Environmentally induced dispersal under heterogeneous logistic growth

Víctor Padrón a,b,*, María Cristina Trevisan b

a School of Mathematics, University of Minnesota, 127 Vincent Hall, 206 Church Street S.E., Minneapolis, MN 55455, United States
b Departamento de Matemáticas, Facultad de Ciencias, Universidad de Los Andes, Mérida 5101, Venezuela

Received 17 June 2005; received in revised form 24 October 2005; accepted 22 November 2005

Communicated by Eberhard Voit

Abstract

We consider a single-species model which is composed of several habitats connected by linear migration rates and having logistic growth. A spatially varying, temporally constant environment is introduced by the non-homogeneity of its carrying capacity. Under this condition any type of purely diffusive behavior, characterized in our model by symmetric migration rates, produces an unbalanced population distribution, i.e. some locations receive more individuals than can be supported by the environmental carrying capacity, while others receive less. Using an evolutionarily stable strategy (ESS) approach we show that an asymmetric migration mechanism, induced by the heterogeneous carrying capacity of the environment, will be selected. This strategy balances the inflow and outflow of individuals in each habitat (balanced dispersal), as well as ‘balancing’ the spatial distribution relative to variation in carrying capacity (the Ideal Free Distribution from habitat selection theory). We show that several quantities are maximized or minimized by the evolutionarily stable dispersal strategy.

© 2005 Elsevier Inc. All rights reserved.

* Corresponding author.
E-mail addresses: padron@ula.ve, padro005@umn.edu (V. Padrón), trevisan@ula.ve (M.C. Trevisan).

0025-5564/$ - see front matter © 2005 Elsevier Inc. All rights reserved.
doi:10.1016/j.mbs.2005.11.004
1. Introduction

Dispersal is a life history trait that has profound effects on both species persistence and evolution, with important implications in population and community dynamics. The question of how dispersal influences the evolutionary distribution of organisms between habitats has been the subject of considerable empirical and theoretical investigation (see [1,2] for a review).

Two different perspectives dominate the evolutionary explanations for adaptive dispersal. According to the source-sink model [3–6], populations in the source habitat produce a surplus of immigrants that disperse to nearby sinks. In the view of the balanced dispersal model [7–11], an evolutionarily stable dispersal strategy emerges when the total number of individuals emigrating out of a habitat is balanced by an equivalent number of individuals that immigrate. A third and inclusive alternative, reciprocating dispersal introduced by Morris et al. [12], predicts a dispersal strategy where individuals flow from one habitat to another during population increase, and flow in the reverse direction during population decline. In this paper we consider a continuous time model of balanced dispersal, and obtain analytical results that are similar to the results obtained in [7,13,9,10] for discrete time generations. Our model is based on differential equations, which in effect assume that the population size in each habitat is large enough to be treated as a continuous variable, and the distances between adjacent habitats are small enough for dispersion to take place almost instantaneously. This is in contrast to the models considered in [7,13,9,10], where the population size at each patch habitat is a discrete quantity, and the distances between habitats are relatively large. Our model generalizes the model considered in [14] by allowing asymmetric dispersal rates.

When dispersal rates are modeled by passive diffusion [14,4] the results suggest that dispersal is selected against. Contrary to this, McPeek and Holt [7] show that in a two-patch system some level of dispersal is favored by selection in environments where the dispersal rates are free to vary between patches (asymmetrical dispersal). The model predicts that the evolutionary stable strategy (ESS) is one in which the ratio of the dispersal rates is inversely proportional to the ratio of the carrying capacities of the habitats. Thus, the number of individuals emigrating from a habitat equals the number of individuals immigrating (balanced dispersal). Similar results are obtained in [13,9,10]. The outcome of an evolutionarily stable dispersal strategy is an Ideal Free Distribution (IFD) [15]. The IFD is a description of how organisms would distribute themselves in space if they were free to move so as to maximize fitness.

This paper focus on the evolution of dispersal as modeled by asymmetric dispersal rates in an environment that is spatially variable, but constant in time. The variability of the space is introduced by the non-homogeneity of its carrying capacity. The question of the evolution by natural selection of dispersal rates is studied using an ESS approach based on an analytical invasibility criteria (4). For that purpose, we develop a model for a single species with logistic growth, in which organisms move between habitats with linear dispersal rates. We show that
an evolutionarily stable dispersal strategy is selected (Theorem 3), under which the population evolves to the best spatial distribution that can be supported by the carrying capacity. When the environment is homogeneous, passive diffusion is selected. However, in the general case, the ESS is characterized by an analytical relation that combines the dispersal rates and the carrying capacities (condition (2)). This condition shows that the flow of individuals is balanced and in concordance with the IFD. Thus, our results generalize those for two-patch models. We also exhibit several quantities that are maximized or minimized by the evolutionary process that yields the ESS.

The rest of the article is organized as follows: Section 2 describes the dynamic model, states the main mathematical results, and considers the question of which quantities are maximized or minimized at the evolutionary equilibrium; Section 3 analyzes the ecological implications of these results and characterizes the evolutionarily stable dispersal strategies; Section 4 shows some numerical experiments to complement the theory; Section 5 discusses the results and related problems. The proof of the results are presented in the Appendix.

