Mathematical Biology

Evolutionary stability of ideal free dispersal strategies in patchy environments

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Abstract   A central question in the study of the evolution of dispersal is what kind of dispersal strategies are evolutionarily stable. Hastings (Theor Pop Biol 24:244–251, 1983) showed that among unconditional dispersal strategies in a spatially heterogeneous but temporally constant environment, the dispersal strategy with no movement is convergent stable. McPeek and Holt's (Am Nat 140:1010–1027, 1992) work suggested that among conditional dispersal strategies in a spatially heterogeneous but temporally constant environment, an ideal free dispersal strategy, which results in the ideal free distribution for a single species at equilibrium, is evolutionarily stable. We use continuous-time and discrete-space models to determine when the dispersal strategy with no movement is evolutionarily stable and when an ideal free dispersal strategy is evolutionarily stable, both in a spatially heterogeneous but temporally constant environment.

Keywords   Evolution of dispersal · Ideal free distribution · Evolutionary stability · Neighborhood invader strategy · Patchy environments

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1 Introduction

Dispersal is an essential aspect of ecology. It is important because it affects population interactions, biological invasions, and the geographical distributions of populations, and their response to habitat fragmentation, among other things. The effects and evolution of dispersal have been studied extensively by theoretical ecologists (Clobert et al. 2001). The problem of understanding the evolution of dispersal strategies in spatially heterogeneous but temporally constant environments has received considerable attention (Averill et al. 2011; Cantrell et al. 2006, 2007a,b, 2008, 2010; Chen and Lou 2008; Chen et al. 2008; Cosner 2005; Cressman and Krivan 2006; Dockery et al. 1998; Hambrock and Lou 2009; Hastings 1983; Holt and Barfield 2001; Kirkland et al. 2006; Krivan et al. 2008; Lam 2011a,b; Lam and Ni 2010; McPeek and Holt 1992; Padrón and Trevisan 2006). In this paper we will examine that question in the context of discrete diffusion models. The corresponding problem in the case of spatial and temporal variation was considered in Holt and McPeek (1996), Hutson et al. (2001), see also Evans et al. (2011), Schreiber (2010, 2011), Schreiber and Li (2011) for some recent important progress in this direction, but we will not address that in the current paper. An important distinction among dispersal strategies is whether they are conditional (depending on environmental factors) or unconditional (effectively random, or at least not based on response to the environment). We will see that when dispersal is favored at all, conditional dispersal of a certain type is favored over unconditional dispersal. Our results extend and refine previous work on that topic. We will take the viewpoint of adaptive dynamics (Dieckmann 1997; Dieckmann and Law 1996; Diekmann 2003; Geritz and Gyllenberg 2008; Geritz et al. 1998; Metz et al. 1996). An important idea in adaptive dynamics is the idea of evolutionarily stable strategies (ESS). A strategy is said to be evolutionarily stable if a population using it cannot be invaded by any small population using a different strategy. A related but different idea is that of convergent stable strategies (CSS). A strategy is convergent stable if small changes in nearby strategies are only favored (i.e., able to invade a resident population) if they are closer to the convergent stable strategy than the resident strategy. The key idea is whether a small population of mutants using a new strategy can invade a resident population using another strategy. Results from Averill et al. (2011), Cantrell et al. (2007a, 2010) show that in some classes of dispersal strategies those that are evolutionarily or convergent stable are those that lead to a distribution of the population which can be described in terms of the ideal free distribution (IFD).

The ideal free distribution, introduced in Fretwell and Lucas (1970), is a description of how organisms should distribute themselves so that individuals optimize their fitness, taking into account the presence of other individuals. The term "ideal free" refers to the idea that such a distribution would be expected if individuals have complete knowledge of their environment and are free to locate themselves wherever they want, specifically under the assumption that the presence of other individuals influences fitness. In the context of modeling population dynamics with dispersal, the IFD thus corresponds to an equilibrium distribution where all individuals have equal fitness, because otherwise some would move to increase their fitness, and where there is no net movement at equilibrium, since no individual can improve its fitness by moving. Since IFD reflects a movement strategy where individuals locate themselves

in response to the presence of others, it can be viewed in the framework of game theory (Cressman and Krivan 2010; Krivan et al. 2008; Krivan and Cressman 2009). Such studies indicate that in many cases the strategies that should be ESS are those leading to IFD. Those studies confirm the idea that the ideal free distribution is the same as what would arise if movement was not allowed, which is consistent with the formulation that we will use in this paper; see also Cantrell et al. (2007a).

The game theory approach is based on comparing payoffs at equilibrium, so it does not address the mechanisms and dynamics that might lead to IFD. Those limitations motivate the adaptive dynamics approach. An important observation arising from this characterization of the IFD is that one strategy that can produce it in population dynamical models is the strategy of no dispersal at all.

Our analysis builds on the ideas developed in Cantrell et al. (2007a), Hastings (1983), McPeek and Holt (1992). Our models consider an arbitrary number of competing populations dispersing among an arbitrary number of patches. We examine both simple Lotka–Volterra competition models and models that also explicitly incorporate the dynamics of both the competitors and their common resource. Our results show not only that strategies producing an IFD resist invasion by other strategies (that is, they are evolutionarily stable) but also that they can invade non-IFD strategies and replace them. In other words, such a strategy is also a neighborhood invader strategy (NIS). (See Apaloo et al. 2009 for a discussion of terminology.) The concepts from adaptive dynamics such as CSS and NIS are typically introduced for strategy dynamics (e.g. dispersal strategies) when population densities are at equilibrium values for the current strategy distribution (see references Dieckmann and Law 1996; Geritz et al. 1998; Metz et al. 1996) whereas the dynamical systems in current paper emphasize population dynamics at fixed dispersal strategies. Our approach to understanding the stability of strategies is to show that if a resident population uses a certain class of strategies, it will achieve a distribution that is an ecologically stable equilibrium (ESE) (Vincent and Brown 2005; Vincent et al. 1996) relative to invasion by any competitor using any strategy outside that class. Because populations using strategies in this class can resist invasion by any other strategy, we interpret the results as implying that this class of strategies is noninvasible, which is a key aspect to evolutionary stability. Because we examine the ecological stability of an equilibrium arising from a given strategy relative to other populations using any other possible strategy, our results effectively amount to a pairwise invasibility analysis.

This paper is organized as follows. In Sect. 2 we describe the mathematical models and state the main results. Sections 3, 4, 5–6 are devoted to the proofs of our main results. Finally in Sect. 7 we discuss the meaning of our results.

2 Model formulations and statement of result

In this section we describe our modeling approach, discuss our terminology, and formulate our main results. We address two problems:

(1) determine when the dispersal strategy with no movement is evolutionarily stable;
(2) determine when an ideal free dispersal strategy is evolutionarily stable.

2.1 Competition model for m-species

We consider a competition model in n patches, in which m-species compete for the same resource, and these species have the same population dynamics but different movement strategies.

Let u_{ki} denote the population density of species k in patch i, $1 \leq k \leq m$ and $1 \leq i \leq n$, where m is the total number of species and n is the total number of patches. We assume that $m \geq 2$ and $n \geq 2$. Let d_{ij}^k denote the proportion of individuals of species k which move from patch j to patch i, where $d_{ij}^k \geq 0$ and $d_{ii}^k = 0$. For each $1 \leq k \leq m$, define the movement matrix D_k for species k by

$$D_k := \left(d_{ij}^k \right)_{1 \leq i, j \leq n}.$$

We say that a matrix is irreducible if it is not similar to a block upper triangular matrix with two blocks via a permutation.

Suppose that u_{ki} satisfies

$$\frac{du_{ki}}{dt} = \sum_{j=1}^{n} \left(d_{ij}^k u_{kj} - d_{ji}^k u_{ki} \right) + u_{ki} f_i \left(\sum_{l=1}^{m} u_{li} \right), \quad t > 0, \tag{2.1}$$

and $u_{ki}(0) > 0$ for every $1 \leq k \leq m$ and $1 \leq i \leq n$.

We assume that species interactions occur only within patches and functions f_i are only patch-dependent. We further assume that for every i, function f_i is continuous and strictly monotone decreasing in $[0, \infty)$, and $\lim_{x \to +\infty} f_i(x) = -\infty$. Hence, if $f_i(0) > 0$, there exists a unique positive constant K_i such that $f_i(K_i) = 0$. Define

$$N_+ = \{1 \leq i \leq n : f_i(0) > 0\}, \quad N_- = \{1 \leq i \leq n : f_i(0) \leq 0\}.$$

Biologically we can view N_+ as the union of source patches (high quality habitat) and N_- as the union of sink patches (low quality habitat).

