



# Evolutionary stability of ideal free dispersal under spatial heterogeneity and time periodicity<sup>☆</sup>

Robert Stephen Cantrell<sup>a,b</sup>, Chris Cosner<sup>\*,a</sup>

<sup>a</sup> Department of Mathematics, The University of Miami, USA

<sup>b</sup> Institute of Mathematical Sciences, Renmin University of China, China

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## ABSTRACT

Roughly speaking, a population is said to have an ideal free distribution on a spatial region if all of its members can and do locate themselves in a way that optimizes their fitness, allowing for the effects of crowding. Dispersal strategies that can lead to ideal free distributions of populations using them have been shown to exist and to be evolutionarily stable in a number of modeling contexts in the case of habitats that vary in space but not in time. Those modeling contexts include reaction-diffusion-advection models and the analogous models using discrete diffusion or nonlocal dispersal described by integro-differential equations. Furthermore, in the case of reaction-diffusion-advection models and their nonlocal analogues, there are strategies that allow populations to achieve an ideal free distribution by using only local information about environmental quality and/or gradients. We show that in the context of reaction-diffusion-advection models for time-periodic environments with spatially varying resource levels, where the total level of resources in an environment remains fixed but its location varies seasonally, there are strategies that allow populations to achieve an ideal free distribution. We also show that those strategies are evolutionarily stable. However, achieving an ideal free distribution in a time-periodic environment requires the use of nonlocal information about the environment such as might be derived from experience and memory, social learning, or genetic programming.

## 1. Introduction

The ideal free distribution is a now long-established construct in ecological theory with significant ramifications in the study of the evolution of dispersal [1–5,7,15–17]. Initially, the ideal free distribution was formulated as a verbal description of the way organisms located themselves [10,11] motivated by observation of territorial patterns of birds. It asserts that if the members of a species have complete knowledge of the environment (ideal) and may locate themselves as they wish (free), they will do so in a manner that maximizes fitness, here thought of as local per capita reproductive success. Fitness is assumed to be discounted by the presence of conspecifics. In this framework, an ideal free distribution is achieved by the species in a given habitat once its fitness is constant in all occupied parts of the habitat. At this point, in a temporally constant habitat, there can be no further net movement of the species in question, as net movement would lower fitness in some locations and raise it in others. In a temporally varying habitat the situation is somewhat different, because the location of regions where fitness is maximized may change over time, so individuals may need to keep moving to optimize their fitness. However,

it turns out that in certain time periodic environments, it is possible for a population to achieve a generalized version of an ideal free distribution by dispersing in an appropriate way.

Movement leading to an ideal free distribution need not be coupled to population dynamics, and, in principle, the equilibrated fitness characterizing an ideal free distribution may be positive. However, in situations wherein dispersal and population dynamics are coupled, the species in question should continue increasing in abundance so long as fitness remains positive. Consequently, in such a setting, fitness could only be expected to equilibrate at 0. Suppose now that the environment is spatially heterogeneous but temporally constant and that dispersal and population dynamics are coupled additively. Then the local population growth should be zero and the ideal free distribution should correspond to a spatially varying equilibrium of the system in the absence of dispersal. In the particular but common situation of a mathematical model with logistic growth in a habitat with a favorable resource distribution, under appropriate scaling, such an equilibrium coincides with perfect alignment to resource distribution. Consequently, in that case, having no net movement when achieving an ideal free distribution translates to the resource distribution being a

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\* Corresponding author.

E-mail address: [gcc@math.miami.edu](mailto:gcc@math.miami.edu) (C. Cosner).

zero of the dispersal term. In this case, we say that the species in question exhibits an ideal free dispersal strategy. In the corresponding time periodic case there will not generally be an equilibrium but there will be a periodic steady state. We will show that under certain conditions a population can still align itself perfectly to the resource distribution, but in general that will not correspond to a zero of the dispersal term, since the resources can move. We will use perfect alignment with the resource distribution as a generalization of the classical definition of an ideal free distribution.

Work by a number of researchers (including ourselves) has shown that ideal free dispersal offers a distinct evolutionary advantage in a number of spatially heterogeneous but temporally constant modeling frameworks including reaction-diffusion-advection [1,2,15–17], discrete diffusion [3], integro-differential [4], and integro-difference [6]. This advantage is expressed through the parlance of adaptive dynamics and focuses on the pairwise invasibility of competing species. We say that species 1 can invade species 2 if it can increase its abundance when it is introduced at low densities in a habitat in which species 2 is at its carrying capacity. We examine evolutionary advantage of dispersal strategies if the competitors are ecologically identical, in essence mutants of each other differing only in their modes of movement. In such a case, we say that a dispersal strategy is evolutionarily stable (an ESS) relative to some class of strategies if a species adopting this strategy cannot be invaded by an ecologically identical competitor adopting any other strategy from this class. A dispersal strategy is a neighborhood invader strategy (an NIS) if it can invade any nearby strategy. Strategies which are both ESS and NIS have a clear evolutionary advantage. The work in [1–7,15–17] shows that ideal free dispersal is both an ESS and an NIS robustly across a range of mathematical modeling frameworks in the spatially heterogeneous but temporally constant setting.

The purpose of this article is two-fold. First, we determine conditions under which ideal free dispersal can be realized in the reaction-diffusion-advection setting when there is temporal periodicity in addition to spatial heterogeneity. We find that there is some restriction on the spatio-temporal variation possible in the distribution of the resource but that the restriction is not biologically unreasonable. Second, we establish that when ideal free dispersal is possible, it indeed is an ESS and NIS, globally among the class of strategies we consider.

