal strategies as specified by the rate of movement $\ell_{ij}^k(t)$ of species k from patch j to patch i. We assume throughout this paper that, for each $1 \leq k \leq N$, the dispersal matrix $L^k(t) = (\ell_{ij}^k(t))$ satisfies

(C) $L^k \in C(\mathbb{R}; \mathbb{R}^{n\times n})$, $\ell_{ij}^k(t) \geq 0$ for $i \neq j$, and $\ell_{ii}^k(t) = -\sum_{j\in\Omega, j\neq i} \ell_{ij}^k(t)$ for $t \in [0, T]$. Moreover, L^k is T-periodic in t and irreducible for some t.

We further assume, for simplicity, that the fitness function is given by

$$\tilde{F}_i(t, s) = r_i(t)\left(1 - \frac{s}{K_i(t)}\right) \quad \text{for some positive and } T\text{-periodic functions } r_i(t) \text{ and } K_i(t),$$

where $r_i(t)$ is the local intrinsic growth rate of patch i, and $K_i(t)$ is the carrying capacity of patch i.

Remark 1.1. *The results of this paper can be extended to any* $\tilde{F}_i(t, s)$ *which is differentiable and such that* $s \mapsto \tilde{F}_i(t, s)$ *is a diffeomorphism of* $\mathbb{R}$ *and* $\frac{\partial}{\partial s}\tilde{F}_i(t, s) < 0$. *In such cases, our proofs can be repeated with the choice of* T*-periodic functions* $M(t)$ *and* $u_i^*(t)$ *such that*

$$\sum_{i\in\Omega} u_i^*(t) = M(t) \quad \textit{and} \quad \frac{M'(t)}{M(t)} = \tilde{F}_i(t, u_i^*(t)) \quad \textit{for all } i \in \Omega,\ t \in \mathbb{R}.$$

Unlike the temporally constant case, there exists periodic environments in which it is impossible for any dispersing population to perfectly match the environment, see [35] for some discussions in two patch environment. It is therefore necessary to clarify the meaning of IFD in time-periodic environments from first principles. To derive the notion of IFD for model (1.1), we start by considering the following single population model:

$$\begin{cases} \dfrac{du_i}{dt} = \displaystyle\sum_{j\in\Omega} \ell_{ij}(t) u_j + r_i(t) u_i \left(1 - \frac{u_i}{K_i(t)}\right), & i \in \Omega,\ t > 0, \\ u_i(0) = u_{i0}, & i \in \Omega. \end{cases} \tag{1.2}$$

It is well known that for given T-periodic coefficients such that $L = (\ell_{ij}(t))$ is irreducible and $\ell_{ij}(t) \geq 0$ for $i \neq j$, and that $r_i(t), K_i(t) > 0$, model (1.2) has a unique positive T-periodic solution $\boldsymbol{u}^*(t)$ (which depends on the choice of dispersal strategy L) (e.g., see [21, Theorem 28.1]). Suppose the population is at a steady state $\boldsymbol{u}(t) = \{u_i(t)\}_{i\in\Omega}$, then the fitness function of an individual (at patch i at time t) is given by the per-capita growth rate $F_i(t) = r_i(t)\left(1 - \frac{u_i(t)}{K_i(t)}\right)$. Hence, we infer that the individual traveling along $I(t) : [0, T] \to \Omega$ receives the fitness given by the quantity (see discussion in [5, Sect. 2])

$$I(t) \mapsto \int_0^T r_{I(t)}(t)\left(1 - \frac{u_{I(t)}(t)}{K_{I(t)}(t)}\right) dt. \tag{1.3}$$

Now, if the population is at an IFD, then we expect that individuals cannot improve their fitness by choosing a different path over the time period $[0, T]$. Therefore, the above quantity (1.3) ought to be independent of the choice of path $I(t)$. This leads to the following definition of IFD.

Definition 1.2. (i) *For a positive, T-periodic distribution $\boldsymbol{u}^*(t) = \{u_i^*(t)\}_{i\in\Omega}$, we say that $\boldsymbol{u}^*(t)$ is an IFD if*

$$r_i(t)\left(1 - \frac{u_i^*(t)}{K_i(t)}\right) = r_j(t)\left(1 - \frac{u_j^*(t)}{K_j(t)}\right) \quad \text{for any} \;\; i, j \in \Omega,\;\; t \in \mathbb{R}. \tag{1.4}$$

(ii) *We say that $L(t) = (\ell_{ij}(t))$ is an ideal free dispersal strategy if the corresponding unique positive, T-periodic solution of model* (1.2) *is an IFD.*

When multiple species are present, indexed by k, their combined distribution may form an IFD even though each species individually cannot not achieve an IFD (see [18, 36]). Thus, we introduce the concept of a joint IFD which will be central to understanding the evolutionary dynamics.

Definition 1.3. *Let $\mathcal{K}$ be a nonempty subset of $\{1, \cdots, N\}$. We say that the competition model* (1.1) *has a $\mathcal{K}$-joint IFD $\boldsymbol{u}^*(t) = (\boldsymbol{u}^{1*}(t), \cdots, \boldsymbol{u}^{N*}(t)) \in [C^1(\mathbb{R}; \mathbb{R}^n)]^N$ if $\boldsymbol{u}^*(t)$ is a positive T-periodic solution of* (1.1) *such that*

$$\boldsymbol{u}^{k*}(t) > \mathbf{0} \;\; \text{for } k \in \mathcal{K} \quad \text{and} \quad \boldsymbol{u}^{k*}(t) \equiv \mathbf{0} \;\; \text{for } k \notin \mathcal{K}, \quad t \in \mathbb{R},$$

and

$$r_i(t)\left(1 - \frac{\sum_{k=1}^N u_i^{k*}(t)}{K_i(t)}\right) = r_j(t)\left(1 - \frac{\sum_{k=1}^N u_j^{k*}(t)}{K_j(t)}\right) \quad \text{for any } i, j \in \Omega,\;\; t \in \mathbb{R}.$$

Remark 1.4. *Throughout this paper, we use the indices $i, j \in \Omega$ to denote spatial locations, the indices k, h, l to distinguish between species, and boldface symbols to denote vector of population distribution indexed by $i \in \Omega$.*

This paper has three main objectives:

- (Subsect. 2.1) To derive a necessary and sufficient condition in environmental functions $\boldsymbol{r}(t)$ and $\boldsymbol{K}(t)$ for IFD to be feasible, see Corollary 2.6.
- (Subsect. 2.2) To prove that IFD is evolutionarily stable in the sense that if model (1.1) has a $\mathcal{K}$-joint IFD, then the spatial distribution of the total population converges to IFD distribution as $t \to \infty$, i.e. the spatial distribution

$$\boldsymbol{U}(t) := \lim_{m\to\infty} \sum_{k=1}^N \boldsymbol{u}^k(t + mT) \tag{1.5}$$

qualifies as an IFD. If, in addition, there exists a unique nonempty $\mathcal{K}'$ achieving a joint IFD, then the species in $\mathcal{K}'$ competitively excludes all the other species, i.e. (1.5) holds and

$$\lim_{m\to\infty} \boldsymbol{u}^k(t+mT) \to \mathbf{0} \quad \text{for all } k \notin \mathcal{K}',$$

see Theorem 2.8. This generalizes the main results established in [5] where the case $N = 2$ and $|\mathcal{K}'| = 1$ was treated for a reaction-diffusion-advection system.

- (Subsect. 2.3) To prove that only the ideal free dispersal strategy can be ESS in the sense that if N-1 competing species are coexisting at steady state but they are not in IFD, then such a steady state can be destabilized by an exotic species with a suitable dispersal strategy, see Theorem 2.11.