Set $u = (u_1, \ldots, u_m)$, where $u_k = (u_{k1}, \ldots, u_{kn})^T$ for every $1 \leq k \leq m$, and A^T denotes the transpose of a matrix A. Define

$$u^* = (u_1^*, 0, \ldots, 0), \tag{2.2}$$

where $u_1^* = (u_{11}^*, \ldots, u_{1n}^*)^T$, and $u_{1i}^* = K_i$ if $i \in N_+$, $u_{1i}^* = 0$ if $i \in N_-$. Note that u^* is an equilibrium of (2.1) when $d_{ij}^1 = 0$ for every $1 \leq i, j \leq n$; i.e, when species 1 has no movement. Our first main result is

Theorem 1 *Suppose that both sets N_+ and N_- are non-empty, $d_{ij}^1 = 0$ for $1 \leq i, j \leq n$, and matrix D_k is irreducible for every $2 \leq k \leq m$. Then, the equilibrium u^* of (2.1) is globally asymptotically stable among all positive initial data; i.e., u^* is locally stable and*

$$\lim_{t \to \infty} u_{ki}(t) = \begin{cases} K_i, & k = 1, \ i \in N_+; \\ 0, & \textit{otherwise.} \end{cases}$$

Hastings (1983) considered a special case of (2.1), namely, $m = 2$ and the dispersals of both species are random; i.e., $d_{ij}^k = \mu_k L_{ij}$, where matrix (L_{ij}) is non-negative, symmetric and irreducible. This case describes random dispersal because the symmetric dispersal rates do not allow organisms to condition their dispersal on habitat quality or other factors. The constant μ_k is the dispersal rate for species k. He envisioned that two phenotypes are competing for the same resource, and the mutant is identical to the resident except for their random dispersal rates. Hastings' result in Hastings (1983) implies that if the environment is spatially heterogeneous but temporally constant (i.e., $K_i \neq K_j$ for some $i \neq j$ and K_i is time-independent for each i), the mutant can invade when rare if and only if it is the slower diffuser. Hence, in terms of the theory of adaptive dynamics (Dieckmann 1997; Dieckmann and Law 1996; Diekmann 2003; Geritz and Gyllenberg 2008; Geritz et al. 1998; Metz et al. 1996), Hastings' result implies that zero movement rate is a convergent stable strategy (CSS). Our Theorem 1 implies that zero dispersal rate (no movement) is an ESS in spatially heterogenous but temporally constant environments, when at least one of the patches is a sink; i.e., $(u^*, 0)$ is locally asymptotically stable. Furthermore, the strategy with no movement can displace strategies with positive movement rate; see Remark 2.2 for further discussions. Interestingly, if N_- is empty, zero dispersal rate may not be an ESS anymore as the following remark shows.

Remark 2.1 If N_- is empty, i.e., $f_i(0) > 0$ for every $1 \le i \le n$, it is tempting to conjecture that

$$\lim_{t \to \infty} u_{ki}(t) = \begin{cases} K_i, & k = 1, \ 1 \le i \le n, \\ 0, & \text{otherwise.} \end{cases}$$

But such conjecture can be false. For example, assume that $d_{ij}^k = \mu_k L_{ij}$, $\mu_1 = 0$ and $\mu_k > 0$ for $k \ge 2$, $\sum_{j=1}^n L_{ij} = \sum_{j=1}^n L_{ji}$ for every $1 \le i \le n$. Let c_k, $2 \le k \le m$, be any positive constants satisfying $\sum_{k=2}^m c_k < \min_{1 \le i \le n} K_i$. Define $\bar{u} = (\bar{u}_1, \dots, \bar{u}_m)$, $\bar{u}_k = (\bar{u}_{k1}, \dots, \bar{u}_{kn})^T$, where $\bar{u}_{ki}$ is given by

$$\bar{u}_{ki} = \begin{cases} K_i - \displaystyle\sum_{l=2}^m c_l, & k = 1, \ 1 \le i \le n, \\ c_k, & 2 \le k \le m, \ 1 \le i \le n. \end{cases}$$

Then $\bar{u}$ is a positive equilibrium of (2.1). Since c_k can be arbitrarily small and $\bar{u} = u^*$ when $c_k = 0$ for every $k \ge 2$, we see that u^* is not locally asymptotically stable when N_- is empty. $\qquad\square$

Next we turn to another class of dispersal strategies which are evolutionarily stable, motivated by the works from Cantrell et al. (2007a), McPeek and Holt (1992). If we restrict ourselves to the situation when N_- is empty, $f_i(x) = 0$ has a unique

positive equilibrium K_i for every i. Following Cantrell et al. (2007a), we first give the following definition:

Definition 1 Species k has an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$ if

$$\sum_{j=1}^{n} d_{ij}^k K_j = \left(\sum_{j=1}^{n} d_{ji}^k \right) K_i \tag{2.3}$$

holds for every $1 \leq i \leq n$. We say that species k does not have an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$ if (2.3) fails to hold for some i.

If species k has an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$, then the system of equations for species k

$$\frac{du_{ki}}{dt} = \sum_{j} \left(d_{ij}^k u_{kj} - d_{ji}^k u_{ki} \right) + u_{ki} f_i (u_{ki}), \quad t > 0 \tag{2.4}$$

has a unique positive equilibrium, precisely given by $(K_1, \ldots, K_n)$. When species k is at this equilibrium, its fitness, which is measured by the per capita growth rate, is equal to zero in all patches; moreover, the species has no net movement. In terms of the ideal free distribution theory Fretwell and Lucas (1970), the spatial distribution of species k at equilibrium is an ideal free distribution. A natural question is whether an ideal free dispersal strategy is evolutionarily stable. A general approach was proposed in Cantrell et al. (2007a) to address this question. It was shown in Cantrell et al. (2007a) that under quite general conditions the only possible evolutionarily stable dispersal strategies are ideal free ones. Furthermore, it was shown in Cantrell et al. (2007a) that under certain conditions ideal free dispersal strategies are evolutionarily stable, by constructing a Lyapunov functional. In this paper we construct a different Lyapunov functional which will enable us to obtain more general results on the evolutionary stability of both ideal free dispersal strategies and the dispersal strategy with no movement.

For two-species ($m = 2$) and n-patch, we have the following result:

Theorem 2 *Suppose that $m = 2$, N_- is empty, matrix D_k is non-negative and irreducible for $k = 1, 2$. If species 1 has an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$ and species 2 does not have an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$, then the equilibrium u^* of (2.1) is globally asymptotically stable among all positive initial data; i.e., u^* is locally stable and*

$$\lim_{t \to \infty} u_{ki}(t) = \begin{cases} K_i, & k = 1, \ 1 \leq i \leq n, \\ 0, & k = 2, \ 1 \leq i \leq n. \end{cases}$$

Remark 2.2 Theorem 1 shows that no movement is evolutionary stable when at least one of the patches is a sink. When all patches are sources, Theorem 2 implies that a species with an ideal free dispersal strategy will outcompete any other species whose dispersal strategy is not ideal free. In particular, ideal free dispersal strategies with respect to $(K_1, \ldots, K_n)$ are evolutionarily stable. It seems that the conclusions of

Theorem 1 are due to the fact that irreducible movement forces some individuals to move to sinks. If the "irreducibility" were restricted to movement among sources and assuming that such restricted movement is an ideal free dispersal strategy with respect to the carrying capacities of sources, we suspect that it is also evolutionarily stable. □

If two species both have ideal free dispersal strategies with respect to $(K_1, \ldots, K_n)$, it is not difficult to see that they can coexist. An immediate question for m competing species ($m \geq 3$) is: if species 1 has an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$ and none of the other species has an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$, can we still conclude that species 1 will drive other species to extinction as in Theorem 2? It turns out that the answer involves a particular combination of dispersal strategies for multiple competitors which enables them to distribute in space so that together they can exactly match the shared resource. To describe our general results for m competing species, we introduce the notion of a joint ideal dispersal strategy for arbitrarily number of species, which generalizes Definition 1 and seems to be of independent interest. In this connection, set $\hat{d}_{ij}^k = d_{ij}^k$ for every $i \neq j$ and $\hat{d}_{ii}^k = -\sum_{j=1}^n d_{ji}$ for every $1 \leq i \leq n$. Let $\hat{D}_k$ denote the $n \times n$ matrix $(\hat{d}_{ij}^k)_{1 \leq i,j \leq n}$, which is irreducible as matrix D_k is irreducible. Since $(1, \ldots, 1)\hat{D}_k = (0, \ldots, 0)$, by the Perron–Frobenius Theorem, zero is the dominant eigenvalue of $\hat{D}_k$ with left eigenvector $(1, \ldots, 1)$. Hence, again by the Perron–Frobenius Theorem, $\hat{D}_k$ has a right vector $\tilde{u}_k := (\tilde{u}_{k1}, \ldots, \tilde{u}_{kn})^T$ (unique up to scalar multiplication) with strictly positive entries. That is,

$$\sum_{j=1}^n d_{ij}^k \tilde{u}_{kj} = \left(\sum_{j=1}^n d_{ji}^k \right) \tilde{u}_{ki} \qquad (2.5)$$

for every $1 \leq i \leq n$. Clearly, (2.3) means that species k has an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$ if and only if $\tilde{u}_k$ can be chosen as the vector $(K_1, \ldots, K_n)^T$.