In the temporally constant setting, the class of reaction-diffusion-advection models we and others have considered are of the form

$$\begin{aligned} \frac{\partial u}{\partial t} &= \nabla \cdot (\mu(x) \nabla u - \alpha(x) u \nabla e(x)) + f(x, u + v) u \\ \frac{\partial v}{\partial t} &= \nabla \cdot (\nu(x) \nabla v - \beta(x) v \nabla h(x)) + f(x, u + v) v \end{aligned} \tag{1}$$

on  $\Omega \times (0, \infty)$ , subject to the no-flux boundary conditions

$$\begin{aligned} (\mu(x) \nabla u - \alpha(x) u \nabla e(x)) \cdot \hat{\eta}(x) &= 0 \\ (\nu(x) \nabla v - \beta(x) v \nabla h(x)) \cdot \hat{\eta}(x) &= 0 \end{aligned} \tag{2}$$

on  $\partial\Omega \times (0, \infty)$ , where  $\Omega$  is a bounded domain in Euclidean space of dimension  $N$  with sufficiently smooth boundary,  $\hat{\eta}(x)$  is the unit outward normal along the boundary  $\partial\Omega$  of  $\Omega$ , and the diffusion coefficients  $\mu(x)$ ,  $\nu(x)$  and advection coefficients  $\alpha(x)$ ,  $\beta(x)$  are smooth on  $\bar{\Omega}$  and positive. The functions  $e(x)$  and  $h(x)$ , whose gradients are advected up by species with densities  $u$  and  $v$  respectively, are sufficiently smooth on  $\bar{\Omega}$ . The function  $f(x, w)$  represents fitness at location  $x \in \bar{\Omega}$  and density  $w \geq 0$ . It is sufficiently smooth in both variables and decreases in  $w$ , with  $f(x, 0) > 0$  on  $\bar{\Omega}$  and  $f(x, K) < 0$  on  $\bar{\Omega}$  for some  $K > 0$ . Our work and that of our collaborators and others [1–7,15–17] has focused on logistic fitness, especially the case where  $f(x, w) = m(x) - w$ , with constant diffusion and advection parameters. The function  $m(x)$  gives the temporally constant, spatially heterogeneous background distribution. It is easy to observe [2] that if  $\mu = \alpha$  and  $e(x) = \log f(x, 0) = \log m(x)$ , the species with density  $u$  exhibits ideal free dispersal in the absence of the species with density  $v$ . Here the

equilibrium density is the resource distribution  $m(x)$ . There is no net movement at equilibrium since  $\nabla(\log m(x)) = \frac{\nabla m(x)}{m(x)}$ , which means advection is in the direction of  $\nabla m(x)$  but with its magnitude modulated by the value of  $m(x)$ . Such movement is conditioned upon purely local information. Nevertheless, as noted [1,2], it aggregates to the population level on the habitat patch  $\Omega$  so that ideal free dispersal is an ESS and NIS. This phenomenon may also be detected in other reaction-diffusion-advection formulations [16,17] and some integro-differential models [8]. This is remarkable in light of the original formulation of the ideal free distribution [10,11]. We shall see that once we incorporate temporal periodicity along with spatial heterogeneity into the resource distribution  $m$ , having an ideal free dispersal strategy will require nonlocal as well as local information.

The remainder of the paper is structured as follows. In Section 2, we will treat analogues to (1) and (2) where  $m(x, t)$  is  $T$ -periodic in time, in the case of one space dimension. We will allow both no-flux and spatially periodic boundary conditions, and determine when ideal free dispersal is possible. It turns out that the condition needed on  $m$  is the same for both types of boundary condition. We then show that ideal free dispersal is an ESS and NIS. In Section 3, we show that in habitats with smooth boundaries, we may extend our results in the no-flux case to higher space dimensions. Finally, in Section 4, we discuss biological ramifications of our results.

## 2. Ideal free dispersal on $[0, L]$

Consider the model

$$\frac{\partial u}{\partial t} = [\mu u_x - uP(x, t)]_x + [m(x, t) - u]u \tag{3}$$

in  $(0, L) \times (0, \infty)$  subject to the no-flux boundary condition

$$\mu u_x(0, t) - u(0, t)P(0, t) = 0 = \mu u_x(L, t) - u(L, t)P(L, t) \tag{4}$$

for  $t > 0$ . Here we require  $\mu > 0$ ,  $P$  and  $m$  smooth and  $T$ -periodic in time with

$$m(x, t) > 0 \text{ for } (x, t) \in [0, L] \times [0, T].$$

It follows from results in [12] that (3)-(4) admits a unique positive  $T$ -periodic solution that is the global attractor for all nonnegative nontrivial initial data. (Direct application of [12] may require a change of variable to obtain classical boundary conditions; see (10).)

We say that (3)-(4) admits an ideal free dispersal strategy whenever  $m(x, t)$  is the positive periodic orbit in question. For in that case,

$$\frac{\partial m}{\partial t} = [\mu m_x - mP(x, t)]_x \tag{5}$$

in  $(0, L) \times (0, \infty)$ , with

$$\mu m_x(0, t) - m(0, t)P(0, t) = 0 = \mu m_x(L, t) - m(L, t)P(L, t) \tag{6}$$

for  $t > 0$ , and the population moves so as to align perfectly with the resource distribution through space and time.