2. The mathematical model

We consider the system of differential equations

\[ u'_i = \sum_{j=1}^{n} [d_{ij}u_j(t) - d_{ji}u_i(t)] + u_i(t)F_i(u_i(t)), \quad i = 1, \ldots, n, \quad t \geq 0, \quad (1) \]

where the coefficients \( d_{ij} \), representing the dispersal rates from location \( j \) to location \( i \), satisfy: (i) \( d_{ij} \geq 0, \quad i, j = 1, \ldots, n \), (ii) \( \sum_{j=1}^{n} d_{ij} > 0 \), (iii) \( \sum_{j=1}^{n} d_{ji} > 0 \), \( i = 1, \ldots, n \). The functions \( F_i(s) \), \( i = 1, \ldots, n \), representing the net rate of population supply, are decreasing functions of \( s \) and verify the following hypothesis:

**Hypothesis 1.** Let \( f_i(s) := sF_i(s) \), \( i = 1, \ldots, n \).

1. \( f_i \), \( i = 1, \ldots, n \), are continuously differentiable.
2. \( f_i(0) = 0, f'_i(0) = F_i(0) > 0 \) and there exists \( 0 < K_i < \infty \), such that \( f_i \) is positive in \((0, K_i)\) and negative in \((K_i, +\infty)\), for \( i = 1, \ldots, n \).
3. There exists a constant \( M > K_i \) such that \( -f_i(s) > \delta s \), for all \( s \geq M \) and \( i = 1, \ldots, n \). Here \( \delta \) is a positive constant such that \( \sum_{j=1}^{n} d_{ij} < \delta \) and \( \sum_{j=1}^{n} d_{ji} < \delta \), \( i = 1, \ldots, n \).

The value \( K_i > 0 \) is called the carrying capacity of the population because it represents the population size that available resources can continue to support. The value \( r_i := F_i(0) > 0 \) is called the *intrinsic growth rate* and represents the per capita growth rate achieved if the population size were small enough to ensure negligible resource limitations. For the standard *logistic growth*, introduced by Verhults [16], \( F_i(s) = r_i(1 - \frac{s}{K_i}) \).

We can write system (1) in the closed form

\[ u' = Au + \mathcal{F}(u), \]
where \( u = (u_1, \ldots, u_n)^T, \mathcal{F}(u) = (f_1(u_1), \ldots, f_n(u_n))^T, \) and \( A = (a_{ij}) \) is the matrix with

\[
a_{ij} = \begin{cases} d_{ij} & \text{for } i \neq j, \\ -\sum_{k=1}^n d_{ki} & \text{for } i = j. \end{cases}
\]

We will call \( A \) the matrix of (1) and we will assume that \( A \) is irreducible. The assumption of the irreducibility of matrix \( A \) is by no means a loss of generality. In fact, under the reciprocal condition that \( d_{ij} \neq 0 \) implies \( d_{ji} \neq 0 \), if \( A \) is reducible, each reducible subset of \( A \) corresponds to a set of isolated habitats which can be treated as single species obeying the irreducibility assumption.

The first condition in Hypothesis 1 is technical and is needed together with the third condition to ensure, given initial data, the existence and uniqueness of solutions for (1) globally defined for \( t \geq 0 \) [17]. Since \( d_{ij} \geq 0 \) and the matrix \( A \) is irreducible, (1) is a cooperative and irreducible system in \( \mathbb{R}_+^n \). This implies that the set \( C := \{ \xi \in \mathbb{R}_+^n : \lim_{t \to \infty} u(t; \xi) \text{ exists} \} \) of convergent points of (1) contains an open and dense subset of \( \mathbb{R}_+^n \) [18, Theorem 4.1.2, p. 57]. Here, \( u(t; \xi) \) denotes the solution of (1) such that \( u(0; \xi) = \xi \). Thus the dynamics of (1) is largely determined by its equilibria.

It is clear that \( u = 0 \) is a steady state solution of (1). Since \( f_i'(0) > 0, i = 1, \ldots, n \), it follows that \( u = 0 \) is unstable. Hence, by the above argument there exists at least one non-trivial equilibria \( \bar{u} \) such that \( \lim_{t \to \infty} u(t; \xi) = \bar{u} \) for some \( \xi \) in an open subset of \( C \). In fact, when

\[
\sum_{j=1}^n d_{ij}K_j = \sum_{j=1}^n d_{ji}K_i, \quad i = 1, \ldots, n,
\]

it follows that \( \bar{u} = (K_1, K_2, \ldots, K_n) \) is the only non-trivial equilibrium of (1) (see Theorem 1). If \( F(s) \) is strictly decreasing for \( s \geq 0 \), and \( i = 1, \ldots, n \), it can be shown, by using monotonicity arguments, that (1) has an unique non-trivial equilibria. This result is well known for reaction–advection–diffusion equations (see [19, Proposition 3.3, p. 148]).

We will prove the following theorem that relates the spatial distribution of the equilibria of (1) with the carrying capacity.

**Theorem 1.** Suppose that \( \bar{u} = (\bar{u}_1, \ldots, \bar{u}_n) \) is a stationary solution of (1) such that \( \bar{u} \neq 0 \).

(a) If (2) holds then \( \bar{u}_i = K_i, i = 1, \ldots, n \).

(b) If there exists \( i_0 \in \{1, \ldots, n\} \) such that \( \sum_{j=1}^n d_{i_0j}K_j \neq \sum_{j=1}^n d_{j_0i}K_{i_0} \), then there exist \( i, j \in \{1, \ldots, n\} \) such that \( \bar{u}_i < K_i \) and \( K_j < \bar{u}_j \).

The following theorem shows several quantities that are maximized (minimized) by the equilibria given by Theorem 1(a).

**Theorem 2.** Let \( \bar{u} = (\bar{u}_1, \ldots, \bar{u}_n) \) be a stationary solution of (1) such that \( \sum_{i=1}^n d_{i_0i}K_i \neq \sum_{i=1}^n d_{i_0i}K_{i_0} \) for some \( i_0 \in \{1, 2, \ldots, n\} \).