Definition 2 Given any integer $l \geq 1$, species $1, \ldots, l$ have a joint ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$ if there exist non-negative constants $c_k, 1 \leq k \leq l$, such that

$$\sum_{k=1}^l c_k \tilde{u}_k = (K_1, \ldots, K_n)^T \qquad (2.6)$$

holds. We say that species $1, \ldots, l$ have no joint ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$ if there are no non-negative constants c_k such that (2.6) holds.

By (2.5) we see that when $l = 1$, (2.6) is reduced to (2.3); i.e., for a single species, the notion of a joint ideal free dispersal strategy is the same as that of an ideal free dispersal strategy as defined in Definition 1. When $l \geq 2$, rather interestingly, it may

happen that none of the species $1, \ldots, l$ can produce an ideal free distribution as a single species but, as a combined effort of all species, a joint ideal free dispersal strategy can produce the ideal free distribution for each species, as the following remark shows.

Remark 2.3 If species $1, \ldots, l$ have a joint ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$, then the system of equations for l species (namely, species $1, \ldots, l$)

$$\frac{du_{ki}}{dt} = \sum_j \left(d_{ij}^k u_{kj} - d_{ji}^k u_{ki} \right) + u_{ki} f_i \left(\sum_{k=1}^l u_{ki} \right), \quad 1 \le k \le l, \; t > 0 \quad (2.7)$$

has a non-negative equilibrium $\hat{u} = (\hat{u}_1, \ldots, \hat{u}_l)$ given by $\hat{u}_k = c_k \tilde{u}_k$, $1 \le k \le l$. When species $1, \ldots, l$ are at this equilibrium, the fitness of each species is equal to zero in all patches:

$$f_i \left(\sum_{k=1}^l \hat{u}_{ki} \right) = f_i \left(\sum_{k=1}^l c_k \tilde{u}_{ki} \right) = f_i(K_i) = 0, \quad 1 \le i \le n.$$

Moreover, (2.5) implies that

$$\sum_j \left(d_{ij}^k \hat{u}_{kj} - d_{ji}^k \hat{u}_{ki} \right) = c_k \left[\sum_{j=1}^n d_{ij}^k \tilde{u}_{kj} - \left(\sum_{j=1}^n d_{ji}^k \right) \tilde{u}_{ki} \right] = 0, \quad \forall \, 1 \le k \le l;$$

$$(2.8)$$

i.e., for every $1 \le k \le l$, species k has no net movement. Hence, a combination of competitors can distribute themselves in space so that together they can exactly match the shared resource. □

Our following result generalizes Theorem 2 to general m competing species:

Theorem 3 *Suppose that N_- is empty and matrix D_k is non-negative and irreducible for $1 \le k \le m$. If species 1 has an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$ and species $2, \ldots, m$ have no joint ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$, then the equilibrium u^* of (2.1) is globally asymptotically stable among all positive initial data; i.e., u^* is locally stable and*

$$\lim_{t \to \infty} u_{ki}(t) = \begin{cases} K_i, & k = 1, \; 1 \le i \le n; \\ 0, & \text{otherwise}. \end{cases}$$

Remark 2.4 Theorem 3 fails if species $2, \ldots, m$ has a joint ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$, even though species 1 has an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$. To see this, let $\tilde{u}_1 = (K_1, \ldots, K_n)^T$ and $\sum_{k=2}^m c_k \tilde{u}_k = (K_1, \ldots, K_n)^T$ for some non-negative constants $c_k, 2 \le k \le m$. For any $0 < s < 1$, set $u^{**} = (u_1^{**}, \ldots, u_n^{**})$, where $u_1^{**} = s(K_1, \ldots, K_n)^T$ and

$u_k^{**} = (1 - s)c_k \tilde{u}_k$. Then u^{**} is an equilibria of (2.1). Since $c_k > 0$ for at least some $2 \leq k \leq m$, at least one of the species other than species 1 can coexist with species 1. As $0 < s < 1$ is arbitrarily and $u^{**}|_{s=1} = u^*$, we see that u^* in Theorem 3 is not even locally asymptotically stable. □

2.2 Consumer-resource models

Our results for the m-species competition model in n-patches can be extended to the following consumer-resource model:

$$
\begin{cases}
\dfrac{dR_i}{dt} = R_i \left(r_i \left[1 - \dfrac{R_i}{\tau_i} \right] - \sum_l u_{li} \right), & t > 0, \\[2mm]
\dfrac{du_{ki}}{dt} = \sum_j \left(d_{ij}^k u_{kj} - d_{ji}^k u_{ki} \right) + u_{ki} \left[g_i(R_i) - d_i \right], & t > 0,
\end{cases}
\tag{2.9}
$$

where R_i denotes the population density of the resource species in patch i, u_{ki} denotes the population density of the consumer species k in patch i, $1 \leq k \leq m$ and $1 \leq i \leq n$. The constants r_i, τ_i, and d_i are assumed to be all positive for every $1 \leq i \leq n$. We assume that for each $1 \leq i \leq n$, $g_i(x)$ is continuously differentiable, strictly monotone increasing in $[0, \infty)$ and $g_i(0) = 0$. Define

$$
\Omega_+ = \{1 \leq i \leq n : g_i(\tau_i) > d_i\}, \quad \Omega_- = \{1 \leq i \leq n : g_i(\tau_i) \leq d_i\}.
$$

For every $i \in \Omega_+$, set

$$
\mathcal{K}_i := r_i \left[1 - \frac{g_i^{-1}(d_i)}{\tau_i} \right] > 0.
$$

Define

$$
u^{**} := (u_1^{**}, 0, \ldots, 0),
\tag{2.10}
$$

where $u_1^{**} := (u_{11}^{**}, \ldots, u_{1n}^{**})^T$, and $u_{1i}^{**} = \mathcal{K}_i$ for $i \in \Omega_+$, $u_{1i}^{**} = 0$ for $i \in \Omega_-$.

Theorem 4 *Suppose that both sets Ω_+ and Ω_- are non-empty, $d_i \neq g_i(\tau_i)$ for every $1 \leq i \leq n$, $d_{ij}^1 = 0$ for every $1 \leq i, j \leq n$, and matrix D_k is non-negative and irreducible for every $k \geq 2$. Then, as $t \to \infty$, $R_i(t) \to \min\{\tau_i, g_i^{-1}(d_i)\}$ for every $1 \leq i \leq n$, and $u(t) \to u^{**}$.*

Similarly to Theorem 1, Theorem 4 shows that the dispersal strategy with no movement is an ESS for the consumer species in the consumer-resource model (2.9). We do not know whether Theorem 4 still holds if the resource species is also mobile.

Similarly to Theorem 2, we have the following result for the consumer-resource model (2.9).

Theorem 5 *Suppose that $\mathcal{K}_i > 0$ for every $1 \leq i \leq n$ (i.e., Ω_- is empty) and matrix D_k is irreducible for every $k \geq 1$. If species 1 has an ideal free dispersal strategy with respect to $(\mathcal{K}_1, \ldots, \mathcal{K}_n)$ and species $2, \ldots, m$ have no joint ideal free dispersal strategy with respect to $(\mathcal{K}_1, \ldots, \mathcal{K}_n)$, then, as $t \to \infty$, $R_i(t) \to g_i^{-1}(d_i)$ for every $1 \leq i \leq n$ and $u(t) \to u^{**}$.*

Again, Theorem 5 might fail if species $2, \ldots, m$ have a joint ideal free dispersal strategy with respect to $(\mathcal{K}_1, \ldots, \mathcal{K}_n)$.