In this way, we generalize previous results concerning the generalized IFD for time-periodic environments [5] to the context of a patch model. In addition, the evolutionary stability of joint IFD in a competition system with *arbitrary number of species* is established here, thanks to a novel construction of Lyapunov function for time-periodic systems. To our knowledge, evolutionary stability and global dynamical attractivity of joint IFD was only treated in the case of three species for an autonomous reaction-diffusion system in [36].

2 Statements of Main results

2.1 Characterization of IFD

Let $\boldsymbol{r}(t)$ and $\boldsymbol{K}(t)$ be given. We define the quantities $M(t)$ and $\tilde{\boldsymbol{K}}(t) = \{\tilde{K}_i(t)\}_{i\in\Omega}$ by

$$M(t) = \left[e^{-\int_0^t a(s)ds} \frac{\int_0^T b(s) e^{-\int_s^T a(\tau)d\tau} ds}{1 - e^{-\int_0^T a(s)ds}} + \int_0^t b(s) e^{-\int_s^t a(\tau)d\tau} ds \right]^{-1}, \tag{2.1}$$

and

$$\tilde{K}_i(t) = \frac{K_i(t)}{r_i(t)M(t)} \left(r_i(t) - \frac{M'(t)}{M(t)} \right) \quad \text{for } \ i \in \Omega. \tag{2.2}$$

Here we set

$$a(t) = \frac{\sum_{i\in\Omega} K_i(t)}{\sum_{i\in\Omega}(K_i(t)/r_i(t))}, \quad b(t) = \frac{1}{\sum_{i\in\Omega}(K_i(t)/r_i(t))}.$$

Remark 2.1. *One can verify that $M(t)$ is the unique positive, periodic solution of*

$$\frac{M'(t)}{M^2(t)} = \frac{a(t)}{M(t)} - b(t), \tag{2.3}$$

since $z(t) = 1/M(t)$ satisfies $z' + a(t)z = b(t)$, which has a unique positive and T-periodic solution. Indeed, $M(t)$ is T-periodic in t since

$$M(0) = M(T) = \left[\frac{\int_0^T b(s) e^{-\int_s^T a(\tau)d\tau} ds}{1 - e^{-\int_0^T a(s)ds}} \right]^{-1}.$$

see [5, Lemma 3.1] *for more details. As a consequence, the functions* $\{\tilde{K}_i(t)\}_{i\in\Omega}$ *satisfy*

$$\sum_{i\in\Omega} \tilde{K}_i(t) \equiv 1 \quad \textit{for all } t. \tag{2.4}$$

Next, consider model (1.1) and recall that $L^k(t) = (\ell^k_{ij}(t))$ is the dispersal matrix of the k-th species.

Lemma 2.2. *For each* $k \in \{1, \cdots, N\}$*, there exists a unique positive and* T*-periodic solution* $\boldsymbol{\phi}^k(t) = \{\phi^k_i(t)\}_{i\in\Omega}$ *to the linear problem*

$$\frac{d}{dt}\boldsymbol{\phi}^k(t) = L^k(t)\boldsymbol{\phi}^k(t) \quad \textit{and} \quad \sum_{i\in\Omega} \phi^k_i(0) \equiv 1. \tag{2.5}$$

In addition, $\phi^k_i(t) > 0$ *for all* i, t *and* $\sum_{i\in\Omega} \phi^k_i(t) \equiv 1$ *for all* t*.*

Proof of Lemma 2.2. Thanks to the cooperativity and irreducibility of $L^k(t)$, we can argue as in [28, Theorem 2.1.1] via the Krein-Rutman theorem [28] to assert that there exists $\lambda_0 \in \mathbb{R}$ and a unique positive T-periodic solution $\boldsymbol{\phi}(t) = \{\phi_i(t)\}_{i\in\Omega}$ such that $\sum_{i\in\Omega} \phi_i(0) = 1$ and

$$\frac{d}{dt}\phi_i(t) = \sum_{j\in\Omega} \ell^k_{ij}(t)\phi_i(t) + \lambda_0\phi_i(t) \quad \text{for each } i \in \Omega. \tag{2.6}$$

Using $\ell^k_{ii}(t) = -\sum_{j\in\Omega,\ j\neq i} \ell^k_{ij}(t)$, we take the summation over i in (2.6) to get

$$\frac{d}{dt}\sum_{i\in\Omega} \phi_i(t) = \lambda_0 \sum_{i\in\Omega} \phi_i(t). \tag{2.7}$$

Since $\boldsymbol{\phi}(t)$ is T-periodic, we integrate (2.7) in t over $[0, T]$ to deduce that $\lambda_0 = 0$. Substitute into (2.7), it follows that $\sum_{i\in\Omega} \phi_i(t) \equiv \sum_{i\in\Omega} \phi_i(0) = 1$ for all t. □

By the definition of $M(t)$ and $\tilde{\boldsymbol{K}}(t)$, and Lemma 2.2, we give some equivalent statements of joint IFD in the following theorem.

Theorem 2.3. *Let* $\boldsymbol{r}(t)$ *and* $\boldsymbol{K}(t)$ *be given, and let* $M(t)$ *and* $\tilde{\boldsymbol{K}}(t)$ *be defined as in* (2.1) *and* (2.2)*, respectively. The following statements are equivalent.*

(i) *There exists a nonempty subset* $\mathcal{K}$ *of* $\{1, \cdots, N\}$ *such that model* (1.1) *has* $\mathcal{K}$*-joint IFD denoted by* $\{\boldsymbol{u}^{k*}(t)\}_{k=1}^N$*.*

(ii) *Model* (1.1) *has a nonnegative,* T*-periodic solution* $\{\boldsymbol{u}^{k*}(t)\}_{k=1}^N$ *such that*

$$\sum_{k=1}^N \boldsymbol{u}^{k*}(t) = M(t)\tilde{\boldsymbol{K}}(t).$$

(iii) *There exist nonnegative constants* $\{c_k\}_{k=1}^N$ *such that* $\sum_{k=1}^N c_k = 1$ *and*

$$\sum_{k=1}^N c_k \boldsymbol{\phi}^k(t) = \tilde{\boldsymbol{K}}(t) \quad \textit{i.e.} \ \sum_{k=1}^N c_k \phi_i^k(t) = \tilde{K}_i(t) \ \ \textit{for all } i \in \Omega, \tag{2.8}$$

where for each k, $\boldsymbol{\phi}^k(t) = \{\phi_i^k(t)\}_{i\in\Omega}$ *is given in Lemma 2.2.*

Proof. (i) ⇒ (ii): Let $\{\boldsymbol{u}^{k*}(t)\}_{k=1}^N$ be a $\mathcal{K}$-joint IFD with some ideal free dispersal strategy $L^{k*}(t)$. Now, by Definition 1.3, there is a scalar function $F(t)$ such that

$$F(t) = r_i(t)\left(1 - \frac{\sum_{k=1}^N u_i^{k*}(t)}{K_i(t)}\right) \quad \text{is independent of } i \in \Omega, \tag{2.9}$$

i.e.

$$\frac{d\boldsymbol{u}^{k*}(t)}{dt} = L^{k*}(t)\boldsymbol{u}^{k*}(t) + F(t)\boldsymbol{u}^{k*}(t) \quad \text{for each } 1 \le k \le N. \tag{2.10}$$

Taking summation in k and i, it follows that the total population $w(t) = \sum_{k=1}^N \sum_{i\in\Omega} u_i^{k*}(t)$ satisfies $w'(t) = F(t)w(t)$ and hence

$$\frac{w'(t)}{w(t)} = r_i(t) - \frac{r_i(t)}{K_i(t)} \sum_{k=1}^N u_i^{k*}(t) \quad \text{for all } i \in \Omega. \tag{2.11}$$

Upon dividing (2.11) by $r_i(t)/K_i(t)$, taking summation in i, we deduce that

$$\frac{1}{b(t)}\frac{w'(t)}{w(t)} = \frac{a(t)}{b(t)} - w(t),$$

where $a(t)$ and $b(t)$ are the same as those in (2.1), which implies that $w(t)$ is a positive T-periodic solution of (2.3). By uniqueness (see Remark 2.1), it follows that $w(t) = M(t)$. Hence, (2.2) and (2.11) imply (ii). In particular, $\tilde{\boldsymbol{K}}(t) > \boldsymbol{0}$.

