

IDEAL FREE DISPERSAL UNDER GENERAL SPATIAL HETEROGENEITY AND TIME PERIODICITY*

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Abstract. A population is said to have an ideal free distribution in a spatially heterogeneous but temporally constant environment if each of its members has chosen a fixed spatial location in a way that optimizes its individual fitness, allowing for the effects of crowding. In this paper, we extend the idea of individual fitness associated with a specific location in space to account for the full path that an individual organism takes in space and time over a periodic cycle, and we extend the mathematical formulation of an ideal free distribution to general time periodic environments. We find that, as in many other cases, populations using dispersal strategies that can produce a generalized ideal free distribution have a competitive advantage relative to populations using dispersal strategies that cannot do so. A sharp criterion on the environmental functions is found to be necessary and sufficient for such ideal free distribution to be feasible. In the case the criterion is met, we show the existence of dispersal strategies that can be identified as producing a time-periodic version of an ideal free distribution, and such strategies are evolutionarily steady and are neighborhood invaders from the viewpoint of adaptive dynamics. Our results extend previous works in which the environments are either temporally constant, or temporally periodic but the total carrying capacity is temporally constant.

Key words. reaction-diffusion-advection, periodic-parabolic problems, principal eigenvalue, ideal free distribution, evolutionarily stable strategy, evolution of dispersal

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1. Introduction. The ideal free distribution (IFD) is by now a well-established concept in ecological theory, with profound ramifications for the understanding of evolution of dispersal [5, 9, 10, 11, 12, 15, 38, 39, 40]. The ideal free distribution was initially formulated as a verbal description of the way organisms located themselves in nature [24, 25] motivated by observing territorial patterns of birds. It asserts that if the members of a species have complete knowledge of the environment (ideal) and may locate themselves without cost (free), then they will do so in a manner that maximizes fitness, here thought of as local per capita reproductive success. Fitness is assumed to be limited by the presence of conspecifics at the same spatial location. In this framework, an IFD is achieved by the population when no individual can improve its fitness by moving in a different way.

Suppose the environment is spatially heterogeneous but temporally constant, and that dispersal and population dynamics are coupled additively. In this case, one can argue formally that the ideal free distribution is equivalent to fitness being equilibrated at zero. To see that, first we make the reasonable assumption that, like the environment, the IFD of the population is also temporally constant. Then the species

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in question should continue to increase in abundance so long as fitness remains positive. Therefore, the local population growth should be zero, and the IFD corresponds to a spatially varying equilibrium of the system in the absence of dispersal. In the particular situation of a mathematical model with logistic growth in a habitat with a favorable resource distribution, under appropriate scaling, such an equilibrium aligns perfectly to the carrying capacity. Indeed, this has been rigorously proven in a number of modeling settings, including reaction-diffusion-advection [5, 9, 38, 39, 40], discrete diffusion [10], integro-differential [11, 16], integro-difference [13], and matrix models [36]. In these papers, the ideal free dispersal, manifesting itself as the perfect alignment with carrying capacity, confers a distinct evolutionary advantage to a residential species adopting such strategy. This advantage is expressed through the parlance of adaptive dynamics [19, 26, 27] and focuses on the pairwise invasibility of competing species. We say that a dispersal strategy is an evolutionarily stable strategy (ESS), also known as evolutionarily steady, relative to some classes of strategies if a species adopting this strategy cannot be invaded by an ecologically identical competitor adopting any other strategy from this class [54]. Precisely, when a rare population of competitors is being introduced into an environment, in which the resident playing the ESS is at equilibrium, the population of competitors decays in time. On the other hand, a strategy is a neighborhood invader strategy (NIS) if it can invade any nearby strategy. Strategies which are both ESS and NIS have a clear evolutionary advantage. The results in [5, 9, 10, 11, 12, 13, 15, 38, 39, 40] show that ideal free dispersal is both an ESS and an NIS robustly across a range of mathematical modeling frameworks in spatially heterogeneous but temporally constant environments.

For the existence of ESS in families of dispersal strategies that do not generate IFD, we refer the reader to [8, 21, 42, 45, 53] and the book chapter [44] for results in the adaptive dynamics framework based on two-species interactions. See also [29, 41, 43, 56, 57] for related results in a framework in which the population is structured by space and a dispersal trait. In the latter framework, the interaction between an infinite number of species is being investigated.