Note that if species 1 has an ideal free dispersal strategy with respect to $(\mathcal{K}_1, \ldots, \mathcal{K}_n)$, we can choose $\tilde{u}_1 = (\mathcal{K}_1, \ldots, \mathcal{K}_n)^T$. Therefore, for the two-species case ($m = 2$), we have

Corollary 2.1 *Suppose that $m = 2, \mathcal{K}_i > 0$ for every $1 \leq i \leq n$, matrix D_k is non-negative and irreducible for $k = 1, 2$. If species 1 has an ideal free dispersal strategy with respect to $(\mathcal{K}_1, \ldots, \mathcal{K}_n)$ and species 2 does not have an ideal free dispersal strategy with respect to $(\mathcal{K}_1, \ldots, \mathcal{K}_n)$, then, $R_i(t) \to g_i^{-1}(d_i)$ as $t \to \infty$ for every $1 \leq i \leq n$, and*

$$\lim_{t \to \infty} u_{ki}(t) = \begin{cases} \mathcal{K}_i, & k = 1, \ 1 \leq i \leq n, \\ 0, & k = 2, \ 1 \leq i \leq n. \end{cases}$$

3 Proof of Theorem 1

This section is devoted to the proof of Theorem 1. Theorem 1 is a consequence of Lemmas 3.1, 3.2 and 3.4 and Theorem 6.

Recall that $u = (u_1, \ldots, u_m)$ and $u_k = (u_{k1}, \ldots, u_{kn})^T$ for every $1 \leq k \leq m$, where $u_{ki} \in \mathbb{R}$. Define $B := \{u : u_{ki} \geq 0, \ \forall \ 1 \leq k \leq m, \ 1 \leq i \leq n\}$ and $G = \{u \in B : u_{1i} > 0 \ \forall \ i \in N_+\}$.

Define $V : G \to \mathbb{R}$ by

$$V(u) = \sum_{i=1}^{n} \sum_{k=1}^{m} u_{ki} - \sum_{i \in N_+} \mathcal{K}_i \ln(u_{1i}).$$

For each $1 \leq k \leq m$ and $1 \leq i \leq n$, define

$$F_{ki}(u) := \sum_j \left(d_{ij}^k u_{kj} - d_{ji}^k u_{ki} \right) + u_{ki} f_i \left(\sum_{l=1}^{m} u_{li} \right).$$

Then for any $u \in G$,

$$\dot{V}(u) := \sum_{k=1}^{m} \sum_{i=1}^{n} \frac{\partial V}{\partial u_{ki}}(u) F_{ki}(u). \tag{3.1}$$

Lemma 3.1 *Suppose that $d_{ij}^1 = 0$ for $1 \le i, j \le n$ and f_i is strictly monotone decreasing. Then $\dot{V}(u) \le 0$, and $\dot{V}(u) = 0$ if and only if*

$$\sum_{l=1}^{m} u_{li} = K_i \quad \forall\, i \in N_+; \quad u_{li} \equiv 0 \quad \forall\, i \in N_-, 1 \le l \le m. \tag{3.2}$$

Proof By the definition of V, $\partial V / \partial u_{ki} = 1$ for $2 \le k \le m$ and $1 \le i \le n$; $\partial V / \partial u_{1i} = 1$ for $i \in N_-$; $\partial V / \partial u_{1i} = 1 - K_i / u_{1i}$ for $i \in N_+$. Hence, by (3.1),

$$\dot{V}(u) = \sum_{k=1}^{m} \sum_{i=1}^{n} F_{ki}(u) - \sum_{i \in N_+} F_{1i}(u) \cdot \frac{K_i}{u_{1i}}.$$

Since

$$\sum_{i,j=1}^{n} \left(d_{ij}^k u_{kj} - d_{ji}^k u_{ki} \right) = 0$$

for every $1 \le k \le m$, we have

$$\sum_{k=1}^{m} \sum_{i=1}^{n} F_{ki}(u) = \sum_{k=1}^{m} \sum_{i=1}^{n} u_{ki} f_i \left(\sum_{l=1}^{m} u_{li} \right)$$

$$= \sum_{i \in N_+} \left(\sum_{l=1}^{m} u_{li} \right) f_i \left(\sum_{l=1}^{m} u_{li} \right) + \sum_{i \in N_-} \left(\sum_{l=1}^{m} u_{li} \right) f_i \left(\sum_{l=1}^{m} u_{li} \right).$$

As $d_{ij}^1 = 0$ for $1 \le i, j \le n$,

$$\sum_{i \in N_+} F_{1i}(u) \cdot \frac{K_i}{u_{1i}} = \sum_{i \in N_+} K_i f_i \left(\sum_{l=1}^{m} u_{li} \right).$$

Hence,

$$\dot{V}(u) = \sum_{i \in N_+} \left[\left(\sum_{l=1}^{m} u_{li} \right) - K_i \right] f_i \left(\sum_{l=1}^{m} u_{li} \right) + \sum_{i \in N_-} \left(\sum_{l=1}^{m} u_{li} \right) f_i \left(\sum_{l=1}^{m} u_{li} \right).$$

Note that, as $f_i(K_i) = 0$ and f_i is strictly monotone decreasing for every $i \in N_+$,

$$\left[\left(\sum_{l=1}^{m} u_{li} \right) - K_i \right] f_i \left(\sum_{l=1}^{m} u_{li} \right) = \left[\left(\sum_{l=1}^{m} u_{li} \right) - K_i \right] \left[f_i \left(\sum_{l=1}^{m} u_{li} \right) - f_i(K_i) \right] \le 0,$$

where equality holds if and only if $\sum_{l=1}^{m} u_{li} = K_i, \forall\, i \in N_+$.

For any $i \in N_-$, since $f_i(0) \le 0$,

$$\left(\sum_{l=1}^{m} u_{li}\right) f_i\left(\sum_{l=1}^{m} u_{li}\right) = f_i(0)\left(\sum_{l=1}^{m} u_{li}\right) + \left(\sum_{l=1}^{m} u_{li}\right)\left(f_i\left(\sum_{l=1}^{m} u_{li}\right) - f_i(0)\right)$$

$$\le \left(\sum_{l=1}^{m} u_{li}\right)\left(f_i\left(\sum_{l=1}^{m} u_{li}\right) - f_i(0)\right) \le 0,$$

where equality holds if and only if $\sum_{l=1}^{m} u_{li} = 0$; that is, $u_{li} = 0, \forall\, 1 \le l \le m,\ i \in N_-$. Hence, $\dot{V}(u) \le 0$ for any $u \in G$, and $\dot{V}(u) = 0$ if and only if (3.2) holds true. $\square$

Recall that u^* is defined as in (2.2). The local stability of u^* is a direct consequence of Lyapunov's stability theorem, Lemma 3.1 and the following result:

Lemma 3.2 $V(u) \ge V(u^*)$ *for any* $u \in G$, *and equality holds for some* $u \in G$ *if and only if* $u = u^*$.

Proof It suffices to notice that for any $u \in G$,

$$V(u) - V(u^*) = \sum_{i \in N_+} \left[u_{1i} - K_i - K_i \ln\left(\frac{u_{1i}}{K_i}\right)\right] + \sum_{i \in N_-} u_{1i} + \sum_{i=1}^{n} \sum_{k \ge 2} u_{ki}.$$

It is well known that for any $a > 0$, the function $x - a - a \ln(x/a)$ is strictly positive in $(0, a) \cup (a, \infty)$ and is equal to zero at $x = a$. This shows that $V(u)$ is strictly larger than $V(u^*)$ for any $u \ne u^*$. $\square$

The asymptotic stability of u^* does not follow from Lyapunov's stability theorem since the set where $\dot{V}$ vanishes contains points other than u^*. It turns out LaSalle's invariant principle (LaSalle 1960) is a proper tool to establish the global convergence of solutions of (2.1) to u^*. There are various versions of LaSalle's invariant principle for ODEs and we shall use the following one:

Theorem 6 *Consider the system of differential equations*

$$\frac{dx}{dt} = f(x),$$

where $f : \mathbb{R}^n \to \mathbb{R}^n$ *is continuous. Suppose that* $V : G \subset \mathbb{R}^n \to \mathbb{R}$ *satisfies:*

(i) V *is continuous on* G;
(ii) V *is not continuous at* $\bar{x} \in \bar{G}$ *(the closure of* G*) implies that* $\lim_{x \to \bar{x}, x \in G} V(x) = +\infty$;
(iii) $\nabla V \cdot f \le 0$ *in* G.