(ii) ⇒ (iii): By $\sum_{k=1}^N \boldsymbol{u}^{k*}(t) = M(t)\tilde{\boldsymbol{K}}(t)$ and (2.2), we derive that

$$r_i(t)\left(1 - \frac{\sum_{k=1}^N u_i^{k*}(t)}{K_i(t)}\right) = r_i(t)\left(1 - \frac{M(t)\tilde{K}_i(t)}{K_i(t)}\right) = \frac{M'(t)}{M(t)} \quad \text{for all } i \in \Omega. \tag{2.12}$$

It follows that (2.10) holds with $F(t) = M'(t)/M(t)$. Then, for each k, $\boldsymbol{u}^{k*}(t)/M(t)$ is a T-periodic solution of (2.5) and hence for each $1 \le k \le N$,

$$\boldsymbol{u}^{k*}(t)/M(t) = c_k \boldsymbol{\phi}^k(t) \quad \text{for some constant } c_k \ge 0,$$

where we used Lemma 2.2. Thus,

$$\sum_{k=1}^N c_k \boldsymbol{\phi}^k(t) = \frac{1}{M(t)} \sum_{k=1}^N \boldsymbol{u}^{k*}(t) = \tilde{\boldsymbol{K}}(t).$$

Summing over $i \in \Omega$, we have

$$\sum_{k=1}^N c_k = \sum_{i\in\Omega}\sum_{k=1}^N c_k \phi_i^k(t) = \sum_{i\in\Omega} \tilde{K}_i(t) = 1.$$

This proves the implication "(ii) $\Rightarrow$ (iii)".

(iii) $\Rightarrow$ (i): Define $\boldsymbol{u}^{k*}(t)=c_kM(t)\boldsymbol{\phi}^k(t)$, then $\boldsymbol{u}^{k*}(t)$ is T-periodic. Due to $\sum_{k=1}^N c_k=1$, there exists $\mathcal{K}\subset\{1,\cdots,N\}$ such that $c_k>0$ for $k\in\mathcal{K}$ and $c_k=0$ for $k\notin\mathcal{K}$. This, together with $M(t)>0$ and $\boldsymbol{\phi}^k(t)>\mathbf{0}$, shows that $\boldsymbol{u}^{k*}(t)>\mathbf{0}$ for $k\in\mathcal{K}$ and $\boldsymbol{u}^{k*}(t)\equiv\mathbf{0}$ for $k\notin\mathcal{K}$. Now, we compute via the definition of $\phi_i^k(t)$ to deduce

$$\frac{d\boldsymbol{u}^{k*}(t)}{dt}=L^{k*}(t)\boldsymbol{u}^{k*}(t)+\frac{M'(t)}{M(t)}\boldsymbol{u}^{k*}(t)\quad\text{for each } 1\le k\le N.$$

By $\sum_{k=1}^N c_k\phi_i^k(t)=\tilde{K}_i(t)$ and the definition of $\tilde{K}_i(t)$, we have

$$r_i(t)\left(1-\frac{\sum_{k=1}^N u_i^{k*}(t)}{K_i(t)}\right)=r_i(t)\left(1-\frac{M(t)\sum_{k=1}^N c_k\phi_i^k(t)}{K_i(t)}\right)=\frac{M'(t)}{M(t)}\quad\text{for any } i\in\Omega.$$

Hence, the above expression is independent of i and $\boldsymbol{u}^{k*}(t)$ is a T-periodic solution of (1.1). This proves (i). □

The next result gives a sufficient condition for the existence of a single species IFD, provided the dispersal strategy is suitably chosen.

Proposition 2.4. *If $\tilde{\boldsymbol{K}}(t)>\mathbf{0}$ for all t, which is equivalent (thanks to (2.2)) to*

$$\inf_{i\in\Omega} r_i(t)>\frac{M'(t)}{M(t)}\quad\textit{for all } t,\tag{2.13}$$

then there exists at least one dispersal strategy $L^*(t)$ given by (2.14) such that the single species model (1.2) admits an IFD.

Remark 2.5. *Note that (2.13) is a condition that depends only on the given environmental parameters Ω, $\boldsymbol{r}(t)$ and $\boldsymbol{K}(t)$.*

Proof of Proposition 2.4. Let $\tilde{\boldsymbol{K}}(t)>\mathbf{0}$ be defined by (2.2). It suffices to construct $L^*(t)$ such that $\boldsymbol{u}^*(t)=M(t)\tilde{\boldsymbol{K}}(t)$ is the corresponding positive T-periodic solution of the single species system. Note that there are multiple such choices of $L^*(t)$, and we choose the simplest one involving a bi-diagonal matrix.

Define $\{q_j(t)\}_{j=2}^n$ by

$$\begin{aligned}q_2(t)&=M_0\frac{\tilde{K}_1}{\tilde{K}_2}+\frac{d\tilde{K}_1(t)}{dt}\cdot\frac{1}{\tilde{K}_2},\\ q_{j+1}(t)&=q_j(t)\frac{\tilde{K}_j}{\tilde{K}_{j+1}}+\frac{d\tilde{K}_j(t)}{dt}\cdot\frac{1}{\tilde{K}_{j+1}}\qquad\text{for } j=2,\cdots,n-1.\end{aligned}$$

Then choose the constant $M_0\gg1$ to ensure that $\{q_j(t)\}_{j=2}^n$ are positive functions.

Next, define the dispersal matrix $L^*(t)=(\ell_{ij}^*(t))$ as follows

$$\ell_{ij}^*(t)=\begin{cases}M_0 & \text{for } (i,j)=(n,1),\\ -M_0 & \text{for } (i,j)=(1,1),\\ q_j(t) & \text{for } i=j-1,\ 2\le j\le n,\\ -q_j(t) & \text{for } i=j,\ 2\le j\le n,\\ 0 & \text{otherwise.}\end{cases}$$

i.e.

$$L^*(t) = \begin{pmatrix} -M_0 & q_2(t) & 0 & 0 & \cdots & 0 \\ 0 & -q_2(t) & q_3(t) & 0 & \cdots & 0 \\ 0 & 0 & -q_3(t) & q_4(t) & 0 & \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ M_0 & 0 & 0 & 0 & \cdots & -q_n(t) \end{pmatrix}. \tag{2.14}$$

It is then clear from the construction of $L^*(t)$ that

$$\frac{d\tilde{\boldsymbol{K}}(t)}{dt} = L^*(t)\tilde{\boldsymbol{K}}(t). \tag{2.15}$$

Combining with (2.2), it follows that $\boldsymbol{u}^*(t) = M(t)\tilde{\boldsymbol{K}}(t)$ satisfies

$$\begin{aligned} \frac{du_i^*(t)}{dt} - \sum_{j\in\Omega} \ell_{ij}^*(t)u_j^*(t) = M'(t)\tilde{K}_i(t) &= M(t)\tilde{K}_i(t)r_i(t)\left(1 - \frac{M(t)\tilde{K}_i(t)}{K_i(t)}\right) \\ &= r_i(t)u_i^*(t)\left(1 - \frac{u_i^*(t)}{K_i(t)}\right). \end{aligned}$$

Therefore, the T-periodic distribution $\boldsymbol{u}^*(t) = M(t)\tilde{\boldsymbol{K}}(t)$ is a (and hence the unique) positive T-periodic solution of the single species adopting the dispersal strategy $L^*(t)$, and it fulfills condition (1.4). □

We state the following corollary of Theorem 2.3 and Proposition 2.4.