(i) If \( F_i'(K_i) = -\frac{n_i}{K_i} \) and \( sF_i'(s) \leq -F_i'(s) \) for any \( s > 0 \) and \( i = 1, \ldots, n \), then

\[
\sum_{i=1}^n r_i\bar{u}_i < \sum_{i=1}^n r_iK_i.
\]
If \( d_{ij} = D_{ij} d_{jk} \) with \( D_{ij} = D_{ji} \), \( P_{0} \), and \( d_j > 0 \), \( i, j = 1, \ldots, n \), then
\[
X_n = 1 F_i \left( \frac{1}{C_2} u_i \right) d_i < 0.
\]

If \( F_i(K_i) = -\frac{r_i}{K_i} \), and \( s F_i''(s) \leq -F_i'(s) \) for any \( s > 0 \) and \( i = 1, \ldots, n \), then
\[
\sum_{i=1}^{n} K_i F_i(\bar{u}_i) > 0.
\]

**Remark 1.** The conditions of items (i) and (iii) are satisfied by the standard logistic growth \( F_i(s) = r_i(1 - \frac{s}{K_i}) \), \( i = 1, \ldots, n \).

3. Evolution of dispersal

Dispersal is a demographic process that modifies the array of ecological conditions that individuals may experience in their interaction with the environment. The outcome of the evolution of dispersal traits should thus be the result of natural selection and reflect the variability of the environment.

Under uniform environmental conditions, i.e. when \( K_i = K, i = 1, \ldots, n \), it is natural to expect that the simplest dispersal strategy, given by the symmetrical condition \( d_{ij} = d_{ji}, i, j = 1, \ldots, n \), or more generally \( \sum_{j=1}^{n} d_{ij} = \sum_{j=1}^{n} d_{ji}, i = 1, \ldots, n \), such that individuals disperse regardless of the environment, will be selected. It is widely known, for this type of diffusive systems, that the only two steady states or equilibria are \( u \equiv 0 \) and \( u \equiv K \). The equilibrium \( u \equiv 0 \) is unstable and \( u \equiv K \) is stable. Therefore, in a generic sense, \( u(t) \to K \) as \( t \to \infty \). That is, the population converges to an spatial distribution that matches the carrying capacity of the environment.

Theorem 1(b) shows that in heterogeneous environments, i.e. when \( K_i, i = 1, \ldots, n \), are not all equal, the previous assumption about a passive dispersal cannot produce this type of balance between the population distribution and the available resources. In this case if \( \sum_{j=1}^{n} d_{i,j} = \sum_{j=1}^{n} d_{j,i}, i = 1, \ldots, n \), then for any non-trivial steady state \( \bar{u} \) of (1) there exist \( i, j \) such that \( \bar{u}_i > K_i \), and \( \bar{u}_j < K_j \). Clearly this situation produces an uneven distribution of resources: while some locations receive more individuals than can be supported by the environmental carrying capacity, others receive less.

This type of source-sink population structure is typical of, but not restricted to, models in which the propensity to disperse is habitat independent. Since more offspring are produced in the better habitat at equilibrium, more individuals move from the better to the poorer habitat than in the opposite direction, simply because the pool of potential dispersers is greater in the former than in the latter. This situation known as under-matching could also arise, as Theorem 1(b) confirms, as a consequence of the asymmetry in the dispersal rates, even in the absence of differences in habitat quality.

There are different ecological factors that promote under-matching: social interactions whereby ‘dominant’ individuals occupying high quality source habitats, inhibit colonization or reproduction by conspecifics [20–22]; the directional influence of environmental agents of dispersal, for
example, gravity, river or ocean current, or prevailing wind direction [23–26]; cost of dispersal [9,27]. See also [28–30] for a general discussion on habitat matching.

However, if there is no cost of dispersal and individuals have a perfect control over their dispersal, natural selection is expected to adjust to a more flexible dispersal rule, one that is sensible to the environmental heterogeneity, resulting in a balanced population distribution, with no sink structure [7,13,9–11].

Theorem 1 (a) shows that when in and out flow is balanced, i.e. when condition (2) holds, then the only non-trivial steady state \( \bar{u} \) of (1) is given by \( \bar{u}_i = K_i, \ i = 1, \ldots, n \). Hence, as in the homogeneous case above, the population converges to the spatial distribution that matches the environmental carrying capacity. This is in concordance with the postulates of the Ideal Free Distribution (IFD) from habitat selection theory.

The IFD [15] describes how the distribution of abundances and fitness across habitats emerges from the evolutionary process of habitat selection strategies of individuals. It assumes that if organisms move freely between habitats, taking into account habitat quality and competition (density dependence), then ideally they select the habitat with the highest mean fitness. This ‘ideal free’ behavior results in a spatial population distribution under which the number of competitors present is proportional to the quality of the habitat, and the resource intake rate is the same across all occupied habitats. This yields the input matching rule which states that the proportion of competitors in a given habitat will be equal to the proportion of resources arriving into that habitat [31,32]. In continuous input models, resources enter a habitat at a fixed rate. Hence, if \( \rho_j \) denotes the resource supply rate, i.e., the amount of resources entering habitat \( j \), and \( \rho \) stands for the lowest resource intake rate, one could assume that the carrying capacity \( K_j \) of habitat \( j \) is given by \( K_j = \rho_j/\rho \). At equilibrium, system (1) under condition (2), has a unique non-zero stationary solution \( \bar{u} = (\bar{u}_1, \ldots, \bar{u}_n) \) with \( \bar{u}_j = K_j, \ j = 1, \ldots, n \). As a consequence, since \( \rho_j/\bar{u}_j = \rho, \ j = 1, \ldots, n \), the resource intake is the same across all occupied habitats. Hence, condition (2), even though it is not a density-dependent ideal free strategy, yields an ideal free distribution. This confirms what was already pointed out by Holt and Barfield [11] that models for the evolution of dispersal in spatially heterogeneous but temporally constant environments also often predict fitness equilibration.