The case of environments that are heterogeneous in both space and time differs from the temporally constant case. In the temporally constant case, a logistically growing population that is initially distributed with a positive density everywhere will grow to exactly match the local carrying capacity everywhere. Thus, if the initial conditions are right, a population can achieve an IFD with no dispersal at all. It is well known that in the case of simple diffusion in continuous environments, or discrete diffusion in patchy environments according to a fixed dispersal matrix, there is selection for slower dispersal, and indeed the strategy of not moving at all is convergence stable in the sense that a population with a smaller dispersal rate can invade an ecologically similar population with a faster dispersal rate [30, 20, 36]. This fact is related to the more general observation that dispersal resulting in mixing across space reduces growth rates, which is known as the reduction phenomenon [2]. In environments that are heterogeneous in both time and space, there may sometimes be selection for faster dispersal, or there may be stable polymorphisms where competitors with different dispersal rates coexist; see [34]. Furthermore, if the local carrying capacity or resource distribution of an environment varies in both space and time, a population cannot match it without some type of dispersal. The motivation for trying to understand the IFD in time-periodic environments is strong. Many environments are seasonal, and in fact one of Fretwell's original works on the IFD is entitled *Populations in a Seasonal Environment* [24]. In the special case of a logistic model in an environment where the total carrying capacity of the environment (or alternatively

the sum of available resources) across space is constant in time, but whose spatial distribution may vary periodically in time, a dispersal strategy that allows a population to match the resource distribution exactly is derived and shown to be an ESS and NIS in [7]. This case differs from the temporally constant case in that matching the resource distribution in space and time requires the use of nonlocal information about the environment, which is not the case in static environments, where dispersal strategies based on purely local cues can produce an IFD.

There is a large literature on periodic-parabolic models in ecology and population dynamics. For the general background, see [32]. More recent results can be found in [3, 4, 6, 51] and the references therein. An interesting recent application to protection zones is given in [52]. There also has been some work on nonspatial models for populations in periodically varying environments where the populations are structured by a trait that is subject to random mutation. Those lead to periodic-parabolic reaction-diffusion equations where the diffusion is in trait space rather than physical space; see, for example, [14, 23].

There are a number of issues that must be addressed in trying to interpret the concept of an IFD and understand the evolution of dispersal in environments that vary in both time and space. It is not immediately clear how individual fitness or an IFD should be defined in that setting. In static environments we can view the local per-capita growth rate at a given location as a proxy for the fitness of individuals at that location. However, that definition is inadequate in time varying environments where the fitness of an individual depends not only on its location but also on how it is moving through space and time. Similarly, an IFD in a static environment can be defined in terms of habitat selection that optimizes fitness, but in a varying environment phenology (that is, the timing of life history events, including migration) also becomes important.

In this article, we continue the investigation of evolution of dispersal strategies in general spatially heterogeneous and time-periodic environments. As is shown by [7], the analogy between IFD and perfect alignment with carrying capacity can hold only under the limitation that the total carrying capacity is constant in time. In section 2, we establish a notion of pathwise fitness, which leads to a broader notion of IFD in the spatially heterogeneous and temporally periodic context. In particular, the generalized version of IFD reduces to and includes the results of [7] when the total level of resources is constant in time (i.e., condition (2.8) below holds). In section 3 we propose a necessary and sufficient condition for the existence of dispersal strategies that enable the species to achieve IFD, and we construct a concrete class of such dispersal strategies. In section 4, we show that the proposed notion of IFD confers the same evolutionary advantage as in the temporally constant case, in the sense that once a strategy enables the species to achieve IFD, then it is both ESS and NIS. Moreover, we will also show that it is necessary in the sense that a time-periodic ecological attractor that is not an IFD can always be invaded by an exotic species equipped with a suitably chosen dispersal strategy. In section 5, we close with some further discussion of the implications of our results.