Let

$$\mathcal{M} := \{x \mid \dot{V}(x) = 0,\ x \in \bar{G}\}$$

and $\mathcal{M}'$ be the largest invariant set in $\mathcal{M}$. Then every bounded (for $t \geq 0$) trajectory of $\dot{x} = f(x)$ which remains in G for $t \geq 0$ tends to the set $\mathcal{M}'$ as $t \to +\infty$.

Theorem 6 was formulated as Theorem 1.2 of Lu and Wolkowicz (1992).

Suppose that $L_{ij} \geq 0$ for $1 \leq i, j \leq n$ and the $n \times n$ matrix (L_{ij}) is irreducible. By the Perron–Frobenius Theorem, there exists a vector $w^* := (w_1^*, \ldots, w_n^*)^T$ (unique up to scalar multiplication) with strictly positive entries such that

$$\sum_{j=1}^{n} L_{ij} w_j^* = \left(\sum_{j=1}^{n} L_{ji} \right) w_i^*$$

for every $1 \leq i \leq n$. We have the following result (see Arino 2008, Theorem 2.2):

Lemma 3.3 *Suppose that $L_{ij} \geq 0$ for $1 \leq i, j \leq n$ and (L_{ij}) is irreducible. Let $w_i(t)$, $1 \leq i \leq n$, satisfy*

$$\frac{dw_i}{dt} = \sum_{j=1}^{n} \left(L_{ij} w_j - L_{ji} w_i \right), \quad t > 0, \quad w_i(0) \geq 0. \tag{3.3}$$

Then, for each $1 \leq i \leq n$,

$$\lim_{t \to \infty} w_i(t) = \frac{w_i^*}{\sum_{j=1}^{n} w_j^*} \sum_{i=1}^{n} w_i(0).$$

Lemma 3.4 *Let $\mathcal{M} := \{u \mid \dot{V}(u) = 0, \ u \in \bar{G}\}$. The largest invariant subset, $\mathcal{M}'$, of $\mathcal{M}$ is $\{u^*\}$.*

Proof Note that

$$\mathcal{M} = \left\{ u \in B : \sum_{l=1}^{m} u_{li} = K_i \ \forall i \in N_+; u_{li} = 0 \ \forall i \in N_-, 1 \leq l \leq m \right\}.$$

Let $u(0) \in \mathcal{M}'$. Then, $u(t) \in \mathcal{M}$ for any $t \geq 0$; i.e., $\sum_{l=1}^{m} u_{li}(t) = K_i \ \forall i \in N_+$ and $u_{li}(t) = 0$ for every $i \in N_-, 1 \leq l \leq m$. We observe that $u_{ki} f_i(\sum_{l=1}^{m} u_{li}) = 0$ for every $1 \leq i \leq n$ and $1 \leq k \leq m$. For $i \in N_-$, this follows from $u_{li}(t) = 0$ for every $i \in N_-, 1 \leq l \leq m$. For $i \in N_+$, it follows from $f_i(K_i) = 0$ and $\sum_{l=1}^{m} u_{li}(t) = K_i$ for every $i \in N_+$ that $f_i(\sum_{l=1}^{m} u_{li}) = f_i(K_i) = 0$. Therefore, for every $1 \leq i \leq n$ and $1 \leq k \leq m$,

$$\frac{du_{ki}}{dt} = \sum_{j} \left(d_{ij}^k u_{kj} - d_{ji}^k u_{ki} \right)$$

for $t \geq 0$. We show that $u_{ki}(0) = 0$ for every $1 \leq i \leq n$ and $2 \leq k \leq m$. If not, suppose that $u_{\bar{k}\bar{i}}(0) > 0$ for some $\bar{i} \in \{1, \ldots, n\}$ and some $\bar{k} \in \{2, \ldots, m\}$. Then,

$\sum_{j=1}^{n} u_{\bar{k}j}(0) > 0$. Since matrix (d_{ij}^{k}) is irreducible for $k \geq 2$, by Lemma 3.3, $u_{\bar{k}i}(t) \rightarrow a_{\bar{k}} \bar{u}_{\bar{k}i}$ for every $1 \leq i \leq n$ as $t \rightarrow \infty$, where $a_{\bar{k}} = \sum_{j} u_{\bar{k}j}(0)/(\sum_{j} \bar{u}_{\bar{k}j}) > 0$. This contradicts $u_{\bar{k}j}(t) = 0$ for every $j \in N_{-}$. Hence, $u_{ki}(0) = 0$ for every $1 \leq i \leq n$ and $2 \leq k \leq m$. Since $\sum_{l=1}^{m} u_{li}(t) = K_{i}$ for every $i \in N_{+}$, we obtain $u_{1i}(0) = K_{i}$ for every $i \in N_{+}$. Recall that $u_{1i}(0) = 0$ for every $i \in N_{-}$. Therefore, $u(0) = u^{*}$. This completes the proof. $\qquad\square$

4 Proof of Theorem 3

This section is devoted to the proof of Theorem 3. Theorem 3 is a consequence of Lemmas 4.1, 4.2 and 4.3 and Theorem 6.

We first introduce a class of matrices which is a natural generalization of symmetric matrices. A $n \times n$ matrix A is called line-sum-symmetric if for every $1 \leq i \leq n$, the sum of the elements in the i-th row of A equals the sum of the elements in the i-th column of A. The following result gives a classification of line-sum-symmetric matrices (Eaves et al. 1985; Corollary 3).

Theorem 7 *Let A be an $n \times n$ nonnegative matrix. Then A is line-sum-symmetric if and only if*

$$\sum_{i,j=1}^{n} a_{ij} \frac{x_i}{x_j} \geq \sum_{i,j=1}^{n} a_{ij} \tag{4.1}$$

for all $x_i > 0, 1 \leq i \leq n$. Moreover, if A is irreducible and line-sum-symmetric, equality in (4.1) holds if and only if all the coordinates of $x = (x_1, \ldots, x_n)$ coincide, i.e., $x_i = x_j$ for any $1 \leq i, j \leq n$.

In this section we define $B := \{u : u_{ki} \geq 0, \forall 1 \leq k \leq m, 1 \leq i \leq n\}$ and $G = \{u \in B : u_{1i} > 0 \forall i\}$. Define $V : G \rightarrow \mathbb{R}$ by

$$V(u) = \sum_{i=1}^{n} \sum_{k=1}^{m} u_{ki} - \sum_{i=1}^{n} K_i \ln(u_{1i}).$$

Lemma 4.1 *Suppose that $\sum_{j}(d_{ij}^{1} K_j - d_{ji}^{1} K_i) = 0$ for every $1 \leq i \leq n$, i.e., the species 1 is adopting an ideal free dispersal strategy with respect to $(K_1, \ldots, K_n)$. Then $\dot{V}(u) \leq 0$, and $\dot{V}(u) = 0$ if and only if there exists some $\kappa > 0$ such that $u_{1i} = \kappa K_i$ and $\sum_{l=2}^{m} u_{li} = (1 - \kappa)K_i$ for every $1 \leq i \leq n$.*

Proof Recall that $\dot{V}(u)$ is defined as in (3.1). Similarly to the proof of Lemma 3.1, after some calculations we have

$$\dot{V}(u) = \sum_{i=1}^{n} \left(\sum_{l=1}^{m} u_{li} - K_i \right) f_i \left(\sum_{l=1}^{m} u_{li} \right) - \left[\sum_{i,j=1}^{n} \frac{K_i}{u_{1i}} d_{ij}^{1} u_{1j} - \sum_{i,j=1}^{n} K_i d_{ji}^{1} \right].$$

Note that, as $f_i(K_i) = 0$ and f is strictly monotone decreasing, for every i,

$$\left[\left(\sum_{l=1}^m u_{li}\right) - K_i\right] f_i\left(\sum_{l=1}^m u_{li}\right) = \left[\left(\sum_{l=1}^m u_{li}\right) - K_i\right]\left[f_i\left(\sum_{l=1}^m u_{li}\right) - f_i(K_i)\right] \leq 0,$$

where equality holds if and only if $\sum_{l=1}^m u_{li} = K_i, \forall i$.