Since we are in one space dimension  $P(x, t)$  is necessarily a spatial gradient. From (6), it is clear that  $P(0, t)$  can only be

$$P(0, t) = \mu \frac{m_x(0, t)}{m(0, t)} = \mu \frac{\partial \log m}{\partial x}(0, t). \tag{7}$$

To obtain  $P(x, t)$  so that (3)-(4) admits an ideal free dispersal strategy, we must integrate (5) with respect to  $x$ . The resulting function  $P(x, t)$  needs to be  $T$ -periodic in time and the second condition in (6) needs to be satisfied. It follows from (5) that our candidate for  $P$  is given by

$$P(x, t) = \frac{1}{m(x, t)} \left[ \mu m_x(x, t) - \int_0^x m_t(y, t) dy \right]. \tag{8}$$

for  $(x, t) \in [0, L] \times (0, \infty)$ . Since  $m$  is  $T$ -periodic in time, it follows immediately from (8) that so is  $P$ . Notice here that  $P$  depends on non-local as well as local information about resource distribution.

It remains to see if it is possible for  $m$  to satisfy (6) at  $x = L$ . We have from (8) that

$$m(x, t)P(x, t) - \mu m_x(x, t) = - \int_0^x m_t(y, t) dy \quad \text{for } x \in [0, L].$$

Consequently,  $m$  satisfies (6) at  $x = L$  if and only if

$$\frac{\partial}{\partial t} \int_0^L m(y, t) dy = 0, \tag{9}$$

meaning that the overall total amount of resource is constant in time. We consider the ramifications of (9) in Section 4. The upshot is that we get ideal free dispersal for (3)-(4) with  $P$  given by (7) if and only if (9) holds.

Remark: If we considered the form of dispersal leading to an ideal free distribution treated in [15–17], based on carrying capacity driven diffusion, the problem analogous to solving (5) for  $P$  would be finding a positive solution  $D$  for

$$\frac{\partial m}{\partial t} = (D(x, t)m)_{xx}$$

where  $Dm$  also satisfies no-flux boundary conditions. This can be done if  $m > 0$  and (9) holds, but the solution again involves an integration that requires nonlocal spatial information on  $m(x, t)$ .

We now want to show that this strategy is an ESS and NIS. To this end, we will employ methods of monotone dynamical systems theory [12,18]. To justify this approach, we need to know that solutions to problems of the form (3)-(4) for arbitrary  $T$ -periodic and smooth  $P(x, t)$  admit a maximum principle. To this end, define a function  $w$  by

$$w = e^{-\frac{1}{\mu} \int_0^x P(y,t) dy} u. \tag{10}$$

A straightforward calculation shows that

$$\mu e^{\frac{1}{\mu} \int_0^x P(y,t) dy} w_x(x, t) = \mu u_x(x, t) - u(x, t)P(x, t).$$

So if  $u$  satisfies (4) and  $w$  is given by (10),  $w$  satisfies a homogeneous Neumann boundary condition. Since

$$w_t = e^{-\frac{1}{\mu} \int_0^x P(y,t) dy} u_t(x, t) - \frac{\int_0^x P(y,t) dy}{\mu} w(x, t),$$

it follows from (3) and (10) that  $w$  satisfies a maximum principle. Consequently, so does  $u$ . So now consider

$$\begin{aligned} \frac{\partial u}{\partial t} &= [\mu u_x - uP(x, t)]_x + [m(x, t) - u - v]u \\ \frac{\partial v}{\partial t} &= [\mu v_x - vQ(x, t)]_x + [m(x, t) - u - v]v \end{aligned} \tag{11}$$

on  $(0, L) \times (0, \infty)$ , subject to the no-flux boundary conditions

$$\begin{aligned} \mu u_x(0, t) - u(0, t)P(0, t) &= 0 = \mu u_x(L, t) - u(L, t)P(L, t) \\ \mu v_x(0, t) - v(0, t)Q(0, t) &= 0 = \mu v_x(L, t) - v(L, t)Q(L, t) \end{aligned} \tag{12}$$

for  $t > 0$ . As before,  $\mu$  is a positive constant,  $m$  is smooth,  $T$ -periodic in time and positive on  $[0, L] \times [0, T]$ , and  $P$  and now  $Q$  are smooth and  $T$ -periodic in time. The results of [12,13] enable us to view (11)-(12) as generating a monotone discrete dynamical system [18] on  $C^1[0, L] \times C^1[0, L]$ . We have the following result.

**Theorem 1.** Consider  $C^1[0, L] \times C^1[0, L]$  and assume that (5)-(6) holds. Then if  $Q \neq P$ , for any nonnegative, nontrivial initial data  $(u_0, v_0) \in C^1[0, L] \times C^1[0, L]$ , the solution to  $C^1[0, L] \times C^1[0, L]$  with  $u(x, 0) = u_0(x)$  and  $v(x, 0) = v_0(x)$  converges in  $C^1[0, L] \times C^1[0, L]$  to the periodic steady state  $(m(x, t), 0)$  as  $t \rightarrow \infty$ .

**Remark.**

(i) Let us refer to the species with density  $u$  as species 1 and the species with density  $v$  as species 2. The dispersal strategy for species 2 in (11)-(12) is ideal free precisely when  $Q = P$ . Consequently, species 1 excludes species 2 in (11)-(12) so long as species 2 does not employ an ideal free dispersal strategy. Hence the ideal free dispersal strategy is an ESS and NIS among strategies of the form  $[\mu w_x - wQ(x, t)]_x$ .