2. Pathwise fitness and IFD in spatially heterogeneous and temporally periodic environments.

2.1. The single-species model. We consider the following class of reaction-diffusion-advection models in the spatially heterogeneous and temporally periodic

setting, which models the dynamics of the density $\theta(x, t)$ of a single species:

$$(2.1) \quad \begin{cases} \frac{\partial \theta}{\partial t} = \nabla \cdot [\mu(x, t) \nabla \theta - \theta \vec{P}(x, t)] + r(x, t) \theta \left(1 - \frac{\theta}{K(x, t)}\right) & \text{in } \Omega \times (0, \infty), \\ n \cdot [\mu(x, t) \nabla \theta - \theta \vec{P}(x, t)] = 0 & \text{on } \partial \Omega \times (0, \infty), \\ \theta(x, 0) = \theta_0(x) & \text{in } \Omega, \end{cases}$$

where Ω is a bounded domain in \mathbb{R}^k with smooth boundary $\partial \Omega$ and unit outer normal vector $n = n(x)$; $\mu(x, t)$ is the diffusion rate; $\vec{P}(x, t)$ is the vector field describing the directed movement; $r(x, t)$ is the local intrinsic growth rate; $K(x, t)$ is the carrying capacity. We call (r, K) the environmental functions and (μ, \vec{P}) the dispersal strategy. We assume that μ, r, K, \vec{P} are smooth and T -periodic in t , and μ, r, K are positive. The no-flux boundary condition says that there is no net movement into or out of the domain, as is reflected by an application of the divergence theorem:

$$(2.2) \quad \int_{\Omega} \nabla \cdot [\mu(x, t) \nabla \theta - \theta \vec{P}(x, t)] dx = 0.$$

It is well known that, for given positive, T -periodic coefficients μ, r, K and T -periodic vector field \vec{P} , equation (2.1) has a unique positive periodic solution $\theta^*(x, t)$, which is globally asymptotically stable among all nonnegative, nontrivial solutions [32].

2.2. A notion of fitness. One characterization of the IFD in a spatially heterogeneous but temporally constant environment is that when a population is at a steady state, individuals at all locations should have equal fitness, since otherwise some would change their behavior to increase their fitness. For theoretical models we need to have a notion of fitness so that we can compare the fitness of individuals using different strategies. If we consider a population where individuals do not move but have spatial locations, a simple population model for population growth at locations x , time t , and density u would take the form

$$(2.3) \quad \frac{du}{dt} = F(x, t, u)u,$$

where $F(x, t, u)$ represents the per-capita growth rate of a population at location x , time t , and density u , which is a commonly used proxy for reproductive fitness. If F does not depend on t and either u is held fixed (for example, if a population is at equilibrium) or F does not depend on u , we can interpret $F = F(x)$ as the average fitness of individuals at location x and use $F(x)$ to model reproductive fitness. In the case of a time-periodic environment with period T we can still define fitness at location x by considering the period map $u(x, 0) \rightarrow u(x, T)$. In the case $F = F(x, t)$ we obtain from (2.3) that

$$(2.4) \quad u(x, T) = e^{\int_0^T F(x, s) ds} u(x, 0).$$

If we let $R(x) = e^{\int_0^T F(x, s) ds}$, then in the case where F does not depend on t we can recover our original fitness proxy $F(x)$ for that case as $F(x) = (1/T) \log(R(x))$. Since we are interested only in comparing fitness between different individuals rather than determining absolute fitness, and T will be fixed throughout the paper, we will drop the scale factor $1/T$ and just use

$$(2.5) \quad \log R(x) = \int_0^T F(x, s) ds$$

as our fitness proxy over a time period in the remainder of our discussion. (It is worth noting that in studies of evolution in simple discrete time models for a population x_t , for example, models of the form $x_{t+1} = r(x_t, \dots)x_t$, fitness is defined as $\log(r(x_t, \dots))$; see, for example, [17, equations (4) and (5)].) Suppose now that the local per-capita growth rate is still given by $F(x, t)$ and is still T -periodic, but that individuals do not remain at fixed locations. Instead, suppose that each individual follows a path $x = \gamma(t)$ through space as t goes from 0 to T . Substituting into (2.5) gives

$$(2.6) \quad F_{\text{path}}(\gamma) = \int_0^T F(\gamma(s), s) ds.$$

A somewhat similar but distinct definition of fitness based on the path that an individual takes through space and time was used in [58], where the authors considered optimal migration from a different modeling viewpoint.