A particular instance where condition (2) holds is given when

\[
d_{i,j} = (\alpha K_i)^{\theta} (\beta K_j)^{\theta-1}, \quad i, j = 1, \ldots, n, \quad \alpha > 0, \ \beta > 0, \ \ 0 < \theta < 1. \tag{3}
\]

That is, the decision about moving between two successive habitats is based on the conditions prevailing at the two locations, measured by the carrying capacity, and weighted by an interpolating exponent. This includes the three standard cases; i.e. the movement from the location \( j \) to the location \( i \) is affected only by conditions at \( j \) (attractive: the better the local conditions the lesser the chances of leaving), at \( i \) (repulsive: the better the non-local conditions the greater the chances of leaving), and at both with equal weight (neutral) corresponding to \( \theta = 0, \ \theta = 1, \) and \( \theta = 1/2 \) respectively. This type of dispersal strategy is similar to the one described in [33] for a spatially continuous population model based on advection-diffusion equations. Condition (3) is a particular instance of the type of dispersal strategy considered in Theorem 2(ii) with \( D_{ij} = (\alpha \beta K_i K_j)^{\theta} \) and \( d_j = (\beta K_j)^{-1} \).

Using an invasibility (of a resident type by a variant) criteria we show that condition (2) on the migration rates is indeed an ESS. As defined by Maynard Smith [34], an ESS is a strategy that has the property that no other type can increase when rare. In a few words, a strategy \( x \) is an ESS if a
population of individuals with strategy $x$ cannot be invaded by another small population with a different strategy $y$. Whether the values $d_{ij}$ in (1) correspond to an ESS is determined by the ability of strategies, represented by different values of $d_{ij}$, to invade. Hence, for system (1) at equilibrium, we are led to consider the superposition of a new population having a size $v_i$, initially small, and different migration rates $\tilde{d}_{ij}$. Suppose that system (1) is at equilibrium in the non-trivial stationary solution $\tilde{u} = (\tilde{u}_1, \ldots, \tilde{u}_n)$. We postulate that a dispersal strategy given by migration rates $d_{ij}$ is an ESS for system (1) if for any other dispersal matrix $(\tilde{d}_{ij})$ with $\tilde{d}_{ij} \neq d_{ij}$ for some $i, j$, the null solution of

$$v'_i(t) = \sum_{j=1}^{n} [\tilde{d}_{ij}v_j(t) - \tilde{d}_{ji}v_i(t)] + v_iF_i(v_i + \tilde{u}_i), \quad i = 1, \ldots, n, \ t \geq 0,$$

is locally asymptotically stable under small perturbations in $\mathbb{R}^n_+$. Notice that this definition assumes the presence of two different time scales; one implicit, the ecological time scale, corresponding to the convergence to the stationary point and another, the evolutionary time scale acting explicitly on Eq. (4), corresponding to the introduction of the small population (invader). The invader is not included in the original model (1), but added once the ecological system has reached the equilibrium [35].

In [14] it is shown that when $d_{ij} = d_{ji}$, $i, j = 1, \ldots, n$, dispersal will be selected against. The following theorem states that evolution can favor dispersal only if organisms are allowed to choose among a broader range of non-diffusive mechanisms induced by the asymmetry of migration rates.

A similar result was obtained in [7,10] for a model with discrete time generations (see also [9]).

**Theorem 3.** Let $\tilde{u} = (\tilde{u}_1, \ldots, \tilde{u}_n)$ be a stationary solution of (1) such that

$$F_i(\tilde{u}_i) = 0, \quad i = 1, \ldots, n.$$  

Suppose that there exists $\gamma > 0$ such that

$$u^T\nabla F(\tilde{u})u < -\gamma|u|^2,$$  

for any $u \in \mathbb{R}^n_+$ such that $u \neq 0$. Here $\nabla F(\tilde{u})$ is the Jacobian matrix of $F(\tilde{u}) = (F_1(u_1), F_2(u_2), \ldots, F_n(u_n))^T$ at $\tilde{u}$. Then condition (2) on the coefficients $d_{ij}$ of system (1) is an ESS.

**Remark 2.** If $F_i(K_i) = -\frac{r_i}{K_i}$, $i = 1, \ldots, n$, including the standard logistic growth $F_i(u_i) = r_i \left(1 - \frac{u_i}{K_i}\right)$, conditions (5) and (6) are satisfied with $\tilde{u} = K = (K_1, \ldots, K_n)$. In fact, in this case $u^T\nabla F(K)u = -\sum_{i=1}^{n} \frac{r_i}{K_i^2} u_i^2$.

Note that (5) is a condition of equilibration of fitness among habitats [11], and if it fails, i.e. $F_i(\tilde{u}_i) \neq 0$, say $F_i(\tilde{u}_i) > 0$, for some $i_0$, then $\tilde{u}$ can not be an ESS. This can be seen by choosing a strategy $d_{ij}$ in (4) such that $\tilde{d}_{i_0} = \tilde{d}_{j_0}, j = 1, \ldots, n$. If $v_{i_0}(0)$ is small enough then $v_{i_0}'(t) > 0$ for $t > 0$ small. Hence the strategy $d_{ij}$ can invade. This supports the suggestion given in [11] that the evolution of dispersal tends towards an equilibration of fitness among habitats.