Corollary 2.6. *Condition* (2.13) *(or equivalently $\tilde{\boldsymbol{K}}(t) > \boldsymbol{0}$) on the environmental parameters $\Omega, \boldsymbol{r}, \boldsymbol{K}$ is necessary and sufficient for the existence of a $\mathcal{K}$-joint IFD.*

Remark 2.7. *In particular, a T-periodic solution $\boldsymbol{u}^*(t)$ of the single species model is an IFD if and only if* (2.13) *holds and $\boldsymbol{u}^*(t) = M(t)\tilde{\boldsymbol{K}}(t)$, which is also equivalent to $\boldsymbol{\phi}(t) = \tilde{\boldsymbol{K}}(t)$.*

2.2 Evolutionary Stability of IFD: Sufficiency

In this section, we discuss the evolutionary stability of IFD. Our basic assumption is that there is a coalition of species indexed by $k \in \mathcal{K}$ forming a joint IFD. Our first main result shows that dispersal strategies that generate a $\mathcal{K}$-joint IFD (or a single species IFD if $|\mathcal{K}| = 1$) are evolutionarily stable. Hereafter, we say that $\{\boldsymbol{u}^k(t)\}_{k=1}^N$ is a nonnegative, nontrivial solution of (1.1) if it is componentwise nonnegative, and that for each k, $\max_{i\in\Omega} u_i^k(0) > 0$. Recall also that a group of species form a $\mathcal{K}$-joint IFD if and only if $\sum\limits_{k\in\mathcal{K}} \boldsymbol{u}^k = M(t)\tilde{\boldsymbol{K}}(t)$, where $M(t)$ and $\tilde{\boldsymbol{K}}(t)$ be defined in terms of $\boldsymbol{r}(t)$ and $\boldsymbol{K}(t)$ in (2.1) and (2.2), respectively.

Theorem 2.8. *Suppose that there is a nonempty subset $\mathcal{K}$ of $\{1, \cdots, N\}$ such that model* (1.1) *has a $\mathcal{K}$-joint IFD. Then for any nonnegative, nontrivial solution $\{\boldsymbol{u}^k(t)\}_{k=1}^N$ of* (1.1)*, the following conclusions hold.*

(a) *The collection of species converges to IFD distribution given by the environment:*

$$\lim_{t\to\infty}\sup_{i\in\Omega}\left|\sum_{k=1}^{N}u_i^k(t)-M(t)\tilde{K}_i(t)\right|=0.$$

(b) *Passing to subsequences* $\{m'\}\subset\mathbb{N}$ *with* $m'\to\infty$, $\lim\limits_{m'\to\infty}\boldsymbol{u}^k(t+m'T)$ *is a* $\mathcal{K}'$*-joint IFD for some* $\mathcal{K}'\subset\{1,\cdots,N\}$*, i.e. there exists* $\boldsymbol{c}=\{c^k\}_{k=1}^N\in[0,1]^N$ *such that* $\sum_{k=1}^N c^k=1$, $c^k>0$ *for* $k\in\mathcal{K}'$ *and* $c^k=0$ *for* $k\notin\mathcal{K}'$ *and*

$$\begin{cases}\lim_{m'\to\infty}\sup_{\substack{i\in\Omega\\1\le k\le N}}\sup_{t\in[0,T)}\left|u_i^k(t+m'T)-c^kM(t)\phi_i^k(t)\right|_{C_{loc}(\mathbb{R})}=0, & \textit{and}\\ \sum_{k=1}^N c^k\boldsymbol{\phi}^k(t)=\tilde{\boldsymbol{K}}(t),\end{cases}$$

where $\boldsymbol{\phi}^k(t)$ *is given in Lemma 2.2.*

(c) *If, in addition, there is a unique subset* $\mathcal{K}_0\subset\{1,\cdots,N\}$ *such that model* (1.1) *has a* $\mathcal{K}$*-joint IFD if and only if* $\mathcal{K}=\mathcal{K}_0$*, then there exists a unique set of coefficients* $\{c_k\}_{k=1}^N\in[0,1]^N$ *such that* $c_k>0$ *for* $k\in\mathcal{K}_0$ *and* $c_k=0$ *for* $k\notin\mathcal{K}_0$ *and*

$$\lim_{t\to\infty}\sup_{\substack{i\in\Omega\\1\le k\le N}}\left|u_i^k(t)-c_kM(t)\phi_i^k(t)\right|=0.$$

As a direct consequence of Theorem 2.8 and Remark 2.7, when only one species adopts an ideal free dispersal strategy, it can drive other $N-1$ species to be extinct, see the following result. This is an extension of [36, Theorem 2.2] and [7, Theorem 3].

Corollary 2.9. *Let* $M(t)$ *and* $\tilde{\boldsymbol{K}}(t)$ *be defined in terms of* $\boldsymbol{r}(t)$ *and* $\boldsymbol{K}(t)$ *in* (2.1) *and* (2.2)*, respectively. Suppose that the first species achieves an IFD (i.e.* $\boldsymbol{\phi}^1(t)\equiv\tilde{\boldsymbol{K}}(t)$*). Then for any nonnegative, nontrivial solution of model* (1.1)*, the following statements hold.*

(a) *The collection of species converges to IFD distribution, i.e.*

$$\lim_{t\to\infty}\sup_{i\in\Omega}\left|\sum_{k=1}^{N}u_i^k(t)-M(t)\tilde{K}_i(t)\right|=0.$$

(b) *If, in addition, no subset* $\mathcal{K}'\subset\{2,\cdots,N\}$ *form a* $\mathcal{K}'$*-joint IFD, then*

$$\lim_{t\to\infty}\sup_{i\in\Omega}\left|u_i^1(t)-M(t)\phi_i^1(t)\right|=0\qquad\textit{and}\qquad\lim_{t\to\infty}\boldsymbol{u}^k(t)=\boldsymbol{0}\ \textit{for}\ k\in\{2,\cdots,N\},$$

where $\boldsymbol{\phi}^1(t)$ *is given in Lemma 2.2.*

Remark 2.10. *Assertion* (b)*, applied to the case* $N=2$*, implies that ideal free dispersal strategies are non-invadable by non-ideal free dispersal strategies, i.e. they are evolutionarily stable.*

Proof of Theorem 2.8. First of all, let $\{\phi_i^k(t)\}_{i\in\Omega,1\le k\le N}$ be as given in Lemma 2.2. By the dissipativity assumption in Remark 1.1, we have

$$\exists\ a_0 > 0 \quad \text{such that} \quad \sup_{\substack{i\in\Omega,\ 1\le k\le N,\\ t\in\mathbb{R}}} \tilde{F}_i(t, s\phi_i^k(t)) < 0 \quad \text{for} \quad s \ge a_0. \tag{2.16}$$

Then, for each t, define the subset $\mathcal{T}(t) \subset \mathbb{R}^{n\times N}$ by

$$\mathcal{T}(t) = \left\{\boldsymbol{Z}(t) = \{z_i^k(t)\} \in \mathbb{R}^{n\times N} : \boldsymbol{Z}(t) > \boldsymbol{0} \ \text{ and } \ z_i^k(t) < a_0\phi_i^k(t) \ \text{ for all } \ i\in\Omega,\ 1\le k\le N\right\}, \tag{2.17}$$

$$\overline{\mathcal{T}}(t) = \left\{\boldsymbol{Z}(t) \in \mathbb{R}^{n\times N} : \boldsymbol{Z}(t) \ge \boldsymbol{0} \ \text{ and } \ z_i^k(t) \le a_0\phi_i^k(t) \ \text{ for all } i\in\Omega,\ 1\le k\le N\right\}. \tag{2.18}$$