Now, we specialize to the reaction-diffusion setting of (2.1). When the environment is temporally constant (i.e., $r = r(x)$ and $K = K(x)$), the stable population will be at equilibrium $\theta^*(x)$, so that the per-capita growth rate depends on location only:

$$F(x) = r(x) \left(1 - \frac{\theta^*(x)}{K(x)} \right).$$

In such a case the IFD is realized when fitness is equilibrated, so that the IFD equilibrium corresponds to the perfect alignment with carrying capacity:

$$\theta^*(x) \equiv K(x).$$

In contrast, when the environment is time periodic, we expect the population density to stabilize at a time-periodic solution $\theta^*(x, t)$, so that the per-capita growth rate varies in both space and time:

$$(2.7) \quad F(x, t) = r(x, t) \left(1 - \frac{\theta^*(x, t)}{K(x, t)} \right).$$

In case $r(x, t) = K(x, t)$, the first two authors [7] show that, under the additional assumption that the carrying capacity is everywhere positive and that the total level of resources in the environment remains constant in time, precisely,

$$(2.8) \quad \int K(x, t) dx = \text{const.},$$

then there exists a class of dispersal strategies (i.e., choices of μ and \vec{P}) under which the IFD can be achieved in the form of perfect alignment with carrying capacity, i.e., $\theta^*(x, t) = K(x, t)$. The authors went on to show that such dispersal strategies are both ESS and NIS. However, as observed in [7], perfect alignment with carrying capacity is impossible if (2.8) is false.

Substituting (2.7) into (2.6), the pathwise fitness of an individual traveling a path $\gamma(t)$ during the time period $[0, T]$ can be defined as

$$F_{\text{path}}(\gamma) = \int_0^T \left[r(x, t) \left(1 - \frac{\theta^*(x, t)}{K(x, t)} \right) \right]_{x=\gamma(t)} dt.$$

Suppose the population achieves IFD. Then we expect that no individual can gain proliferative advantage by dispersing itself differently within the time period $[0, T]$,

so that the pathwise fitness $F_{\text{path}}(\gamma)$ will be equilibrated among all possible paths γ ; i.e., a distribution $\theta^*(x, t)$ is IFD if and only if the corresponding pathwise fitness $F_{\text{path}}(\gamma)$ is independent of paths γ . Observe that

$$(2.9) \quad \inf_{\gamma} F_{\text{path}}(\gamma) = \int_0^T \inf_{x \in \Omega} F(x, t) dt \quad \text{and} \quad \sup_{\gamma} F_{\text{path}}(\gamma) = \int_0^T \sup_{x \in \Omega} F(x, t) dt,$$

where the infimum and supremum are taken over all continuous paths $\gamma : [0, T] \rightarrow \Omega$. See Appendix B for the proof of (2.9). (We remark that the set of test functions can be further reduced to the class of all C^∞ paths by a density argument.) This motivates the following definition.

DEFINITION 2.1. *Suppose the population density stabilizes at a positive periodic solution $\theta^*(x, t)$. We say that $\theta^*(x, t)$ is an ideal free distribution (IFD) if*

$$F(x, t) = r(x, t) \left(1 - \frac{\theta^*(x, t)}{K(x, t)} \right) \quad \text{is independent of } x.$$

Observe that total alignment with resource (i.e., $\theta^*(x, t) = K(x, t)$ for all x and t) is a sufficient, but not necessary, condition for IFD in the sense of Definition 2.1. For example, when $r(x, t) \equiv 1$, then $\theta^*(x, t) = p(t)K(x, t)$ is IFD for some $p(t)$. See Remark 3.4(a) for details.

In section 4, we will give two pieces of evidence in support of the validity of the above definition of an IFD. First, we show that a species that is able to achieve IFD, in the absence of competitors, can always competitively exclude a species that does not achieve IFD. Conversely, if a given resident species does not achieve IFD, then it can be invaded by an exotic species with a suitably chosen dispersal strategy.

3. The existence of IFD strategy. The goal of this section is to give a sufficient and necessary condition, in terms of the environmental functions $r(x, t)$ and $K(x, t)$, so that there exists a class of dispersal strategies (μ, \vec{P}) whose corresponding positive T -periodic solution of (2.1) is an IFD.