What quantity, if any, is maximized by the evolutionary process that leads to the strategy (2)? Theorem 2(i) shows that in the case that $F_i(K_i) = -\frac{r_i}{K_i}$, and $sF'_{ij}(s) \leq -F'_i(s)$ for any $s > 0$ and $i = 1, \ldots, n$, including the standard logistic growth, the mean number of offspring produced at equilibrium by adult females in the absence of competition, $\frac{1}{n}\sum_{i=1}^{n} r_i \tilde{u}_i$, is maximized.
It has been known since Haldane [36], that there are many ways that selection can fail to maximize population size (see [14,4]). Our result suggests that the variability of the intrinsic growth rates \( r_i \) are not all equal, Theorem 2(i) shows that maximizing fitness, as measured by the quantity \( \frac{1}{n} \sum_{i=1}^{n} r_i \bar{u}_i \), is in general in conflict with maximizing population size. One can expect, as the example below shows, that a non-ESS strategy could yield a total population that is larger than the population that maximizes fitness by inducing the stabilization of a relatively high population in the locations with lower intrinsic growth rates and relatively low population in the locations with higher intrinsic growth rates. In terms of maximizing fitness such a strategy seems to be ineffective, but it could manage to produce a higher population size.

Consider the system

\[
\begin{align*}
    x' &= -x + 3y + 4x(1 - x), \\
    y' &= x - 3y + 9y(1 - y).
\end{align*}
\]

(7)

Here \( K_1 = K_2 = 1, d_{12} = 3, d_{21} = 1 \) and hence \( d_{12} K_2 \neq d_{21} K_1 \). Nevertheless, the vector \((\bar{x}, \bar{y}) = (\frac{3}{4}, \frac{1}{4})\) is a stationary solution of (7) for which \( \bar{x} + \bar{y} = \frac{3}{2} > 2 = K_1 + K_2 \).

In general, when the intrinsic growth rate is not necessarily constant, Theorem 2(iii) shows that the ESS described by condition (2) minimizes the net growth sustained by the carrying capacity.

In the case that \( d_{ij} = D_{ij} d_{ij} \), with \( D_{ij} = D_{ji} \geq 0 \) and \( d_{ij} > 0 \), \( i, j = 1, \ldots, n \), Theorem 2(ii) shows that the weighted average \( \sum_{i=1}^{n} \frac{F_i(\bar{u}_i)}{d_i} \) is maximized by the ESS described by condition (2). If there is no cost of dispersal and individuals have perfect control over their dispersal, one could assume that \( d_i \) represents the component of the dispersal rule that is sensitive to habitat type, and other predictors of local fitness [7]. Hence, \( d_i \) is inversely proportional to the organism perception of habitat quality, and the quantity \( \sum_{i=1}^{n} \frac{F_i(\bar{u}_i)}{d_i} \) could be seen as a ‘measure of the perceived mean fitness across habitats’.

4. Numerical experiments

Now we present some numerical simulations that illustrate the results contained in Theorem 1. We consider a habitat of \( n^2 \) localities distributed into a square grid of points \((h, k)\) where \( h = \left\lfloor \frac{n-1}{n} \right\rfloor + 1 \) and \( k = i \text{ mod } n \) with \( i = 1, \ldots, n^2 \). The notation \([p]\) means the greatest integer less than \( p \) and \( p \mod q \) is the remainder of \( p \) divided by \( q \). The population density \( v(h, k, t) \) at the point \((h, k)\) at time \( t \) is given by \( v(h, k, t) = u_{\delta(h-1)+k}(t) \), \( h, k = 1, \ldots, n \), where \( u \) is the solution of system (1).

We will assume that individuals move only to the four adjacent cells (three or two when they are located in the boundary). That is, for instance, if \((h, k)\) is an interior point of the grid, then for \( j = n(h-1) + k \) we have \( d_{ij} \neq 0 \) for \( i = j \pm 1, j \pm n \) and \( d_{ij} = 0 \) otherwise.

Under these conditions, the matrix of (1) is described by a sparse matrix \( A = (a_{ij}) \) with

\[
a_{ij} = \begin{cases} 
    d_{ij} & \text{for } j = i \pm 1, i \pm n, \\
    -(d_{i-n,j} + d_{i-1,i} + d_{i+1,i} + d_{i+n,j}) & \text{for } i = j, \\
    0 & \text{otherwise.}
\end{cases}
\]

(8)
For the experiments we choose $n^2 = 36$ localities. The heterogeneity of the environment is represented by a randomly selected vector $K$ of carrying capacities, whose values are shown in Table 1.

For the first example we consider the diffusive case, in particular when the migration rates are symmetric ($d_{i,j} = d_{j,i}$). Fig. 1 (Left) shows the steady solution $v(h, k, t)$ at $t = 50$ and the environmental carrying capacities. We observe that some locations receive more individuals than can be supported by the carrying capacity, while others receive less. This uneven population distribution is not predictable to be within a certain range, as depicted in Fig. 1 (Right).

Table 1 shows the numerical values for the steady state $v(h, k, t)$ together with the carrying capacities.

In the next example, the migration rates $d_{i,j}$ are computed according to formula (3). Fig. 2 shows a sequence of graphs of the solutions $v(h, k, t)$ of system (1) at different times, with initial data $v(h, k, 0) = .5$, $h, k = 1, \ldots, 6$, $\theta = 0.1$ and $\alpha = 9/950$ and $\beta = 10/9$. As it was expected, after a time ($t = 20$), the population reaches the distribution of the carrying capacities.