(ii) If we define  $p$  and  $q$  by  $p(x, t) = \int_0^x P(y, t) dy$  and  $q(x, t) = \int_0^x Q(y, t) dy$ , then the advection term in the dispersal strategy of species 1 (respectively species 2) is advection up the gradient of  $p$  (respectively  $q$ ).

(ii) The results of [12,13] employ an interplay between viewing (11)-(12) as a non-autonomous system of pde's and a discrete time dynamical system. As a result, we may employ monotone dynamical systems theory [18] to establish Theorem 1, so long as we show there is no component-wise positive periodic orbit for (11)-(12) and that  $(0, v^*)$  is unstable, where  $v^*$  is the unique globally attracting periodic orbit of

$$\begin{aligned} \frac{\partial v}{\partial t} &= [\mu v_x - vQ(x, t)]_x + [m(x, t) - v]v \text{ on } (0, L) \times (0, \infty) \text{ with} \\ \mu v_x(0, t) - v(0, t)Q(0, t) &= 0 = \mu v_x(L, t) - v(L, t)Q(L, t) \text{ for } t > 0. \end{aligned}$$

The existence of such a  $v^*$  follows from [12].

**Proof.** We first show there is no component-wise positive periodic orbit for (11)-(12). Suppose to the contrary that  $(u(x, t), v(x, t))$  is such an orbit. Then

$$\frac{\partial u}{\partial t} = [\mu u_x - uP(x, t)]_x + [m(x, t) - u - v]u \tag{13}$$

and

$$\frac{\partial m}{\partial t} = [\mu m_x - mP(x, t)]_x \tag{14}$$

on  $(0, L) \times (0, \infty)$ . Multiplying (13) by  $m/u$  and (14) by  $\log u$ , we obtain that

$$\begin{aligned} \frac{\partial(m \log u)}{\partial t} &= (m/u)(\mu u_x - uP(x, t))_x + \log u(\mu m_x - mP(x, t))_x \\ &\quad + [m - u - v]m. \end{aligned} \tag{15}$$

Now integrate (15) over  $[0, L] \times [0, T]$ . Since  $m$  and  $u$  are  $T$ -periodic, the left hand side of the resulting equation is zero. We can employ integration by parts on the first two terms of the right hand side, using the no-flux boundary conditions on  $m$  and  $u$  to obtain

$$\begin{aligned} 0 &= \int_0^T \int_0^L [\mu m(u_x)^2/(u^2) - 2\mu m_x(u_x/u) + m_x P \\ &\quad + m(m - u - v)] dx dt \\ &= \int_0^T \int_0^L [\mu m(u_x)^2/(u^2) - 2\mu m(u_x/u)(m_x/m) + \mu m(m_x)^2/(m^2) \\ &\quad - \mu m(m_x)^2/m^2 + m_x P + m(m - u - v)] dx dt \\ &= \int_0^T \int_0^L [\mu m((u_x/u) - (m_x/m))^2 + m(m - u - v) + m_x P \\ &\quad - \mu(m_x)^2/m] dx dt. \end{aligned} \tag{16}$$

Now consider  $\int_0^T \int_0^L (m_x P - \mu(m_x)^2/m) dx dt$ . Recall that

$$P(x, t) = \frac{\mu m_x}{m} - \frac{1}{m} \int_0^x m_t(y, t) dy.$$

Consequently

$$\begin{aligned} m_x P - \mu(m_x)^2/m &= -\frac{m_x}{m} \int_0^x m_t(y, t) dy \\ &= -(\log m)_x \int_0^x m_t(y, t) dy. \end{aligned}$$

Thus

$$\begin{aligned} \int_0^T \int_0^L (m_x P - \mu(m_x)^2/m) dx dt &= \int_0^T \int_0^L [-(\log m)_x \int_0^x m_t(y, t) dy] dx dt \\ &= \int_0^T [-(\log m(L, t) \int_0^L m_t(y, t) dy) dt \\ &\quad + \int_0^T \int_0^L \log m(x, t) m_t(x, t) dx dt \\ &= \int_0^T \int_0^L \log m(x, t) m_t(x, t) dx dt \end{aligned}$$

since  $\int_0^L m_t(y, t) dy = 0$ . Since  $\log m(x, t)m_t(x, t) = (m \log m - m)_t$ , we get

$$\int_0^T \int_0^L (m_x P - \mu(m_x)^2/m) dx dt = \int_0^L \int_0^T (m \log m - m)_t dx dt = 0$$

since  $m$  is  $T$ -periodic in time. Consequently (16) reduces to

$$0 = \int_0^T \int_0^L [\mu m((u_x/u) - (m_x/m))^2 + m(m - u - v)] dx dt. \tag{17}$$

Integrating the equations for  $u$  and  $v$  in (11) over  $[0, L] \times [0, T]$  and employing  $T$ -periodicity and no-flux boundary conditions leads us to

$$\int_0^T \int_0^L u(m - u - v) dx dt = \int_0^T \int_0^L v(m - u - v) dx dt = 0.$$

Adding these last equations to (17) gives

$$0 = \int_0^T \int_0^L [\mu m((u_x/u) - (m_x/m))^2 + (m - u - v)^2] dx dt. \tag{18}$$