We outline our main ideas as follows. First, we define a periodic function $M(t)$ by solving a Bernoulli-type equation (see Lemma 3.1). Second, we consider the transformation $\tilde{\theta}(x, t) = \theta(x, t)/M(t)$, which transforms the single-species problem (2.1) into the following:

$$(3.1) \quad \begin{cases} \frac{\partial \tilde{\theta}}{\partial t} = \nabla \cdot [\mu(x, t) \nabla \tilde{\theta} - \tilde{\theta} \vec{P}(x, t)] + \tilde{r}(x, t) \tilde{\theta} \left(1 - \frac{\tilde{\theta}}{K(x, t)} \right) & \text{in } \Omega \times (0, \infty), \\ n \cdot [\mu(x, t) \nabla \tilde{\theta} - \tilde{\theta} \vec{P}(x, t)] = 0 & \text{on } \partial\Omega \times (0, \infty), \\ \tilde{\theta}(x, 0) = \tilde{\theta}_0(x) & \text{in } \Omega, \end{cases}$$

where

$$(3.2) \quad \tilde{r}(x, t) = r(x, t) - \frac{M'(t)}{M(t)}$$

and

$$(3.3) \quad \tilde{K}(x, t) = \frac{K(x, t)}{M(t)r(x, t)} \left(r(x, t) - \frac{M'(t)}{M(t)} \right) = \frac{K(x, t)}{M(t)} - \frac{K(x, t)}{r(x, t)} \cdot \frac{M'(t)}{M(t)^2}.$$

Then we have an equivalent system where the new carrying capacity $\tilde{K}(x, t)$ satisfies, by our choice of $M(t)$ in Lemma 3.1,

$$(3.4) \quad \int \tilde{K}(x, t) dx = 1 \quad \text{for all } t.$$

Provided that the positivity conditions $\tilde{r}, \tilde{K} > 0$ (see (3.9)) hold, we can apply the results in [7] to yield an IFD of (3.1) that perfectly matches the new carrying capacity $\tilde{K}(x, t)$. This gives a mathematically natural way of extending the notion of IFD to general time-periodic environments. Condition (3.9), which corresponds to the positivity of carrying capacity in the transformed problem (3.1), can be interpreted as a criterion that prevents the appearance of generalized sinks in the original problem (2.1).

In subsection 3.1, we state condition (3.9), under which we can define an IFD $\theta^*(x, t) = M(t)\tilde{K}(x, t)$, where $M(t)$ and $\tilde{K}(x, t)$ are defined in terms of the environmental data $r(x, t), K(x, t)$ by solving a Bernoulli-type equation. In subsection 3.2, we will show that condition (3.9) is necessary, and that the IFD $\theta^*(x, t) = M(t)\tilde{K}(x, t)$ is the only possible form of IFD for the class of population dynamics as described by the reaction-diffusion-advection equation (2.1). In subsection 3.3, we construct a class of dispersal strategies which generates IFD.

3.1. The Bernoulli equation. Let the environmental functions $r(x, t), K(x, t)$ be given. We define $M(t)$ as follows.

LEMMA 3.1. *There exists a unique, positive, T-periodic function $M(t)$ such that*

$$(3.5) \quad \frac{\overline{K}(t)}{M(t)} - \overline{(K/r)}(t) \frac{M'(t)}{M(t)^2} = 1,$$

where, hereafter, $\bar{f}(t)$ denotes the spatial average of $f(x, t)$, as given by $\frac{1}{|\Omega|} \int_{\Omega} f(x, t) dx$.

Proof. It remains to solve

$$\frac{M'(t)}{M(t)} + b(t)M(t) = a(t),$$

where

$$(3.6) \quad a(t) := \frac{\overline{K}(t)}{\overline{(K/r)}(t)} \quad \text{and} \quad b(t) = \frac{1}{\overline{(K/r)}(t)}.$$

First we show uniqueness. Suppose $M(t)$ is a positive T -periodic solution of (3.5). Then $w(t) = 1/M(t)$ satisfies

$$-w' + b(t) = a(t)w$$

so that

$$\left[\exp \left(\int_0^t a(s) ds \right) w(t) \right]' = b(t) \exp \left(\int_0^t a(s) ds \right).$$

Integrating the above, we obtain

$$w(t) = \exp \left(- \int_0^t a(s) ds \right) w(0) + \int_0^t b(s) \exp \left(- \int_s^t a(\tau) d\tau \right) ds.$$

By invoking the periodicity $w(0) = w(T)$, we further determine $w(0)$ uniquely. That is,

$$(3.7) \quad \frac{1}{M(t)} = w(t) = \exp \left(- \int_0^t a(s) ds \right) \frac{\int_0^T b(s) \exp \left(- \int_s^T a(\tau) d\tau \right) ds}{1 - \exp \left(- \int_0^T a(s) ds \right)} + \int_0^t b(s) \exp \left(- \int_s^t a(\tau) d\tau \right) ds.$$

This proves uniqueness. Conversely, (3.7) also defines a solution to (3.5), so that existence follows immediately. \square

Next, we define $\tilde{K}(x, t)$ in terms of $r(x, t)$, $K(x, t)$, and $M(t)$, by (3.3), and define

$$(3.8) \quad \theta^*(x, t) := M(t)\tilde{K}(x, t).$$

We show that θ^* defines an IFD.