Set $h_{ij} = d_{ij}^1 K_j$. By our assumption, (h_{ij}) is line-sum-symmetric, non-negative and irreducible. Set $b_i := K_i/u_{1i} > 0$. Then by Theorem 7,

$$\sum_{i,j=1}^n \frac{K_i}{u_{1i}} d_{ij}^1 u_{1j} - \sum_{i,j=1}^n K_i d_{ji}^1 = \sum_{i,j=1}^n h_{ij} \frac{b_i}{b_j} - \sum_{i,j=1}^n h_{ij} \geq 0,$$

where equality holds if and only if $b_i = b_j$ for every $1 \leq i, j \leq n$; i.e., $u_{1,i}/K_i = \kappa$ for some $\kappa > 0$ and every $1 \leq i \leq n$. Hence, $\dot{V}(u) \leq 0$. Moreover, $\dot{V}(u) = 0$ if and only if for every $1 \leq i \leq n$, $\sum_{l=1}^m u_{li} = K_i$ and there exists some $\kappa > 0$ such that $u_{1,i}/K_i = \kappa$ for some $\kappa > 0$, which hold if and only if $u_{1i} = \kappa K_i$ and $\sum_{l=2}^m u_{li} = (1 - \kappa)K_i$ for every $1 \leq i \leq n$. □

Recall that u^* is defined as in (2.2). The local stability of u^* is a direct consequence of Lyapunov's stability theorem, Lemma 4.1 and the following result:

Lemma 4.2 $V(u) \geq V(u^*)$ *for any* $u \in G$, *and equality holds for some* $u \in G$ *if and only if* $u = u^*$.

Proof It suffices to notice that for any $u \in G$,

$$V(u) - V(u^*) = \sum_{i=1}^n \left[u_{1i} - K_i - K_i \ln\left(\frac{u_{1i}}{K_i}\right)\right] + \sum_{i=1}^n \sum_{k\geq 2} u_{ki},$$

and $u_{1i} - K_i - K_i \ln\frac{u_{1i}}{K_i} \geq 0$ for any $u_{1i} > 0$, where the equality holds if and only if $u_{1i} = K_i$. □

We apply LaSalle's invariant principle to establish the global convergence of solutions of (2.1) to u^*.

Lemma 4.3 *Suppose that* $\sum_j \left(d_{ij}^1 K_j - d_{ji}^1 K_i\right) = 0$ *for every* $1 \leq i \leq n$, D_k *is irreducible for every* $1 \leq k \leq m$, *and there exist no non-negative constants* $\tau_k, 2 \leq k \leq m$, *such that* $\tilde{u}_1 = \sum_{k=2}^m \tau_k \tilde{u}_k$. *Let* $\mathcal{M} := \{u|\ \dot{V}(u) = 0, u \in \bar{G}\}$. *Then, the largest invariant subset* $\mathcal{M}'$ *of* $\mathcal{M}$ *is* $\{u^* = (u_1^*, 0, \ldots, 0) : u_{1i}^* = K_i > 0, \forall\ 1 \leq i \leq n\}$.

Proof By Lemma 4.1,

$$\mathcal{M} = \left\{u \in B : u_{1i} = \kappa K_i, \sum_{l=2}^m u_{li} = (1 - \kappa)K_i, 1 \leq i \leq n\right\}.$$

Let $u(0) \in \mathcal{M}'$. Then, $u(t) \in \mathcal{M}$ for any $t \geq 0$; i.e., $u_{1i}(t) = \kappa(t)K_i$, and $\sum_{l=2}^{m} u_{li}(t) = (1 - \kappa(t))K_i$ for $1 \leq i \leq n$. This implies that $f_i \left(\sum_{l=1}^{m} u_{li}(t)\right) = f_i(K_i) = 0$ for every $1 \leq i \leq n$. Therefore, for every $1 \leq i \leq n$ and $1 \leq k \leq m$, u_{ki} satisfies

$$\frac{du_{ki}}{dt} = \sum_{j} \left(d_{ij}^{k} u_{kj} - d_{ji}^{k} u_{ki}\right), \quad t > 0. \tag{4.2}$$

Substituting $u_{1i} = \kappa(t)K_i$, $1 \leq i \leq n$, into the Eq. (4.2), as $\sum_{j} \left(d_{ij}^{1} K_j - d_{ji}^{1} K_i\right) = 0$, we have $\kappa'(t)K_i = 0$, i.e., κ is a constant. In particular, this implies that

$$\sum_{l=2}^{m} u_{li}(t) = (1 - \kappa)K_i \tag{4.3}$$

for $1 \leq i \leq n$. Since u_{li} are all non-negative, we see that $\kappa \in (0, 1]$.

We claim that $\kappa = 1$. To establish our assertion, we argue by contradiction: if not, suppose that $\kappa < 1$. By Lemma 3.3, for every $k \geq 2$, $\lim_{t \to \infty} u_{ki}(t) = a_k \tilde{u}_{ki}$, where $a_k := \sum_{i} u_{ki}(0) / \left(\sum_{j} \tilde{u}_{kj}\right)$. By letting $t \to \infty$ in (4.3) we have $\sum_{l=2}^{m} a_l \tilde{u}_{li} = (1 - \kappa)K_i$ for every $1 \leq i \leq n$. Since $\kappa < 1$, we have $\sum_{l=2}^{m} [a_l/(1 - \kappa)]\tilde{u}_{li} = K_i$ for every $1 \leq i \leq n$. That is, $\sum_{l=2}^{m} [a_l/(1 - \kappa)]\tilde{u}_l = \tilde{u}_1$ since $\tilde{u}_1$ can be chosen as the vector $(K_1, \ldots, K_n)$. This contradicts our assumption. Therefore, $\kappa = 1$. In particular, (4.3) implies that $u_{li}(t) = 0$ for every $2 \leq l \leq m$ and $1 \leq i \leq n$. Also, we have $u_{1i}(t) = K_i$. This proves that $u(t) = u^*$ and thus completes the proof. $\square$

5 Proof of Theorem 4

This section is devoted to the proof of Theorem 4. Theorem 4 is a consequence of Lemmas 5.1, 5.2 and Theorem 6.

In this section we define $B := \{(R, u) : R_i \geq 0, \ u_{ki} \geq 0, \ \forall \ 1 \leq k \leq m, \ 1 \leq i \leq n\}$ and $G = \{(R, u) \in B : R_i > 0 \ \forall \ i, \ u_{1i} > 0 \ \forall \ i \in \Omega_+\}$. Define $V : G \to \mathbb{R}$ by

$$V(R, u) = \sum_{i=1}^{n} \sum_{k=1}^{m} u_{ki} - \sum_{i \in \Omega_+} \mathcal{K}_i \ln(u_{1i}) + \sum_{i} G_i(R_i),$$

where G_i is a scalar function satisfying $G_i(0) = 0$ and

$$G_i'(x) = \frac{g_i(x) - \min\{g_i(\tau_i), d_i\}}{x}, \quad x > 0,$$

for every $1 \leq i \leq n$. As g_i is C^1 and $g_i(0) = 0$, the functions G_i behave like negative multiples of the logarithm near 0 and hence V will satisfy hypothesis (ii) of Theorem 6.