Consequently, (18) implies that  $u + v \equiv m$  and  $u_x/u \equiv m_x/m$  or  $(\log u)_x \equiv (\log m)_x$ . Hence  $\log u = \log m + c(t)$ , where  $c(t)$  is  $T$ -periodic and thus  $u = s(t)m$ , where  $s(t)$  is  $T$ -periodic and positive. As  $u + v \equiv m$ ,  $v = (1 - s(t))m$  and  $s(t) \in [0, 1]$  for all  $t \in [0, T]$ . The equation for  $u$  in (11) becomes

$$(sm)_t = (\mu(sm)_x - smP)_x = s(\mu(m)_x - mP)_x$$

so that

$$ms_t = s(\mu(m)_x - mP)_x - sm_t = 0$$

because (5) is satisfied due to our choice of  $P$ . Since we assume  $m > 0$ , it follows that in  $[0, L] \times [0, T]$ . Thus  $s(t) \equiv s(0)$ . If  $s(0) = 1$ , then  $v \equiv 0$ , contradicting our assumption that  $(u(x, t), v(x, t))$  is a componentwise-positive steady state for (11)-(12). Hence we must have  $s(0) < 1$ . Consequently the equation for  $v$  in (11) reduces to

$$m_t = [\mu m_x - mQ]_x.$$

It then follows from (5) that  $[m(x, t)(Q(x, t) - P(x, t))]_x \equiv 0$  for  $x \in (0, L)$  and  $t > 0$ . Since the boundary conditions (12) imply  $m(0, t)(Q(0, t) - P(0, t)) = 0$ , it follows that  $Q(x, t) \equiv P(x, t)$  for  $x \in (0, L)$  and  $t \geq 0$ , contrary to the hypotheses of Theorem 1. So there can be no such component-wise positive steady state for (11)-(12).

To address the instability of  $(0, v^*)$ , we need  $\gamma < 0$  in

$$\phi_t = [\mu\phi_x - \phi P]_x + (m - v^*)\phi + \gamma\phi \tag{19}$$

where  $\phi$  is  $T$ -periodic in time,  $\phi$  is smooth and positive on  $[0, L] \times [0, T]$  and satisfies

$$\mu\phi_x(0, t) - \phi(0, t)P(0, t) = \phi_x(L, t) - \phi(L, t)P(L, t) \tag{20}$$

for  $t > 0$ . We may calculate in manner analogous to (15) that

$$(m \log \phi)_t = \log \phi [\mu m_x - mP]_x + (m/\phi)[\mu\phi_x - \phi P]_x + m(m - v^*) + m\gamma \tag{21}$$

Here, as before, we have made use of (5). Integrating over  $[0, L] \times [0, T]$  and proceeding as with (15) we obtain

$$0 = \int_0^T \int_0^L [\mu m((\phi_x/\phi) - (m_x/m))^2 + m(m - v^*) + m\gamma] dx dt. \tag{22}$$

Integrating the equation for  $v^*$  over  $[0, L] \times [0, T]$  yields

$$0 = \int_0^T \int_0^L (m - v^*)v^* dx dt. \tag{23}$$

Adding (22) and (23), we obtain

$$0 = \int_0^T \int_0^L [\mu m((\phi_x/\phi) - (m_x/m))^2 + (m - v^*)^2] dx dt + \gamma \int_0^T \int_0^L m dx dt. \tag{24}$$

It is clear from (24) that  $\gamma < 0$  unless  $m \equiv v^*$ . But in that case we have

$$m_t = (\mu m_x - mP)_x \text{ and}$$

$m_t = (\mu m_x - mQ)_x$  which implies that  $(m(P - Q))_x \equiv 0$ . As before, since  $m(0, t)(P(0, t) - Q(0, t)) = 0$  for  $t > 0$ , we conclude that  $P(x, t) \equiv Q(x, t)$ , a contradiction. Thus  $\gamma < 0$ , and  $(0, v^*)$  is unstable.

We conclude that all solutions to (11)-(12) corresponding to non-negative, nontrivial initial data converge to the periodic steady state  $(m(x, t), 0)$  as  $t \rightarrow \infty$ . Consequently, ideal free dispersal is an ESS and NIS in this context.  $\square$

**Remark.** We may also obtain ideal free dispersal if  $m$  is  $L$ -periodic in space as well as  $T$ -periodic in time. In this case there is no restriction on  $P(0, t)$  and no issue regarding the maximum principle. The proof of the result corresponding to Theorem 1 in this case requires only modest changes from that of Theorem 1 and is therefore omitted.

### 3. Extension to higher space dimensions

The analogue to (3)-(4) in higher space dimensions is

$$\frac{\partial u}{\partial t} = \nabla \cdot (\mu \nabla u - u \vec{P}(x, t)) + (m(x, t) - u)u \tag{25}$$

in  $\Omega \times (0, \infty)$  subject to the no-flux boundary condition

$$(\mu(x) \nabla u - u \vec{P}(x, t)) \cdot \hat{\eta}(x) = 0 \tag{26}$$

on  $\partial\Omega \times (0, \infty)$ , where  $\Omega$  is the focal habitat patch in question and  $\hat{\eta}$  is the outward normal to  $\partial\Omega$ . If the space dimension is higher than 1, it is imminently possible to construct a vector valued function  $\vec{P}(x, t)$  which is  $T$ -periodic in time and such that