LEMMA 3.2. *Assume*

$$(3.9) \quad K(x, t) > (K/r)(x, t) \frac{M'(t)}{M(t)}.$$

Then the distribution θ^* is an IFD. Precisely, the fitness function satisfies

$$(3.10) \quad r(x, t) \left[1 - \frac{\theta^*(x, t)}{K(x, t)} \right] = r(x, t) \left[1 - \frac{M(t)\tilde{K}(x, t)}{K(x, t)} \right] = \frac{M'(t)}{M(t)}.$$

Proof. By (3.9), the function $\tilde{K}(x, t)$ defined in (3.3) is positive, so that $\theta^*(x, t) = M(t)\tilde{K}(x, t)$ is also positive. Finally, (3.10) follows by rewriting (3.3). \square

Remark 3.3. Condition (3.9) can also be written as $r(x, t) > M'(t)/M(t)$. We prefer the above formulation, in view of the fact that K and K/r have already appeared in the definition of $M(t)$. Also, by combining (3.3) and (3.5), we have

$$(3.11) \quad \tilde{K}(x, t) = \frac{K(x, t) - \bar{K}(t)}{M(t)} + \frac{(K/r)(x, t)}{(K/r)(t)} - \frac{\bar{K}(t)}{M(t)} \left[\frac{(K/r)(x, t)}{(K/r)(t)} - 1 \right].$$

This gives yet another equivalent formulation of (3.9), which is

$$(3.12) \quad \frac{K(x, t) - \bar{K}(t)}{M(t)} > \frac{\bar{K}(t)}{M(t)} \left[\frac{(K/r)(x, t)}{(K/r)(t)} - 1 \right] - \frac{(K/r)(x, t)}{(K/r)(t)}.$$

Remark 3.4.

- (a) If $r \equiv 1$, then (3.12) and thus (3.9) hold for any $K(x, t) > 0$. The corresponding IFD is given by

$$\theta^*(x, t) = \frac{M(t)}{\bar{K}(t)} K(x, t).$$

Note that $\theta^*(x, t)$ is proportional in space to $K(x, t)$ for each t .

- (b) If $K \equiv 1$, then $a(t) = b(t) = [(1/r)(t)]^{-1}$ and $M(t) \equiv 1$ and the IFD is homogeneous 1, and the IFD strategy can simply be taken to be the homogeneous diffusion operator.
- (c) If $(\overline{K/r})(t) \equiv 1$ and $\bar{K}(t) = \text{const.}$, then $M(t) = \bar{K}(t)$, so that (3.12) and (3.9) are reduced to the requirements $r(x, t), K(x, t) > 0$. This includes the results in [7], where $r(x, t) = K(x, t)$ and condition (2.8) are enforced.
- (d) Consider the special case $r(x, t) \equiv K(x, t)$, which is the simplified logistic model considered in [7]. Fix an arbitrary $\rho(t)$ which is positive, periodic, and nonconstant, and define $M(t)$ to be the unique periodic solution to

$$\frac{M'(t)}{M(t)} + M(t) = \rho(t).$$

Then it is easy to see that $M'(t)/M(t)$ changes sign in t . Hence, the condition (3.9) fails if we choose $K(x, t) = r(x, t)$ such that

$$\bar{K}(t) = \rho(t), \quad \text{and} \quad \inf_{x \in \Omega} K(x, t) - \frac{M'(t)}{M(t)} \text{ changes sign.}$$