For $1 \leq i \leq n$, set

$$H_i(R, u) := R_i \left(r_i \left[1 - \frac{R_i}{\tau_i} \right] - \sum_l u_{li} \right).$$

For $1 \leq k \leq m$ and $1 \leq i \leq n$, set

$$\tilde{F}_{ki}(R, u) := \sum_j \left(d_{ij}^k u_{kj} - d_{ji}^k u_{ki} \right) + u_{ki} \left[g_i(R_i) - d_i \right].$$

Then for any $(R, u) \in G$,

$$\dot{V}(R, u) = \sum_{i=1}^n \frac{\partial V}{\partial R_i}(R, u) H_i(R, u) + \sum_{k=1}^m \sum_{i=1}^n \frac{\partial V}{\partial u_{ki}}(R, u) \tilde{F}_{ki}(R, u). \quad (5.1)$$

Lemma 5.1 *Suppose that $d_i \neq g_i(\tau_i)$ for every $1 \leq i \leq n$ and $d_{ij}^1 = 0$ for every $1 \leq i, j \leq n$. Then, $\dot{V}(R, u) \leq 0$ for any $(R, u) \in G$. Furthermore, $\dot{V}(R, u) = 0$ if and only if*

$$R_i = \min\{g_i^{-1}(d_i), \tau_i\} \quad \forall 1 \leq i \leq n; \quad u_{li} = 0 \quad \forall 1 \leq l \leq m, \ \forall i \in \Omega_-. \quad (5.2)$$

Proof By the definition of V, $\partial V / \partial u_{ki} = 1$ for $2 \leq k \leq m$ and $1 \leq i \leq n$; $\partial V / \partial u_{1i} = 1$ for $i \in \Omega_-$; $\partial V / \partial u_{1i} = 1 - \mathcal{K}_i / u_{1i}$ for $i \in \Omega_+$. Hence, as in the proof of Lemma 3.1,

$$\sum_{k=1}^m \sum_{i=1}^n \frac{\partial V}{\partial u_{ki}} \tilde{F}_{ki} = \sum_{i=1}^n \left(\sum_{l=1}^m u_{li} \right) [g_i(R_i) - d_i] - \sum_{i \in \Omega_+} \mathcal{K}_i [g_i(R_i) - d_i].$$

Since

$$\frac{\partial V}{\partial R_i} = \frac{g_i(R_i) - \min\{g_i(\tau_i), d_i\}}{R_i},$$

we obtain

$$\sum_{i=1}^n \frac{\partial V}{\partial R_i} H_i = \sum_{i=1}^n [g_i(R_i) - \min\{g_i(\tau_i), d_i\}] \cdot \left[r_i \left(1 - \frac{R_i}{\tau_i} \right) - \left(\sum_{l=1}^m u_{li} \right) \right]$$

$$= \sum_{i \in \Omega_+} [g_i(R_i) - d_i] \left[r_i \left(1 - \frac{R_i}{\tau_i} \right) - \left(\sum_{l=1}^m u_{li} \right) \right]$$

$$+ \sum_{i \in \Omega_-} [g_i(R_i) - g_i(\tau_i)] \left[r_i \left(1 - \frac{R_i}{\tau_i} \right) - \left(\sum_{l=1}^m u_{li} \right) \right].$$

Hence, after some direct calculations,

$$\dot{V}(R, u) = - \sum_{i \in \Omega_+} \frac{r_i}{\tau_i} [g_i(R_i) - d_i] \left[R_i - g_i^{-1}(d_i) \right]$$
$$- \sum_{i \in \Omega_-} \frac{r_i}{\tau_i} [g_i(\tau_i) - g_i(R_i)] [\tau_i - R_i]$$
$$- \sum_{i \in \Omega_-} \left(\sum_{l=1}^{m} u_{li} \right) [d_i - g_i(\tau_i)].$$

Since g_i is strictly monotone increasing,

$$\sum_{i \in \Omega_+} [g_i(R_i) - d_i] \left[R_i - g_i^{-1}(d_i) \right] \geq 0,$$

and equality holds if and only if $R_i = g_i^{-1}(d_i)$ for every $i \in \Omega_+$. Similarly,

$$\sum_{i \in \Omega_-} [g_i(\tau_i) - g_i(R_i)] [\tau_i - R_i] \geq 0,$$

and equality holds if and only if $R_i = \tau_i$ for every $i \in \Omega_-$. Finally,

$$\sum_{i \in \Omega_-} \left(\sum_{l=1}^{m} u_{li} \right) [d_i - g_i(\tau_i)] \geq 0,$$

and equality holds if and only if $u_{li} = 0$ for every l and every $i \in \Omega_-$. Hence, $\dot{V}(R, u) \leq 0$, and $\dot{V}(R, u) = 0$ if and only if (5.2) hold. $\qquad \square$

Set $R^* = (R_1^*, \ldots, R_n^*)$, where $R_i^* = \min\{g_i^{-1}(d_i), \tau_i\}$. Recall that u^{**} is defined as in (2.10).

Lemma 5.2 *Suppose that Ω_+ and Ω_- are non-empty, $d_i \neq g_i(\tau_i)$ for every $1 \leq i \leq n$, $d_{ij}^1 = 0$ for every $1 \leq i, j \leq n$ and D_k is irreducible for every $k \geq 2$. Let $\mathcal{M} := \{(R, u) | \dot{V}(R, u) = 0, (R, u) \in \bar{G}\}$. Then, the largest invariant subset $\mathcal{M}'$ of $\mathcal{M}$ is $\{(R, u) = (R^*, u^{**})\}$.*

Proof Note that by Lemma 5.1,

$$\mathcal{M} = \left\{ (R, u) : R = R^*, \quad u_{li} = 0 \quad \forall i \in \Omega_-, 1 \leq l \leq m \right\}.$$

Let $(R(0), u(0)) \in \mathcal{M}'$. Then, $R(t) = R^*$ for any $t \geq 0$, and $u_{ki}(t) = 0$ for every $i \in \Omega_-$ and $1 \leq k \leq m$. Hence, for $i \in \Omega_+$, $g_i(R_i(t)) - d_i = 0$. This implies that for every $i \in \Omega_+$ and $1 \leq k \leq m$,

$$\frac{d u_{ki}}{dt} = \sum_{j} \left(d_{ij}^k u_{kj} - d_{ji}^k u_{ki} \right), \quad t > 0. \tag{5.3}$$

Since $u_{ki}(t) = 0$ for every $1 \leq k \leq m$ and $i \in \Omega_-$, we see that (5.3) holds for every $1 \leq k \leq m$ and $1 \leq i \leq n$. For $k \geq 2$, as matrix D_k is non-negative and irreducible, by Lemma 3.3 and $u_{ki}(t) = 0$ for every $1 \leq k \leq m$ and $i \in \Omega_-$, we see that the only possibility is that $u_{ki} = 0$ for every $2 \leq k \leq m$ and $1 \leq i \leq n$.

By the equation of R_i and $R_i(t) = R_i^*$, we have

$$\sum_{l=1}^{m} u_{li} = r_i \left(1 - \frac{R_i^*}{\tau_i}\right)$$

for every $1 \leq i \leq n$. As $u_{li} = 0$ for every $i \in \Omega_+$ and $l \geq 2$, we have $u_{1i} = \mathcal{K}_i$ for $i \in \Omega_+$. As $u_{1i} = 0$ for every $i \in \Omega_-$, we see that $u(t) = u^{**}$ for all t. This completes the proof. $\qquad\square$

6 Proof of Theorem 5

This section is devoted to the proof of Theorem 5. Theorem 5 is a consequence of Lemmas 6.1, 6.2 and Theorem 6.

In this section we define $B := \{(R, u) : R_i \geq 0, \ u_{ki} \geq 0, \ \forall\, 1 \leq k \leq m, \ 1 \leq i \leq n\}$ and $G = \{(R, u) \in B : R_i > 0, \ u_{1i} > 0 \ \forall\, i\}$.

Recall that $\mathcal{K}_i$ is defined by

$$\mathcal{K}_i = r_i \left(1 - \frac{g_i^{-1}(d_i)}{\tau_i}\right),$$

which is positive for every i if we assume that $g_i(\tau_i) > d_i$ for every i.

Define $V : G \rightarrow \mathbb{R}$ by

$$V(R, u) = \sum_{i=1}^{n} \sum_{k=1}^{m} u_{ki} - \sum_{i=1}^{n} \mathcal{K}_i \ln(u_{1i}) + \sum_{i=1}^{n} G_i(R_i),$$

where G_i is a scalar function which satisfies

$$G_i'(x) = \frac{g_i(x) - d_i}{x}, \quad G_i(0) = 0.$$

Recall that $\dot{V}$ is defined as in (5.1).