$$m_t = \nabla \cdot (\mu \nabla m - m \vec{P}) \tag{27}$$

in  $\Omega \times (0, \infty)$  with

$$(\mu \nabla m - m \vec{P}) \cdot \hat{\eta}(x) = 0 \tag{28}$$

on  $\partial\Omega \times (0, \infty)$ . Indeed, one may choose

$$\vec{P}(x, t) = \frac{1}{m(x, t)} [\mu \nabla m(x, t) - \nabla q(x, t)] \tag{29}$$

where  $q$  is such that

$$\nabla \cdot (\nabla q) = m_t \tag{30}$$

with  $\nabla q \cdot \hat{\eta}(x) = 0$  on  $\partial\Omega \times (0, \infty)$ , so long as

$$\int_{\Omega} m_t(y, t) dy = 0$$

for all  $t$ . As in the case of one space dimension, to achieve an ideal free distribution requires the use of nonlocal information. Again, an analogous construction could be used in the case of the type of models considered in [15–17] but would still use nonlocal information. If positive solutions to (25)-(26) with  $\vec{P}(x, t)$  given by (29)-(30) satisfy a maximum principle, the analogue to Theorem 1 obtains in higher space dimensions. Moreover, the proof is a straightforward adaptation of that of Theorem 1. However,  $\vec{P}(x, t)$  given by (29)-(30) need not be a gradient so that the change of variables analogous to (10), namely  $w = e^{p(x,t)}u$  where  $\nabla p(x, t) = \vec{P}(x, t)$ , can not be employed for this purpose.

To circumvent this limitation on  $\vec{P}$ , we look for a sufficiently smooth function  $\alpha(x, t)$  which is  $T$ -periodic in  $t$ , so that

$$w = e^{\alpha(x,t)}u \tag{31}$$

satisfies a maximum principle. Again, if  $w$  satisfies a maximum principle, so will  $u$ .

It is easy to show that  $w$  satisfies



$$\begin{aligned}
 w_t &= \mu \Delta w - 2\mu \nabla \alpha \cdot \nabla w - \nabla w \cdot \vec{P} \\
 &+ [\mu |\nabla \alpha|^2 - \mu \Delta \alpha + \nabla \alpha \cdot \vec{P} - \nabla \cdot \vec{P}] w \\
 &+ \alpha_t w + [m(x, t) - e^{-\alpha} w] w
 \end{aligned} \tag{32}$$

in  $\Omega \times (0, \infty)$  with

$$[\mu \nabla w - \mu (\nabla \alpha) w - w \vec{P}] \cdot \hat{\eta} = 0 \tag{33}$$

on  $\partial \Omega \times (0, \infty)$ .

We see from (32)-(33) that  $w$  will satisfy the maximum principle on  $\Omega$  if (33) is a classical Robin boundary condition; i.e., if  $\alpha(x, t)$  can be chosen so that

$$-\mu \nabla \alpha \cdot \hat{\eta} - \vec{P} \cdot \hat{\eta} > 0 \tag{34}$$

on  $\partial \Omega \times (0, \infty)$ .

Note that  $\vec{P}$  given in (29)-(30) is a fixed function. Hence (34) will hold provided

$$\mu \nabla \alpha(x, t) \cdot \hat{\eta} < -p_0 \tag{35}$$

for a sufficiently large constant  $p_0$ . Consequently the change of variables (31) may be employed to show that  $u$  in (25)-(26) satisfies a maximum principle (and consequently Theorem 1 extends to higher space dimensions) so long as  $\alpha(x, t)$  can be chosen so that (35) holds for sufficiently large  $p_0$ . To this end, we have the following result.

**Proposition 1.** *Suppose  $\Omega \subseteq \mathbb{R}^n$ , where  $n \geq 2$ , is a bounded domain with  $\partial \Omega$  of class  $C^1$ . Then given fixed  $T$ -periodic  $\vec{P}(x, t)$  satisfying (29)-(30), there is a smooth function  $\alpha: \bar{\Omega} \rightarrow \mathbb{R}$  satisfying (34).*

Note: We establish that we can choose  $\alpha$  depending only on  $x$  independent of  $t$ . Such a function is clearly  $T$ -periodic in time.

**Proof.** We first observe that we may construct a  $C^1$  function  $F: \bar{\Omega} \rightarrow \mathbb{R}$  so that

$\partial \Omega = \{x: F(x) = 0\}$  with  $F(x) > 0$  in  $\Omega$  and  $\nabla F(x) \neq \vec{0}$  for  $x \in \partial \Omega$ . We then show how to construct the required  $\alpha$ .

Let  $x_0$  be an arbitrary point on  $\partial \Omega$ . Since  $\partial \Omega$  is of class  $C^1$ , there is a  $C^1$  diffeomorphism  $\vec{\phi}$  from some ball  $B_\epsilon(x_0)$  about  $x_0$  into a region containing a ball  $B_\delta(0)$  so that  $\vec{\phi}(x_0) = 0$  and  $\vec{\phi}$  maps  $(int \Omega) \cap B_\epsilon(x_0)$  to  $\{(y_1, \dots, y_n): y_n > 0\} \cap B_\delta(0)$ . So  $y_n = \phi_n(x)$ , the  $n^{th}$  coordinate of  $\vec{\phi}$ , is positive for  $x \in (int \Omega) \cap B_\epsilon(x_0)$  and

$$\nabla_{\vec{x}} \phi_n = \nabla_{\vec{y}} y_n = (0, 0, \dots, 1).$$

Since  $\vec{\phi}$  is a diffeomorphism, so is  $\vec{\phi}^{-1}$ . Thus the Jacobian ( $Jac \phi^{-1}$ ) is invertible, with