We claim that $\mathcal{T}(t)$ is forward invariant[1] with respect to the semiflow generated by the model (1.1), i.e., for any $t_0 \ge 0$, and any solution $\boldsymbol{u}(t) = \{u_i^k(t)\}_{i\in\Omega,1\le k\le N}$ of model (1.1), we have

$$\boldsymbol{u}(t_0) \in \mathcal{T}(t_0) \quad \Longrightarrow \quad \boldsymbol{u}(t) \in \mathcal{T}(t) \quad \text{for all } t \ge t_0. \tag{2.19}$$

Indeed, fix $t_0 \ge 0$ and fix a solution $\boldsymbol{u}(t)$ of model (1.1) such that $\boldsymbol{u}(t_0) \in \mathcal{T}(t_0)$. We easily obtain $\boldsymbol{u}(t) > \boldsymbol{0}$ for $t > t_0$ (resp. $\boldsymbol{u}(t) \ge \boldsymbol{0}$ for $t > t_0$) using the irreducibility and cooperativity of the dispersal matrix $L^k(t)$.

Next, denote $w_i^k(t) = u_i^k(t)/\phi_i^k(t)$, then

$$\frac{d}{dt}w_i^k = \sum_{j\in\Omega} \tilde{\ell}_{ij}^k(t) w_j^k + w_i^k F_i\left(t, \sum_{h=1}^N \phi_i^h w_i^h\right) \tag{2.20}$$

where

$$\tilde{\ell}_{ij}^k(t) = \ell_{ij}^k(t)\frac{\phi_j^k(t)}{\phi_i^k(t)} \quad \text{for } j \ne i \quad \text{ and } \quad \tilde{\ell}_{ii}^k(t) = -\frac{1}{\phi_i^k(t)} \sum_{\substack{j\in\Omega,\\ j\ne i}} \ell_{ij}^k(t)\phi_j^k(t). \tag{2.21}$$

We claim that $\boldsymbol{u}(t) \in \mathcal{T}(t)$ for all $t > t_0$. Suppose not, there exist $t^* \in (t_0, \infty)$ and k^*, i^* such that $\boldsymbol{u}(t) \in \mathcal{T}(t)$ for $t \in [t_0, t^*)$ and

$$w_i^k(t^*) \le a_0 \ \text{ for all } 1 \le k \le N,\ i\in\Omega, \quad w_{i^*}^{k^*}(t^*) = a_0 \quad \text{ and } \quad \frac{d}{dt}w_{i^*}^{k^*}(t^*) \ge 0.$$

Substitute into (2.20), and take $(i,k) = (i^*, k^*)$, we have

$$0 \le \frac{d}{dt}w_{i^*}^{k^*}(t^*) \le \sum_{j\in\Omega} \tilde{\ell}_{i^*j}^{k^*}(t^*)a_0 + a_0\tilde{F}_{i^*}(t^*, a_0\phi_{i^*}^{k^*}(t^*)). \tag{2.22}$$

However, $\sum_{j\in\Omega} \tilde{\ell}_{i^*j}^{k^*}(t^*)a_0 = 0$ (thanks to the definition of $(\tilde{\ell}_{ij}^k(t))$ in (2.21)) and $\tilde{F}_{i^*}(t^*, a_0\phi_{i^*}^{k^*}(t^*)) < 0$ by (2.16), which is a contradiction to (2.22). This proves the forward-invariance of $\mathcal{T}(t)$. By continuous dependence, it follows that $\overline{\mathcal{T}}$ is also forward-invariant. Note also that $a_0 \gg 1$ can be chosen arbitrarily large.

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[1] An equivalent formulation is that the Poincaré map is forward invariant with respect to $\mathcal{T}(0)$.

Let $\{\boldsymbol{u}^{k*}(t)\}_{k=1}^N$ be the $\mathcal{K}$-joint IFD, with the convention that

$$\boldsymbol{u}^{k*}(t) > \mathbf{0} \quad \text{for} \quad k \in \mathcal{K} \quad \text{and} \quad \boldsymbol{u}^{k*}(t) \equiv \mathbf{0} \quad \text{for} \quad k \notin \mathcal{K}.$$

Then, we see that $\sum_{k=1}^N \boldsymbol{u}^{k*}(t) = M(t)\tilde{\boldsymbol{K}}(t)$ (by Theorem 2.3 (ii)), and

$$\frac{du_i^{l*}(t)}{dt} = \sum_{j\in\Omega} l_{ij}^l(t) u_j^{l*}(t) + u_i^{l*}(t)\frac{M'(t)}{M(t)}, \quad \text{for all } i \in \Omega,\ l \in \mathcal{K}. \tag{2.23}$$

Here $M(t)$ and $\tilde{\boldsymbol{K}}(t)$ are defined in terms of $\boldsymbol{r}(t)$ and $\boldsymbol{K}(t)$ in (2.1) and (2.2), respectively. Let $G(s) = s - \ln s$ for $s > 0$, and denote $\mathcal{K}^c = \{1, \cdots, N\} \setminus \mathcal{K}$. Fix an arbitrary solution $(\boldsymbol{u}^1(t), \cdots, \boldsymbol{u}^N(t))$ with initial data belonging to the forward-invariant set $\mathcal{T}(0)$, then define $V(\boldsymbol{u}^1(t), \cdots, \boldsymbol{u}^N(t)) = V_1 + V_2$, where

$$V_1 = \sum_{i\in\Omega}\sum_{l\in\mathcal{K}} \frac{u_i^{l*}(t)}{M(t)} G\left(\frac{u_i^l(t)}{u_i^{l*}(t)}\right) \geq 0 \quad \text{and} \quad V_2 = \sum_{i\in\Omega}\sum_{k\in\mathcal{K}^c} \frac{u_i^k(t)}{M(t)} \geq 0.$$

For $l \in \mathcal{K}$, denote

$$G_i^l = G\left(\frac{u_i^l(t)}{u_i^{l*}(t)}\right) \quad \text{and} \quad (G_i^l)' = (G_i^l)'(s)|_{s=u_i^l(t)/u_i^{l*}(t)} = 1 - \frac{u_i^{l*}(t)}{u_i^l(t)}.$$