---

**Table 1**

<table>
<thead>
<tr>
<th>$h\backslash k$</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>$v$</td>
<td>93.4</td>
<td>24.9</td>
<td>58.8</td>
<td>50.0</td>
<td>87.4</td>
<td>76.2</td>
</tr>
<tr>
<td>$K$</td>
<td>95</td>
<td>23</td>
<td>61</td>
<td>49</td>
<td>89</td>
<td>76</td>
</tr>
<tr>
<td>$v$</td>
<td>47.1</td>
<td>9.8</td>
<td>19.6</td>
<td>41.2</td>
<td>41</td>
<td>91.5</td>
</tr>
<tr>
<td>$K$</td>
<td>46</td>
<td>2</td>
<td>82</td>
<td>44</td>
<td>44</td>
<td>62.8</td>
</tr>
<tr>
<td>$v$</td>
<td>89.4</td>
<td>27</td>
<td>74</td>
<td>18</td>
<td>41</td>
<td>94</td>
</tr>
<tr>
<td>$K$</td>
<td>92</td>
<td>9.8</td>
<td>19.6</td>
<td>41</td>
<td>41</td>
<td>90.9</td>
</tr>
<tr>
<td>$v$</td>
<td>42.3</td>
<td>47.7</td>
<td>19.6</td>
<td>41</td>
<td>41</td>
<td>92</td>
</tr>
<tr>
<td>$K$</td>
<td>41</td>
<td>47.7</td>
<td>19.6</td>
<td>41</td>
<td>41</td>
<td>92</td>
</tr>
<tr>
<td>$v$</td>
<td>14.7</td>
<td>21.5</td>
<td>20</td>
<td>25.2</td>
<td>60</td>
<td>28.4</td>
</tr>
<tr>
<td>$K$</td>
<td>14</td>
<td>21.5</td>
<td>20</td>
<td>25.2</td>
<td>60</td>
<td>28.4</td>
</tr>
<tr>
<td>$v$</td>
<td>7.0</td>
<td>3.2</td>
<td>45.0</td>
<td>45</td>
<td>45</td>
<td>45</td>
</tr>
<tr>
<td>$K$</td>
<td>2</td>
<td>43.2</td>
<td>45.0</td>
<td>45</td>
<td>45</td>
<td>45</td>
</tr>
</tbody>
</table>

Fig. 1. (Left) Population density $v(h, k, t)$ at the steady state, started with initial data $v(h, k, 0) = 10$, $h, k = 1, \ldots, 6$, in stars $\star$ and carrying capacities in circles $\bigcirc$. (Right) Difference between the population density solution at each locality of system (1) and the corresponding carrying capacity.
5. Discussion

We study a model for the evolution of dispersal of a single species in spatially heterogeneous but temporally constant environments. We showed that a dispersal strategy will be selected. This strategy is characterized by an analytical condition on the dispersal rates that involves the carrying capacity of the environment. At equilibrium this strategy yields a balanced dispersal and equilibration of fitness across habitats. These results agree with previous results obtained for models with discrete time generations, and support the suggestion that the evolution of dispersal tends towards an equilibration of fitness among habitats.

Models for the evolution of dispersal for competing populations show that for organisms which disperse unconditionally (passive dispersal), slower dispersing population competitively excludes a faster dispersing population. For conditional dispersers experiencing no dispersal costs, an evolutionarily stable dispersal strategy will be selected, and the population adopting these strategies exhibit an ideal free distribution at equilibrium: the per-capita growth rate is constant across the landscape [37–39]. Similar results are obtained for models including age structure in spatially varying but temporally constant environments [9,27].

The results of this paper seem to be a common feature of models for the evolution of dispersers experiencing no dispersal costs in spatially heterogeneous but temporally constant environments. For example, Theorem 3 is still true if we replace condition (5) with the more general condition \( F_i(\bar{u}) = 0, i = 1, \ldots, n \), which applies to systems of interacting species and age structure. This
suggests that we should be able to obtain general theorems of this type for models that fit in any one of the possible categories of being continuous or discrete, in space and time. This is part of an ongoing research project of V. Padron with R.S. Cantrell and C. Cosner.

If cost of dispersal can be compensated with differences of survival rates between immigrants and residents, then similar results can be obtained. Otherwise, philopatry, i.e. non-dispersal, is selected [9,27].

When the environment varies across space and through time, previous numerical studies [7,11] suggest that the evolution of dispersal can produce a distribution characterized by approximate equilibration of local fitness measures, such as geometric means of local reproductive success or spatial reproductive values, among habitats. A combined analytical and numerical treatment of a similar problem was given by Hutson et al. [40]. Here a reaction diffusion model for two phenotypes is studied, and showed that either the lower or higher diffuser rate may be selected, or there may be coexistence of phenotypes. The technical complexities arising when we include time variability in carrying capacity in our model make it more difficult to obtain analytical results similar to the ones given in this paper.

Acknowledgments

This research was partially supported by the Consejo de Desarrollo Cientı́fico, Humanı́stico y Técnico (CDCHT) de la Universidad de Los Andes through project C-1002-00-05-B. We are deeply indebted to Peter A. Abrams, Douglas W. Morris, and Hans Weinberger for their valuable observations and criticisms which helped us to substantially improve this paper.

Proofs of the results

The following lemma will be needed in the proofs of Theorems 1 and 2.

Lemma 1. If \( \tilde{u} = (\tilde{u}_1 \ldots \tilde{u}_n) \) is a stationary solution of (1), then \( \sum_{i=1}^{n} f_i(\tilde{u}_i) = 0 \).

Proof. Since \( \tilde{u} \) is a stationary solution of (1), we have that

\[
\sum_{j=1}^{n} [d_{ij} \tilde{u}_j(t) - d_{ji} \tilde{u}_i(t)] + f_i(\tilde{u}_i(t)) = 0, \quad i = 1, \ldots, n.
\]

Hence,

\[
\sum_{i=1}^{n} \sum_{j=1}^{n} d_{ij} \tilde{u}_j - \sum_{i=1}^{n} \sum_{j=1}^{n} d_{ji} \tilde{u}_i + \sum_{i=1}^{n} f_i(\tilde{u}_i(t)) = 0.
\]

But,

\[
\sum_{i=1}^{n} \sum_{j=1}^{n} d_{ij} \tilde{u}_j = \sum_{j=1}^{n} \sum_{i=1}^{n} d_{ij} \tilde{u}_j = \sum_{i=1}^{n} \sum_{j=1}^{n} d_{ji} \tilde{u}_i.
\]

It follows that \( \sum_{i=1}^{n} f_i(\tilde{u}_i(t)) = 0 \). \( \Box \)
Proof of Theorem 1. It will be enough to prove the theorem in the case in which $K_i = 1$, $i = 1, \ldots, n$. The change of variables $v_i = u_i/K_i$, $i = 1, \ldots, n$, reduces the original problem to this case.