$\nabla_{\vec{x}} \phi_n = (Jac \phi^{-1}) \nabla_{\vec{y}} y_n$  for  $x \in \bar{B}_{\epsilon_1}(x_0)$ ,  $y \in \bar{B}_{\delta_1}(0)$  for sufficiently small  $\epsilon_1 < \epsilon$  and  $\delta_1 < \delta$ . Moreover,  $\nabla_{\vec{x}} \phi_n$  is an inward pointing normal vector to  $\partial \Omega$ , since  $\phi_n(x) > 0$  in  $\Omega$  and  $\phi_n(x) = 0$  on  $\partial \Omega$ . Since  $\vec{\phi}$  and  $\vec{\phi}^{-1}$  are  $C^1$ ,  $|\nabla_{\vec{x}} \phi_n|$  is continuous, hence bounded below, say by  $g_0 > 0$ .

Now modify  $\phi_n$  by multiplying by  $\psi(x)$ , where  $\psi(x)$  is smooth, defined on all of  $\mathbb{R}^n$  and satisfies  $\psi(x) \equiv 1$  on  $B_{\epsilon_1/4}(x_0)$ ,  $\psi \equiv 0$  outside  $B_{\epsilon_1/2}(x_0)$ , and  $\psi(x) > 0$  for  $x \in B_{\epsilon_1/2}(x_0)$ . Then  $\psi \phi_n \geq 0$  inside  $\Omega$  and  $\leq 0$  outside  $\Omega$ . Hence, on the part of  $\partial \Omega$  inside  $B_{\epsilon_1/2}(x_0)$  (where  $\psi > 0$ )  $\nabla_{\vec{x}}(\psi \phi_n)$  remains an inward pointing normal. Elsewhere it is zero. Further, if  $x \in B_{\epsilon_1/4}(x_0)$ , we have  $\nabla_{\vec{x}} \phi_n = \nabla_{\vec{x}}(\psi \phi_n)$ , so that  $|\nabla_{\vec{x}}(\psi \phi_n)| \geq g_0 = g_0(x_0)$ . Let  $\rho_{x_0}(x)$  be defined as  $\psi \phi_n$  inside  $B_{\epsilon_1/2}(x_0)$  and 0 outside  $B_{\epsilon_1/2}(x_0)$ .

The preceding construction can be carried out at any point  $x \in \partial \Omega$ . The balls  $B_{\epsilon_1/4}(x)$  form a cover of  $\partial \Omega$ . We take a finite subcover  $\{B_{\epsilon_1(x_i)/4}(x_i): i = 1, \dots, K\}$ . Define  $F(x) = \sum_{i=1}^K \rho_{x_i}$ . Any  $x \in \partial \Omega$  is in  $B_{\epsilon_1(x_i)/4}(x_i)$  for some  $x_i$ . Consequently,  $\nabla_{\vec{x}} F$  is an inward pointing normal with length  $|\nabla_{\vec{x}} F| \geq \min\{g_0(x_i): i = 1, \dots, K\} > g^*$  for some  $g^* > 0$ . This construction defines  $F$  in a neighborhood of  $\partial \Omega$  with  $F > 0$  inside  $\Omega$  and  $F = 0$  on  $\partial \Omega$ . Standard methods allow us to extend  $F$  to all of  $\bar{\Omega}$ .

We now have that  $F$  satisfies

$$\nabla F(x) = -f(x) \hat{\eta}(x) \tag{36}$$

on  $\partial \Omega$  where  $\hat{\eta}$  is a unit outward normal along  $\partial \Omega$  and  $f(x) > 0$  for  $x \in \partial \Omega$ . Since  $\vec{P}(x, t)$  is  $T$ -periodic,  $\max\{|\vec{P} \cdot \hat{\eta}|: x \in \partial \Omega, t > 0\}$  is bounded, say by  $p^*$ . We may choose  $\alpha$  as

$$\alpha(x) = -\alpha_0 F(x) \tag{37}$$

where  $\alpha_0$  is chosen so that  $\mu \alpha_0 \min\{f(x): x \in \partial \Omega\} > p^*$ .  $\square$

**Remark.** Proposition 1 continues to hold if  $\vec{P}(x, t)$  in (25)-(26) is replaced with an arbitrary smooth  $\vec{Q}(x, t)$  which is  $T$ -periodic in time.

We may now formalize the main result in the higher dimensional case. To this end, we consider

$$\begin{aligned}
 \frac{\partial u}{\partial t} &= \nabla \cdot [\mu \nabla u - u \vec{P}(x, t)] + [m(x, t) - u - v] u \\
 \frac{\partial v}{\partial t} &= \nabla \cdot [\mu \nabla v - v \vec{Q}(x, t)] + [m(x, t) - u - v] v
 \end{aligned} \tag{38}$$