Then direct calculations yield,

$$\begin{aligned}
\dot{V}_1 &= \frac{1}{M}\sum_{i\in\Omega}\sum_{l\in\mathcal{K}} \left[\frac{du_i^{l*}}{dt}\left(G_i^l - \frac{(G_i^l)'u_i^l}{u_i^{l*}}\right) + (G_i^l)'\frac{du_i^l}{dt} - \frac{M'}{M}u_i^{l*}G_i^l\right] \\
&= \frac{1}{M}\sum_{i\in\Omega}\sum_{l\in\mathcal{K}} \left\{G_i^l\left[\frac{du_i^{l*}}{dt} - \frac{M'}{M}u_i^{l*}\right] + (G_i^l)'\left[-\frac{u_i^l}{u_i^{l*}}\frac{du_i^{l*}}{dt} + \frac{du_i^l}{dt}\right]\right\} \\
&= \frac{1}{M}\sum_{i\in\Omega}\sum_{l\in\mathcal{K}} \left\{G_i^l \sum_{j\in\Omega}\ell_{ij}^l u_j^{l*} + (G_i^l)'\left[-\frac{u_i^l}{u_i^{l*}}\sum_{j\in\Omega}\ell_{ij}^l u_j^{l*} + \sum_{j\in\Omega}\ell_{ij}^l u_j^l + u_i^l\frac{r_i}{K_i}\left(\sum_{h=1}^N u_i^{h*} - \sum_{h=1}^N u_i^h\right)\right]\right\} \\
&= \frac{1}{M}\sum_{l\in\mathcal{K}}\sum_{i\in\Omega}\sum_{j\in\Omega}\ell_{ij}^l u_j^{l*}\left\{G_i^l + (G_i^l)'\left(\frac{u_j^l}{u_j^{l*}} - \frac{u_i^l}{u_i^{l*}}\right) - G_j^l\right\} \\
&\quad + \frac{1}{M}\sum_{i\in\Omega}\frac{r_i}{K_i}\left(\sum_{h=1}^N u_i^{h*} - \sum_{h=1}^N u_i^h\right)\sum_{l\in\mathcal{K}}(u_i^l - u_i^{l*}),
\end{aligned}$$

where we use $\sum_{i,j\in\Omega}\ell_{ij}^l u_j^{l*}G_j^l = \sum_{i\in\Omega} u_j^{l*}G_j^l\sum_{i\in\Omega}\ell_{ij}^l = 0$ and $(G_i^l)'u_i^l = u_i^l - u_i^{l*}$ in the last equality.

By the Taylor's theorem, $G_j^l = G_i^l + (G_i^l)'\left(\frac{u_j^l}{u_j^{l*}} - \frac{u_i^l}{u_i^{l*}}\right) + \frac{1}{2}G''(s)|_{s=\xi_{ij}^l(t)}\left(\frac{u_j^l}{u_j^{l*}} - \frac{u_i^l}{u_i^{l*}}\right)^2$, for some $\xi_{ij}^l(t) > 0$ between $u_i^l(t)/u_i^{l*}(t)$ and $u_j^l(t)/u_j^{l*}(t)$, so

$$\dot{V}_1 = \frac{-1}{2M}\sum_{l\in\mathcal{K}}\sum_{i\in\Omega}\sum_{j\in\Omega}\frac{\ell_{ij}^l u_j^{l*}}{|\xi_{ij}^l|^2}\left(\frac{u_i^l}{u_i^{l*}} - \frac{u_j^l}{u_j^{l*}}\right)^2 + \frac{1}{M}\sum_{i\in\Omega}\frac{r_i}{K_i}\left(\sum_{h=1}^N u_i^{h*} - \sum_{h=1}^N u_i^h\right)\sum_{l\in\mathcal{K}}(u_i^l - u_i^{l*}). \tag{2.24}$$

Note that $u_i^l(t)$ is eventually bounded from above, and $u_i^{l*}(t)$ is uniformly bounded away from zero and infinity, so $\xi_{ij}^l(t)$ is uniformly bounded from above for all $l \in \mathcal{K}$.

Next, we use $\sum_{i\in\Omega} \ell_{ij}^k = 0$ to compute

$$\begin{aligned}\dot{V}_2 &= \frac{1}{M}\sum_{i\in\Omega}\sum_{k\in\mathcal{K}^c}\left(\frac{du_i^k}{dt} - \frac{u_i^k M'}{M}\right)\\ &= \frac{1}{M}\sum_{i\in\Omega}\sum_{k\in\mathcal{K}^c}\left[\sum_{j\in\Omega}\ell_{ij}^k u_j^k + u_i^k r_i\left(1-\frac{\sum_{h=1}^N u_j^h}{K_i}\right) - u_i^k r_i\left(1-\frac{\sum_{h=1}^N u_j^{h*}}{K_i}\right)\right]\\ &= \frac{1}{M}\sum_{i\in\Omega}\frac{r_i}{K_i}\left(\sum_{h=1}^N u_i^{h*} - \sum_{h=1}^N u_j^h\right)\sum_{k\in\mathcal{K}^c} u_i^k \end{aligned} \tag{2.25}$$

and use $\boldsymbol{u}^{k*}(t) = \mathbf{0}$ for each $k \in \mathcal{K}^c$ to compute

$$0 = \frac{1}{M}\sum_{i\in\Omega}\frac{r_i}{K_i}\left(\sum_{h=1}^N u_i^{h*} - \sum_{h=1}^N u_j^h\right)\left(-\sum_{k\in\mathcal{K}^c} u_i^{k*}\right). \tag{2.26}$$

By adding (2.24), (2.25) and (2.26), we have

$$\dot{V} = \frac{-1}{2M}\sum_{i\in\Omega}\sum_{j\in\Omega}\sum_{l\in\mathcal{K}}\frac{\ell_{ij}^l u_j^{l*}}{|\xi_{ij}^l|^2}\left(\frac{u_i^l}{u_i^{l*}} - \frac{u_j^l}{u_j^{l*}}\right)^2 - \frac{1}{M}\sum_{i\in\Omega}\frac{r_i}{K_i}\left(\sum_{h=1}^N u_i^{h*} - \sum_{h=1}^N u_i^h\right)^2 \le 0. \tag{2.27}$$

According to (2.27), $\mathcal{M} := \{\dot{V} = 0\}$ is given by

$$\mathcal{M} = \Big\{(\boldsymbol{u}^1(t), \cdots, \boldsymbol{u}^N(t)) \in \mathcal{T}(t) : \text{(2.28) holds for some } \chi_l(t),\ l \in \mathcal{K}\Big\}.$$

where

$$\begin{cases}\sum_{k=1}^N u_i^k(t) = \sum_{h=1}^N u_i^{h*}(t) = M(t)\tilde{K}_i(t) & \text{for } i \in \Omega,\\ u_i^l(t) = \chi_l(t) u_i^{l*}(t) & \text{for } i \in \Omega,\ l \in \mathcal{K}.\end{cases} \tag{2.28}$$

Note that $\chi_l(t)$ is independent of $i \in \Omega$.

It is known from the LaSalle's invariance principle [31, Theorem 5] that, for arbitrary $a_0 \gg 1$ satisfying (2.16), the solution initiating from $\overline{\mathcal{T}}(0)$ tends to the maximal invariant subset $\mathcal{M}'$ of $\mathcal{M}$. In general, for each trajectory $\boldsymbol{u}$ of (1.1) with nonnegative and nontrivial initial value, there exists $m \in \mathbb{N}$ such that $\boldsymbol{u}(mT) \in \overline{\mathcal{T}}(mT) = \overline{\mathcal{T}}(0)$. It follows that $\mathcal{M}'$ attracts the solution initiating from any nonnegative and nontrivial initial value (see, e.g., [46, Theorem 1.2.1]). We further characterize $\mathcal{M}'$. Indeed, let $(\boldsymbol{u}^1(t), \cdots, \boldsymbol{u}^N(t))$ be an entire solution (which is defined for $t \in \mathbb{R}$) and lie in $\mathcal{M}$, then conclusion (a) follows from the first condition in (2.28), and the fact that $a_0 \gg 1$ can be chosen arbitrarily large.