By Lemma 1 we know that the only homogeneous stationary solutions of (1) are $u \equiv 0$ and $u \equiv 1$. Hence to prove (a) it will be enough to prove that all the stationary solutions of (1) are homogeneous.

Denote $I = \{1, 2, \ldots, n\}$ and assume by contradiction that there exist $i, j \in I$ such that $\bar{u}_i \neq \bar{u}_j$. Suppose that $\bar{u}_i > 0$, $i = 1, \ldots, n$. Let $i_0 \in I$ such that $\bar{u}_{i_0} \leq \bar{u}_i$, $i = 1, \ldots, n$. By Lemma 1 we have that $0 < \bar{u}_{i_0} < 1$.

Hence,

$$0 = \sum_{j=1}^{n} (d_{i_0j} \bar{u}_j - d_{j_0j} \bar{u}_{i_0}) + f_{i_0}(\bar{u}_{i_0}) \geq \sum_{j=1}^{n} (d_{i_0j} - d_{j_0j}) \bar{u}_{i_0} + f_{i_0}(\bar{u}_{i_0}) = f_{i_0}(\bar{u}_{i_0}) > 0.$$  

This is a contradiction. Hence there must exist $i \in I$ such that $\bar{u}_i = 0$. Let $I_1 \subseteq I$ such that $\bar{u}_i = 0$ for all $i \in I_1$. We already know that $I_1 \neq \emptyset$, and since we are assuming that $\bar{u}$ is not homogeneous we also have that $I_1 \neq I$. Hence for all $i \in I_1$

$$0 = \sum_{j=1}^{n} (d_{ij} \bar{u}_j - d_{j_0j} \bar{u}_i) + f_i(\bar{u}_i) = \sum_{j \notin I_1} d_{ij} \bar{u}_j.$$  

Since for all $j \notin I_1, \bar{u}_j > 0$, it follows that

$$d_{ij} = 0 \quad \text{for} \quad i \in I_1, j \notin I_1. \quad (9)$$  

This is a contradiction since we are assuming that the matrix of (1) is irreducible. Hence, all the stationary solutions of (1) are homogeneous. This proves (a).

To prove (b) suppose that there exists $i_0 \in I$ such that $\sum_{j=1}^{n} d_{i_0j} \neq \sum_{j=1}^{n} d_{j_0i}$. It follows that there exists $i$ such that $\bar{u}_i \neq 1$, otherwise we would have that

$$0 = \sum_{j=1}^{n} [d_{i_0j} \bar{u}_j(t) - d_{j_0j} \bar{u}_i(t)] + f_{i_0}(\bar{u}_{i_0}(t)) = \sum_{j=1}^{n} [d_{i_0j} - d_{j_0j}] + f_{i_0}(1) = \sum_{j=1}^{n} [d_{i_0j} - d_{j_0i}],$$

and this is a contradiction.

Suppose that $\bar{u}_i \leq 1$, $i = 1, \ldots, n$. There are two possibilities: (1) there exists $I_1 \subseteq I$, $I_1 \neq \emptyset$, such that $\bar{u}_i = 1$ for $i \in I_1$ and $\bar{u}_i = 0$ for $i \notin I_1$, (2) there exists $i_1 \in I$ such that $0 < \bar{u}_{i_1} < 1$.

In the first case we would have for all $i \notin I_1$ that

$$0 = \sum_{j \notin I_1} [d_{ij} \bar{u}_j(t) - d_{j_0j} \bar{u}_i(t)] + \sum_{j \in I_1} [d_{ij} \bar{u}_j(t) - d_{j_0j} \bar{u}_i(t)] + f_i(\bar{u}_i(t)) = \sum_{j \notin I_1} d_{ij}.$$  

This implies that $d_{ij} = 0$ for $i \notin I_1$ and $j \in I_1$. This is a contradiction since we are assuming that the matrix of (1) is irreducible.

Suppose now that there exists $i_1 \in I$ such that $0 < \bar{u}_{i_1} < 1$. Since we are assuming that $\bar{u}_i \leq 1$, $i = 1, \ldots, n$, this implies that $\sum_{j=1}^{n} f_j(\bar{u}_j) > 0$. This is again a contradiction since by Lemma 1, $\sum_{j=1}^{n} f_j(\bar{u}_j) = 0$. Hence we cannot have $\bar{u}_i \leq 1$, $i = 1, \ldots, n$. A similar argument shows that we cannot have $\bar{u}_i \geq 1$, $i = 1, \ldots, n$. Therefore, there exist $i, j \in I$ such that $\bar{u}_i < 1$ and $1 < \bar{u}_j$. □
Proof of Theorem 2. We will proof (i) and (ii). The proof of (iii) is similar to the proof of (i) and it is omitted.

Let \( K = (K_1, K_2, \ldots, K_n) \). For any \( x = (x_1, x_2, \ldots, x_n) \in \mathbb{R}_{+}^n \), let \( f(x) = \sum_{i=1}^{n} r_i x_i \), and \( g(x) = \sum_{i=1}^{n} x_i F_i(x_i) \).