$\Omega \times (0, \infty)$ , subject to the no-flux boundary conditions

$$[\mu \nabla u - u \vec{P}(x, t)] \cdot \hat{\eta} = 0 = [\mu \nabla v - v \vec{Q}(x, t)] \cdot \hat{\eta} \tag{39}$$

on  $\partial \Omega \times (0, \infty)$ , where  $\hat{\eta}$  is a unit outward normal to  $\partial \Omega$ . Assume that  $\mu > 0$ ,  $m(x, t)$  is smooth, positive and  $T$ -periodic in time, and that  $\vec{P}(x, t)$  and  $\vec{Q}(x, t)$  are smooth and  $T$ -periodic in time. Proposition 1 guarantees that the methods of monotone dynamical systems apply to (38)-(39). Consequently, the natural adjustments to the proof of Theorem 1 to the higher dimensional space case guarantee the following

**Theorem 2.** *Consider (38)-(39), where  $\mu$ ,  $m$ ,  $\vec{P}$ , and  $\vec{Q}$  are as above. Assume that  $\int_{\Omega} m(y, t) dy$  is constant in time and that  $\vec{P}(x, t)$  is such that (27)-(28) hold. If  $\vec{Q} \neq \vec{P} + \vec{H}/m$ , where  $\nabla \cdot \vec{H}(x, t) = 0$  in  $\Omega$  and  $\vec{H}(x, t) \cdot \hat{\eta} = 0$  on  $\partial \Omega$ , then for any nonnegative, nontrivial initial data  $(u_0, v_0)$  in  $C^1(\bar{\Omega}) \times C^1(\bar{\Omega})$ , the solution to (38)-(39) with  $u(x, 0) = u_0(x)$  and  $v(x, 0) = v_0(x)$  converges in  $C^1(\bar{\Omega}) \times C^1(\bar{\Omega})$  to the periodic steady state  $(m(x, t), 0)$  as  $t \rightarrow \infty$ .*

**Remark.** Note that if  $\vec{P}$  satisfies (27) and (28) then so does  $\vec{P} + \vec{H}/m$  if  $\vec{H}$  satisfies the hypotheses in Theorem 2. This same type of non-uniqueness of ideal free dispersal strategies in higher space dimensions is also present in the temporally constant case; see [1].

#### 4. Discussion

In the context of spatially heterogeneous but temporally constant bounded habitats, reaction-diffusion-advection models [1,2,15-17] may be used to capture an ideal free distribution at equilibrium. In such cases, the density of an ecological species matches the underlying resource so as to have zero fitness throughout the habitat and to exhibit no net movement. In a formulation such as (1)-(2) this phenomenon is possible when advection is up the gradient of the logarithm of the resource at an appropriate rate relative to the random component of motion. The resulting dispersal strategy-  $\nabla \cdot [\mu(x) \nabla u - \mu(x) u \nabla(\log m(x))]$  - is then an ESS and an NIS against any other strategy  $\nabla \cdot [\nu(x) \nabla v - \beta(x) v \nabla h(x)]$  where  $h(x) = \log m(x)$  is non-constant [1,2].

In this paper we show that it is possible to extend this notion of ideal free dispersal to cases wherein the resource is both spatially heterogeneous and  $T$ -periodic in time provided (9) holds, so that the total resource abundance-  $\int_{\Omega} m(y, t) dy$  - is constant in time. Having total resource abundance constant in time means that the organism in question does not have to consider the timing of reproductive events *per se*. It can reproduce optimally by adjusting its spatial position appropriately over time. If (9) fails to hold, so the total resource abundance varies in time, then the timing of reproductive events, i.e., phenology,

becomes important. In that situation organisms may not be able to optimize their fitness by movement alone, but might be able to do so if they also match their reproductive effort to the resource level. This is an interesting topic for further study. When (9) holds, the density that matches resources is a time dependent steady-state, namely a periodic orbit. Moreover, the advective component of the ideal free movement must take into account the values of the resource over the whole of the habitat; i.e., the species at hand must utilize nonlocal information in order to achieve ideal free dispersal. Such is in distinct contrast to the temporally constant case where advection up the resource at a rate depending upon the level of the resource at the present position leads to ideal free dispersal. Thus, in the temporally constant setting, one can achieve ideal free dispersal in the reaction-diffusion-advection context with only local information. One should note here that the advective component of ideal free dispersal in the time periodic setting does reduce to advection up the gradient of the logarithm of the resource in the limiting case of vanishing time periodicity. In the time periodic case in one space dimension, advection in ideal free dispersal is movement up a (time dependent) gradient. In higher space dimensions, such is generally not the case.

We show that ideal free dispersal in the time periodic setting has the important advantage of being an ESS and an NIS relative to movement strategies with a different advective component. This advantage relies on utilization of temporally dependent nonlocal information. This feature resonates with the original formulations of the ideal free distribution [10,11] with respect to the perceptual range of the species in question. Other settings in which utilization of nonlocal information is advantageous (in the determination of optimal movement strategies in spatially and temporally heterogeneous landscapes) are discussed in [14] and [9]. Here the metrics do not pertain to considerations of pairwise invasibility of ecologically identical competitors but rather focus on the role of nonlocal information in foraging success. In [14] the famous wildebeest migration in Africa is studied by comparing simulation models and data, and the authors conclude that the study “strongly suggest that extended perceptual neighborhoods are a prerequisite for effective landscape-level exploitation of resources by wildebeest”. In [9], models are developed that show that utilization of nonlocal information in determining movement in spatio-temporally heterogeneous landscapes increases foraging success in highly ephemeral landscapes over strategies which rely solely on local cues.

## Supplementary material

Supplementary material associated with this article can be found, in the online version, at [10.1016/j.mbs.2018.09.002](https://doi.org/10.1016/j.mbs.2018.09.002)

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