Moreover, the solution satisfies

$$\frac{d}{dt}\boldsymbol{u}^k(t) - L^k(t)\boldsymbol{u}^k(t) = \frac{M'(t)}{M(t)}\boldsymbol{u}^k(t) \quad \text{for} \quad 1 \le k \le N,\ t \in \mathbb{R}. \tag{2.29}$$

Observe also that $M(t)\boldsymbol{\phi}^k(t)$ is another positive entire solution of (2.29). By the uniqueness of positive entire solution of (2.29) (see [28, Theorem 4.1.2] for the statement for linear parabolic equations and the general exponential separation result due to Polacik et al. [41]), we see that $\boldsymbol{u}^k(t)/M(t) = c_k\boldsymbol{\phi}^k(t)$ for some constant $c_k \geq 0$. This means that $\boldsymbol{u}^k(t)$ is T-periodic in time. Taking the summation over k, we deduce that $\sum_{k=1}^N c_k\boldsymbol{\phi}^k(t) = \sum_{k=1}^N \boldsymbol{u}^k(t)/M(t) = \tilde{\boldsymbol{K}}(t)$ by (2.28). Then, summing over $i \in \Omega$ and using $\sum_{i\in\Omega}\phi_i^k(t) = 1$ and (2.2), we have

$$\sum_{k=1}^N c_k = \sum_{i\in\Omega}\tilde{K}_i(t) = 1.$$

Thus, conclusion (b) holds.

To prove conclusion (c), assume that there is a unique subset $\mathcal{K}_0$ that supports a joint IFD. It follows from (b) that subsequential limits of $\boldsymbol{u}^k(t+mT)/M(t)$ as $m \to \infty$ equal $c_k\boldsymbol{\phi}^k(t)$ with c_k being supported precisely on $\mathcal{K}_0$.

It suffices to show the uniqueness of $\{c_k\}_{k=1}^N$. If there are two distinct combinations of $\{c_k\}_{k=1}^N$ and $\{c'_k\}_{k=1}^N$ whose support is precisely $\mathcal{K}_0$ such that

$$\sum_{k=1}^N c_k\boldsymbol{\phi}^k(t) = \sum_{k=1}^N c'_k\boldsymbol{\phi}^k(t) = \tilde{\boldsymbol{K}}(t).$$

Then define $s' := \min_{k\in\mathcal{K}_0}\{c'_k/c_k\}$, then $0 < s' < 1$. It then follows that

$$c''_k := \frac{1}{1-s}(c'_k - sc_k) \geq 0$$

satisfies $\sum_{k=1}^N c''_k = 1$, $c''_{k_1} = 0$ for some $k_1 \in \mathcal{K}_0$, and

$$\sum_{k=1}^N c''_k\boldsymbol{\phi}^k(t) = \tilde{\boldsymbol{K}}(t),$$

which implies that there is a joint IFD with fewer species. This is a contradiction. □

Theorem 2.8 demonstrates that the long-time limit of each solution to model (1.1) selects an IFD. However, that a subset of multiple species exhibits a joint IFD does not imply immediately that particular subset can drive all other species to extinction. A counter example can be obtained for two-species system: if $\boldsymbol{\phi}^1(t) = \boldsymbol{\phi}^2(t) = \tilde{\boldsymbol{K}}(t)$, then it follows that for each $s \in [0,1]$, $(\boldsymbol{u}_s^1(t), \boldsymbol{u}_s^2(t)) := (sM(t)\tilde{\boldsymbol{K}}(t), (1-s)M(t)\tilde{\boldsymbol{K}}(t))$ is a coexistence periodic solution, indicating that neither species may competitively exclude the other one. The same situation holds if $\mathcal{K}_1 = \{1\}$ and $\mathcal{K}_2 = \{2,3\}$ simultaneously have joint IFD.

On the other hand, sufficient conditions for competition exclusion in three-species reaction-diffusion models with temporally constant environments have been obtained in [36]. For example, $\mathcal{K} = \{1\}$ has IFD while no subset of $\{2,3\}$ has IFD, then the first species competitively excludes the second and third species [36, Theorem 2.2]; if $\mathcal{K} = \{1,2\}$ forms a $\mathcal{K}$-joint IFD, and $\mathcal{K} = \{3\}$ does not, then the third species will be competitively excluded while the first two species coexist stably [36, Theorem 2.3].

Our results (Theorem 2.8 and Corollary 2.9) generalize these previous results to N-species problems with $N > 3$. Namely, if only one specific combination of species can achieve a joint IFD, then the species combination will dominate and competitively exclude all other species.

2.3 Evolutionary Stability of IFD: Necessity

Suppose a positive, T-periodic distribution $(\tilde{\boldsymbol{u}}^1(t), \cdots, \tilde{\boldsymbol{u}}^{N-1}(t), \mathbf{0})$ in an N species system is not an IFD (or a joint-IFD in case it consists of multiple species). We show in this subsection that it can be destablized by certain choices of dispersal strategy of the N species. There are two direct consequences:

- For a time-periodic steady state of a single or multiple sepcies, being an IFD is a necessary condition to keep evolutionary stable;
- When (2.13) does not hold, an IFD is not possible and hence the given environment does not support any evolutionary stable time-periodic steady states.

Theorem 2.11. *Let* $(\tilde{\boldsymbol{u}}^1(t), \cdots, \tilde{\boldsymbol{u}}^{N-1}(t), \mathbf{0})$ *be a T-periodic solution of model* (1.1). *Suppose* $(\tilde{\boldsymbol{u}}^1(t), \cdots, \tilde{\boldsymbol{u}}^{N-1}(t))$ *is not a joint IFD. Then there exists a dispersal strategy* $L^N(t)$ *given in Claim 2.13 such that* $(\tilde{\boldsymbol{u}}^1(t), \cdots, \tilde{\boldsymbol{u}}^{N-1}(t), \mathbf{0})$ *is unstable, i.e., rare N-th species invades.*

Remark 2.12. *If we assume in addition that* (2.13) *holds, then Theorem 2.11 is a consequence of Corollary 2.9. However, we show that Theorem 2.11 holds without imposing* (2.13).

Proof of Theorem 2.11. Let $\{\boldsymbol{u}^k(t)\}_{k=1}^N$ be the solution to the initial value problem (1.1), and define $\boldsymbol{\theta}(t) = \sum_{k=1}^{N-1} \boldsymbol{u}^k(t)$. Then $(\tilde{\boldsymbol{\theta}}(t), \mathbf{0})$, where $\tilde{\boldsymbol{\theta}}(t) = \sum_{k=1}^{N-1} \tilde{\boldsymbol{u}}^k(t)$ and $\{\tilde{\boldsymbol{u}}^k(t)\}_{k=1}^{N-1}$ is given in the statement of the theorem, is the semitrivial T-periodic solution of

$$\begin{cases} \dfrac{d\theta_i}{dt} = \displaystyle\sum_{k=1}^{N-1} \sum_{j\in\Omega} \ell_{ij}^k(t) u_j^k + r_i(t)\theta_i \left(1 - \frac{\theta_i + u_i^N}{K_i(t)}\right), & i \in \Omega,\ t > 0, \\ \dfrac{du_i^N}{dt} = \displaystyle\sum_{j\in\Omega} \ell_{ij}^N(t) u_j^N + r_i(t) u_i^N \left(1 - \frac{\theta_i + u_i^N}{K_i(t)}\right), & i \in \Omega,\ t > 0, \\ \theta_i(0) = \sum_{k=1}^{N-1} u_{i0}^k, \quad u_i^N(0) = u_{i0}^N. \end{cases} \tag{2.30}$$

It is clear that $\tilde{\boldsymbol{\theta}}(t)$ satisfies

$$\begin{cases} \dfrac{d\tilde{\theta}_i}{dt} = \displaystyle\sum_{k=1}^{N-1} \sum_{j\in\Omega} \ell_{ij}^k(t) \tilde{u}_j^k + r_i(t)\tilde{\theta}_i \left(1 - \frac{\tilde{\theta}_i}{K_i(t)}\right), & i \in \Omega,\ t > 0, \\ \tilde{\theta}_i(0) = \sum_{k=1}^{N-1} u_{i0}^k, & i \in \Omega. \end{cases} \tag{2.31}$$

Then $(\tilde{\boldsymbol{\theta}}(t), \mathbf{0})$ is linearly unstable provided that the following eigenvalue problem has a negative principal eigenvalue (see [28, Chap. 7]):

$$\frac{d\varphi_i}{dt} = \sum_{j\in\Omega} \ell_{ij}^N(t)\varphi_j + F(i,t)\varphi_i + \lambda\varphi_i, \quad i \in \Omega. \tag{2.32}$$

where

$$F(i,t) := r_i(t)\left(1 - \frac{\tilde{\theta}_i}{K_i(t)}\right).$$

Let $\lambda_1 \in \mathbb{R}$ be the principal eigenvalue of (2.32) and has positive eigenfunction $\boldsymbol{\varphi}(t)$ normalized by $\int_0^T \sum_{i\in\Omega} \varphi_i(t)\,dt = T$, whose existence can be derived from the Krein-Rutman theorem. It is enough to prove that $\lambda_1 < 0$ for some dispersal strategy $L(t)$, which implies the instability of $(\tilde{\boldsymbol{\theta}}(t), \mathbf{0})$.