It will be enough to show that \( f \) has a strict constrained maximum at \( K \) subject to \( g(x) = 0 \); that is, for any \( x \in \mathbb{R}_{+}^n \) such that \( g(x) = 0 \) and \( x \neq K \) we have \( f(x) < f(K) \). Certainly, if \( \bar{u} = (\bar{u}_1, \ldots, \bar{u}_n) \) is a stationary solution of (1) then by Lemma 1, \( g(u) = 0 \). Moreover, since \( \sum_{j=1}^{n} d_{ij} K_j \neq \sum_{j=1}^{n} d_{ij} K_i \) for some \( i \in \{1, 2, \ldots, n\} \), we have that \( \bar{u} \neq K \). Hence, by our claim, \( f(\bar{u}) < f(K) \), and part (i) of the theorem would follow.

Let \( M := \{x \in \mathbb{R}_{+}^n : g(x) = 0\} \). Since \( M \) is a compact set we know that \( f(x) \) has an absolute maximum on \( M \). Moreover, any relative extremum of \( f \) on \( M \) is a solution of the system

\[
\nabla f(x) = \lambda \nabla g(x),
\]
\[
g(x) = 0.
\]

From (10) we have

\[
\frac{F_i(x_i) + x_i F'_i(x_i)}{r_i} = \frac{1}{\lambda}, \quad i = 1, \ldots, n.
\]

Let \( x \in M \) such that \( x \neq 0 \) and \( x \neq K \). By (11) there are two possibilities: (1) there exist \( i, j \) such that

\[
0 < x_i < K_i \quad \text{and} \quad 0 < K_j < x_j,
\]

or (2) there exist \( i, j \) such that \( x_i = 0 \) and \( x_j = K_j \).

Condition (13) implies that \( F_i(x_i) > 0 \) and \( F_j(x_j) < 0 \). By condition \( s F''_i(s) \leq -F'_i(s) \) for any \( s > 0 \) and \( i = 1, \ldots, n \), we have that \( s F'_i(s) \) is a decreasing function of \( s \). It follows from (13) that

\[
\frac{F_i(x_i) + x_i F'_i(x_i)}{r_i} > \frac{K_i F'_i(K_i)}{r_i} = -1 = \frac{K_j F'_j(K_j)}{r_j} > \frac{F_j(x_j) + x_j F'_j(x_j)}{r_j}.
\]

This implies that \( x \) cannot be a solution of (12).

Similarly, if \( x_i = 0 \) and \( x_j = K_j \) we have

\[
\frac{F_i(x_i) + x_i F'_i(x_i)}{r_i} = 1 > -1 = \frac{K_j F'_j(K_j)}{r_j} = \frac{F_j(x_j) + x_j F'_j(x_j)}{r_j}.
\]

Therefore \( x \) cannot be a solution of (12).

It follows that the only solutions of (10) and (11) are \( x = 0 \) or \( x = K \). Since \( f(0) = 0 \), we conclude that \( f \) attains its strict maximum on \( M \) at the point \( x = K \), as we wanted to prove.

To prove (ii) we first notice that the terms of the sum \( \sum_{i=1}^{n} \frac{F_i(u_i)}{d_i} \) are of the form

\[
-D_{ij} \left( \frac{d_j \bar{u}_j}{d_i \bar{u}_i} - 2 \frac{d_j \bar{u}_i}{d_j \bar{u}_j} \right) = -D_{ij} \frac{d_j \bar{u}_i}{d_j \bar{u}_j} \left( \frac{d_j \bar{u}_j}{d_i \bar{u}_i} - 1 \right)^2.
\]

By Theorem 1(a) there exists \( i_0 \in I := \{1, 2, \ldots, n\} \) such that \( \sum_{j=1}^{n} D_{ij} d_j \bar{u}_j \neq \sum_{j=1}^{n} D_{ij} d_j \bar{u}_{i_0} \). This implies that \( d_{i_0} \bar{u}_{i_0} \neq d_j \bar{u}_j \) for some \( j \in I \). Hence, the set \( I_0 = \{i \in I : d_i \bar{u}_i \neq d_i \bar{u}_{i_0}\} \) is non-empty.
Since the matrix \((D_{ij})\) is irreducible (this follows from the irreducibility of the matrix \((d_{ij})\)), then there exists \(i \in I_0\) and \(j \notin I_0\) such that \(D_{ij} \neq 0\). For such values of \(i, j\) we have

\[
D_{ij} \frac{d_j u_j}{d_i u_i} \left( \frac{d_j u_j}{d_i u_i} - 1 \right)^2 > 0.
\]

This finishes the proof of (ii). \(\square\)

**Proof of Theorem 3.** Suppose that the coefficients \(d_{ij}\) of system (1) satisfy condition (2). By Theorem 1 the only non-trivial stationary solution \(\bar{u}\) of system (1) is \(\bar{u} = (K_1, \ldots, K_n)\).

For any solution \(v(t)\) of (4) let \(V(t) = \sum_{i=1}^{n} v_i(t)\). Assuming \(V_0 = V(0) > 0\) small enough and using the condition on the jacobian of \(F\) we have

\[
\frac{dV}{dt}(t) = \sum_{i=1}^{n} F_i(\bar{u} + v) v_i = \sum_{i=1}^{n} \left[ \int_{0}^{1} \frac{d}{ds} F_i(\bar{u} + sv) \, ds \right] v_i
\]

\[
= \int_{0}^{1} v^T \nabla F(\bar{u} + sv) v \, ds < -\gamma |v|^2 < -\frac{\gamma}{n} V^2(t). \tag{14}
\]

We obtain by integrating (14)

\[
0 \leq V(t) \leq \frac{n V_0}{n + \gamma V_0 t}.
\]

Since \(V(t) > 0\) for \(t \geq 0\), we obtain that \(\lim_{t \to \infty} V(t) = 0\). This proves the theorem. \(\square\)

**References**