Lemma 6.1 *Suppose that $g_i(\tau_i) > d_i$ and $\sum_{j=1}^{n} d_{ij}^1 \mathcal{K}_j = \sum_{j=1}^{n} d_{ji}^1 \mathcal{K}_i$ for every $1 \leq i \leq n$. Then $\dot{V}(R, u) \leq 0$ for $(R, u) \in G$. Furthermore, $\dot{V}(R, u) = 0$ if and only if $R_i = g_i^{-1}(d_i)$ for every $1 \leq i \leq n$ and there exists some constant $\kappa > 0$ such that $u_{1i} = \kappa \mathcal{K}_i$ for every $1 \leq i \leq n$.*

Proof Similar to the proof of Lemma 5.1, we have

$$\dot{V}(R, u) = -\sum_{i=1}^{n} \frac{r_i}{\tau_i}[g_i(R_i) - d_i][R_i - g_i^{-1}(d_i)] - \left[\sum_{i,j=1}^{n} \frac{\mathcal{K}_i}{u_{1i}}d_{ij}^1 u_{1j} - \sum_{i,j=1}^{n} \mathcal{K}_i d_{ji}^1\right].$$

Note that

$$[g_i(R_i) - d_i][R_i - g_i^{-1}(d_i)] \geq 0,$$

where equality holds if and only if $R_i = g_i^{-1}(d_i)$ for every $1 \leq i \leq n$.

Set $h_{ij} = d_{ij}^1 \mathcal{K}_j$. By assumption on the matrix (d_{ij}^1), the matrix (h_{ij}) is line symmetric, non-negative and irreducible. Set $b_i := \mathcal{K}_i/u_{1i} > 0$. Then by Theorem 7,

$$\sum_{i,j=1}^{n} \frac{\mathcal{K}_i}{u_{1i}}d_{ij}^1 u_{1j} - \sum_{i,j=1}^{n} \mathcal{K}_i d_{ji}^1 = \sum_{i,j=1}^{n} h_{ij}\frac{b_i}{b_j} - \sum_{i,j=1}^{n} h_{ij} \geq 0,$$

where the equality holds if and only if $b_i = b_j$ for every $1 \leq i, j \leq n$. Hence, $\dot{V}(R, u) \leq 0$ for $(R, u) \in G$, and $\dot{V}(R, u) = 0$ if and only if $R_i = g_i^{-1}(d_i)$ for every $1 \leq i \leq n$ and there exists some constant $\kappa > 0$ such that $u_{1i} = \kappa \mathcal{K}_i$ for every $1 \leq i \leq n$. $\square$

Let $\mathcal{M} := \{(R, u)| \dot{V}(R, u) = 0, (R, u) \in \bar{G}\}$. By previous lemma, we see that $\mathcal{M}$ is given by

$$\mathcal{M} = \left\{(R, u) \in B : R_i = g_i^{-1}(d_i) \,\forall\, 1 \leq i \leq n, \quad u_{1i}/\mathcal{K}_i = u_{1j}/\mathcal{K}_j \,\forall\, 1 \leq i, j \leq n\right\}.$$

Set $R^* = (R_1^*, \ldots, R_n^*)$, where $R_i^* = g_i^{-1}(d_i)$. Recall that u^{**} is defined as in (2.10).

Lemma 6.2 *Suppose that* $\sum_j \left(d_{ij}^1 \mathcal{K}_j - d_{ji}^1 \mathcal{K}_i\right) = 0$ *for every* $1 \leq i \leq n$, D_k *is irreducible for every* $1 \leq k \leq m$, *and there exist no non-negative constants* $\tau_k, 2 \leq k \leq m$, *such that* $\tilde{u}_1 = \sum_{k=2}^{m} \tau_k \tilde{u}_k$. *Then, the largest invariant subset* $\mathcal{M}'$ *of* $\mathcal{M}$ *is* $\{(R, u) = (R^*, u^{**})\}$.

Proof Let $(R(0), u(0)) \in \mathcal{M}'$. Then, $(R(t), u(t)) \in \mathcal{M}$ for any $t \geq 0$; i.e., $R_i(t) = g_i^{-1}(d_i)$ for every i and there exists some $\kappa(t)$ such that $u_{1i}(t) = \kappa(t)\mathcal{K}_i$ for every i. By the equation of u_{ki} and $R_i(t) = g_i^{-1}(d_i)$, for every $1 \leq i \leq n$ and $1 \leq k \leq m$, u_{ki} satisfies

$$\frac{du_{ki}}{dt} = \sum_j \left(d_{ij}^k u_{kj} - d_{ji}^k u_{ki}\right), \quad t > 0. \tag{6.1}$$

Substituting $u_{1i} = \kappa(t)\mathcal{K}_i, 1 \leq i \leq n$, into (6.1), as $\sum_j \left(d_{ij}^1 \mathcal{K}_j - d_{ji}^1 \mathcal{K}_i\right) = 0$, we have $\kappa'(t)\mathcal{K}_i = 0$, i.e., κ is a constant. By the equation for R_i and $R_i = g_i^{-1}(d_i)$, we have $\sum_k u_{ki}(t) = \mathcal{K}_i$ for every i. Hence,

$$\sum_{l=2}^{m} u_{li}(t) = (1 - \kappa)\mathcal{K}_i \qquad (6.2)$$

for $1 \leq i \leq n$. Since u_{li} are all non-negative, we see that $\kappa \in (0, 1]$.

We claim that $\kappa = 1$. To establish our assertion, we argue by contradiction: if not, suppose that $\kappa < 1$. By Lemma 3.3, for every $k \geq 2$, $\lim_{t\to\infty} u_{ki}(t) = a_k \tilde{u}_{ki}$, where $a_k := \sum_i u_{ki}(0)/\left(\sum_j \tilde{u}_{kj}\right)$. By letting $t \to \infty$ in (6.2) we have $\sum_{l=2}^{m} a_l \tilde{u}_{li} = (1 - \kappa)\mathcal{K}_i$ for every $1 \leq i \leq n$. Since $\kappa < 1$, we have $\sum_{l=2}^{m}[a_l/(1 - \kappa)]\tilde{u}_{li} = \mathcal{K}_i$ for every $1 \leq i \leq n$. That is, $\sum_{l=2}^{m}[a_l/(1 - \kappa)]\tilde{u}_l = \tilde{u}_1$ since $\tilde{u}_1$ can be chosen as $(\mathcal{K}_1, \ldots, \mathcal{K}_n)$ (up to a positive scalar multiplication). This contradicts our assumption. Therefore, $\kappa = 1$. In particular, (6.2) implies that $u_{li}(t) = 0$ for every $2 \leq l \leq m$ and $1 \leq i \leq n$. Also, we have $u_{1i}(t) = \mathcal{K}_i$. This shows that $u(t) = u^{**}$ and thus completes the proof. □

7 Discussion

All of our results are set in the context of discrete-diffusion models on a network consisting of an arbitrary but finite number of patches, under the assumption that all admissible dispersal strategies other than no dispersal at all result in positive population densities in all patches. In all cases we consider a situation where an arbitrary but finite number of populations that are identical in every aspect except for their dispersal strategies compete for a common resource. We consider both models for just the competitors and models that include the dynamics of both the competitors and a shared resource. In all cases we conclude that if one competitor is using a strategy that produces an ideal free distribution, and no other combination of competitors use strategies that produce an ideal free distribution for their combined densities, then the competitor using the ideal free dispersal strategy will exclude all others. If there is another combination of competitors that distribute themselves in space so that together they can exactly match the shared resource, that combination functions like another single competitor using an ideal free dispersal strategy. Such a combination of competitors could be said to be using a joint ideal free dispersal strategy. Our results imply that this would allow them to coexist with other single competitors using IFD strategies. In the case of pairwise competition, the competitor with the IFD dispersal strategy will always exclude the other competitor if the other competitor uses a non-IFD strategy. (If two or more competitors use strategies that can produce ideal free distribution then they can coexist in a neutrally stable state.) We conclude that strategies which produce an ideal free population distribution are evolutionarily stable relative to strategies that do not. Since a population using an ideal free dispersal strategy can invade and exclude populations using other strategies, we can conclude that ideal free dispersal is in some sense a global neighborhood invader strategy (NIS) (see Apaloo et al. 2009).

Our models lead to different specific conclusions in the cases of those environments that include sink habitats versus those that do not. Recall that we consider classes of strategies that lead to positive densities on all patches if there is any dispersal at all. In the case of environments containing sinks there is no such strategy leading to an IFD,

so the only ESS is the strategy of no dispersal at all, and that strategy is evolutionarily stable. That conclusion is consistent with the results of Dockery et al. (1998), Hastings (1983). In the case of environments without sinks, there is a continuum of IFD strategies which can be characterized by an algebraic relationship between patch qualities and dispersal rates between patches. In that case, any IFD strategy is an ESS and an NIS versus any set of strategies within which no combination of other populations can achieve an IFD. In situations where more than one population can achieve an IFD, their dispersal strategies can coexist and are mutually neutrally stable.

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