Take summation over i in (2.31), then

$$\frac{d}{dt}\sum_{i\in\Omega}\tilde{\theta}_i = \sum_{i\in\Omega} F(i,t)\tilde{\theta}_i < \left[\max_{j\in\Omega} F(j,t)\right]\sum_{i\in\Omega}\tilde{\theta}_i,$$

where the strict inequality holds because $(\tilde{\boldsymbol{u}}^1(t), \cdots, \tilde{\boldsymbol{u}}^{N-1}(t))$ is not a joint IFD. Divide both sides of the above equation by $\sum_{i\in\Omega}\tilde{\theta}_i$ and integrate the result in t over $[0,T]$, then there exists some patch choice $I(t) : [0,T] \to \Omega$ such that

$$\int_0^T F(I(t),t)\,dt = \int_0^T \max_{j\in\Omega} F(j,t)dt > 0.$$

Define $\boldsymbol{E}(t) = \{E_i(t)\}_{i\in\Omega}$ by

$$E_i(t) = 1 \ \text{ when } \ I(t) = i, \qquad \text{and} \qquad E_i(t) = 0 \quad \text{otherwise},$$

then we can choose a smooth T-periodic positive function $\boldsymbol{\kappa}(t) = \{\kappa_i(t)\}_{i\in\Omega}$ such that $\sum_{i\in\Omega}\kappa_i(t) \equiv 1$, and $\boldsymbol{\kappa}(t) \approx \boldsymbol{E}(t)$ in L^1. By approximation, one can assume further that

$$\int_0^T \sum_{i\in\Omega} F(i,t)\kappa_i(t)\,dt > 0. \tag{2.33}$$

Now, by a procedure similar to the proof of Proposition 2.4, it is easy to construct a dispersal matrix $A(t) = (a_{ij}(t))$ satisfying condition (C), such that $A(t)\boldsymbol{\kappa}(t) = \mathbf{0}$ for $t \in [0,T]$. For example, if $\boldsymbol{\kappa}(t) = (\kappa_1(t), \kappa_2(t), \kappa_3(t))$, then we can take

$$A(t) = \begin{pmatrix} -\kappa_2(t)/\kappa_1(t) & 1 & 0 \\ 0 & -1 & -\kappa_2(t)/\kappa_3(t) \\ \kappa_2(t)/\kappa_1(t) & 0 & \kappa_2(t)/\kappa_3(t) \end{pmatrix},$$

and note that $A(t)$ is smooth and satisfies condition (C). Furthermore, for each $t \in [0,T]$, $A(t)\boldsymbol{v}(t) = \mathbf{0}$ and $\boldsymbol{v}(t) \geq \mathbf{0}$ implies that $\boldsymbol{v}(t) = c_0\boldsymbol{\kappa}(t)$ for some $c_0 \geq 0$ by Perron-Frobenius Theorem.

Claim 2.13. *Choose $L^N(t) = \alpha A(t)$ in the eigenvalue problem* (2.32)*. Then as $\alpha \to +\infty$, we have $\lambda_1 \to -\frac{1}{T}\int_0^T \sum_{i\in\Omega} F(i,t)\kappa_i(t)\,dt < 0$.*

To see the claim, take $L^N(t) = \alpha A(t)$ in (2.32). Observe that λ_1 is bounded uniformly for $\alpha \geq 0$ by integrating the equation (2.32) in t and summing over $i \in \Omega$ to get

$$|\lambda_1| \int_0^T \sum_{i\in\Omega} \varphi_i(t)\,dt = \left| \int_0^T \sum_{i\in\Omega} F(i,t)\varphi_i(t)\,dt \right| \leq \max_{i\in\Omega} \|F(i,\cdot)\|_\infty \int_0^T \sum_{i\in\Omega} \varphi_i(t)\,dt,$$

so that $|\lambda_1| \leq \max_{i\in\Omega} \|F(i,\cdot)\|_\infty$, and that $\lambda_1 \to \bar\lambda$ upon passing to a subsequence as $\alpha \to \infty$.

Next, denote $q^\alpha(t) := \sum_{i\in\Omega} \varphi_i(t)$, then

$$\frac{d}{dt} \log q^\alpha(t) = \frac{\sum_{i\in\Omega}(F(i,t) + \lambda_1)\varphi_i(t)}{\sum_{i\in\Omega} \varphi_i(t)}. \tag{2.34}$$

Since the right hand side is uniformly bounded by $2\max_{i\in\Omega} \|F(i,\cdot)\|_\infty$, if we also normalize $q^\alpha(0) = 1$, then Ascoli's theorem implies that by passing to a subsequence, there exists a positive function $\bar q(t) \in \mathrm{Lip}([0,T])$ such that $\bar q(0) = \bar q(T) = 1$ and

$$q^\alpha(t) \to \bar q(t) \quad \text{uniformly in } [0,T] \quad \text{as } \alpha \to \infty.$$

Also, the boundedness of $\sum_{i\in\Omega} \varphi_i(t)$ in L^∞ also implies that (again passing to a subsequence) there exists $\boldsymbol{v}(t) = \{v_i(t)\}_{i\in\Omega} \in L^\infty$ such that $\boldsymbol{\varphi} \to \boldsymbol{v}$ weakly in L^p for any $1 < p < \infty$. Divide the equation (2.32) by α,

$$\frac{1}{\alpha}\frac{d\varphi_i}{dt} = \sum_{j\in\Omega} a_{ij}(t)\varphi_j + \frac{1}{\alpha}\left(F(i,t) + \lambda_1\right)\varphi_i, \ i \in \Omega,$$

and then passing to the limit, we deduce $\boldsymbol{v}(t) = \bar q(t)\boldsymbol{\kappa}(t)$. Finally, integrate (2.34) over $[0,T]$, then the left hand side vanishes by periodicity of q^α. We then pass to the limit as $\alpha \to \infty$, so that

$$\begin{aligned} 0 &= \lim_{\alpha\to\infty} \int_0^T \frac{\sum_{i\in\Omega}(F(i,t) + \lambda_1)\varphi_i(t)}{\sum_{i\in\Omega} \varphi_i(t)} dt \\ &= \int_0^T \frac{\sum_{i\in\Omega}(F(i,t) + \bar\lambda)\bar q(t)\kappa_i(t)}{\bar q(t)}\,dt \\ &= \int_0^T \sum_{i\in\Omega}(F(i,t) + \bar\lambda)\kappa_i(t)\,dt. \end{aligned}$$

This proves that $\lambda_1 \to -\frac{1}{T}\int_0^T \sum_{i\in\Omega} F(i,t)\kappa_i(t)\,dt < 0$ as $\alpha \to \infty$. □

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