3.2. Necessary condition for an IFD. In the previous subsection, we saw that $\theta^*(x, t) = M(t)\tilde{K}(x, t)$ is an IFD. In this subsection we will show that this is the only possibility. For this purpose, consider the N -species competition model (3.13)

$$\begin{cases} \frac{du_i}{dt} = \nabla \cdot [\mu_i(x, t)\nabla u_i - u_i\vec{P}_i(x, t)] + r(x, t)u_i \left(1 - \frac{\sum_{j=1}^N u_j}{K(x, t)}\right) & \text{in } \Omega \times (0, \infty), \\ n \cdot [\mu_i(x, t)\nabla u_i - u_i\vec{P}_i(x, t)] = 0 & \text{on } \partial\Omega \times (0, \infty), \\ u_i(x, 0) = u_{i,0}(x) & \text{in } \Omega \end{cases}$$

for $1 \leq i \leq N$, where $\mu_i(x, t), \vec{P}_i$ are smooth, T -periodic in t , $\mu_i(x, t) > 0$, and $r(x, t), K(x, t)$ are as before.

DEFINITION 3.5. Let $(\tilde{u}_i(x, t))_{i=1}^N$ be a positive, T -periodic solution of (3.13). We say that $(\tilde{u}_i(x, t))_{i=1}^N$ is an IFD if $\theta^*(x, t) = \sum_{i=1}^N \tilde{u}_i(x, t)$ is an IFD, i.e.,

$$r(x, t) \left(1 - \frac{\sum_{i=1}^N \tilde{u}_i(x, t)}{K(x, t)}\right) \text{ depends on } t \text{ only.}$$

THEOREM 3.6. Let $(\tilde{u}_i(x, t))_{i=1}^N$ be a positive, T -periodic solution of (3.13). Suppose $(\tilde{u}_i(x, t))_{i=1}^N$ is an IFD. Then (3.9) holds and

$$\sum_{i=1}^N \tilde{u}_i(x, t) = M(t)\tilde{K}(x, t),$$

where the T -periodic functions $M(t)$ and $\tilde{K}(x, t)$ are uniquely determined by $r(x, t)$ and $K(x, t)$, via (3.5) and (3.3), respectively.

Remark 3.7. As noted in Remark 3.4(d), there exists positive functions $r(x, t), K(x, t)$ which are periodic in t such that (3.9) does not hold, and thus Corollary 3.8 shows that IFD is impossible for such environments.

Proof of Theorem 3.6. First, we define $\theta^*(x, t) = \sum_{i=1}^N \tilde{u}_i(x, t)$ and then define $M(t)$ as

$$(3.14) \quad M(t) = \bar{\theta}^*(0) \exp \left[\int_0^t r(x, s) \left(1 - \frac{\theta^*(x, s)}{K(x, s)}\right) ds \right],$$

where $\bar{\theta}^*(0) = \frac{1}{|\Omega|} \int_{\Omega} \theta^*(x, 0) dx$. (Note that the right-hand side of (3.14) is independent of x , since θ^* is an IFD.) Then $M(t)$ is positive and satisfies

$$(3.15) \quad \frac{M'(t)}{M(t)} = r(x, t) \left(1 - \frac{\theta^*(x, t)}{K(x, t)}\right)$$

and the equation of $\tilde{u}_i(x, t)$ becomes

$$(3.16) \quad \frac{\partial \tilde{u}_i}{\partial t} = \nabla \cdot [\mu_i \tilde{u}_i - \tilde{u}_i \vec{P}_i] + \frac{M'(t)}{M(t)} \tilde{u}_i.$$

Using the no-flux boundary conditions of \tilde{u}_i , we can integrate (3.16) in Ω to get

$$\frac{d}{dt} \overline{\tilde{u}_i}(t) = \frac{M'(t)}{M(t)} \overline{\tilde{u}_i}(t).$$

Adding in $i = 1, \dots, N$, we obtain

$$(3.17) \quad \frac{d}{dt} \overline{\theta^*}(t) = \frac{M'(t)}{M(t)} \overline{\theta^*}(t).$$

Dividing (3.17) by $\overline{\theta^*}(t) > 0$ and setting $t = 0$ in (3.14), we have

$$(\log M)'(t) = (\log \overline{\theta^*})'(t) \quad \text{for all } t \geq 0, \quad \text{and} \quad M(0) = \overline{\theta^*}(0).$$

Therefore,

$$(3.18) \quad \overline{\theta^*}(t) = M(t) \quad \text{for all } t.$$

In particular, $M(t)$ is T -periodic in t as well.

Next, we show that $M(t)$ satisfies (3.5). Indeed, multiply both sides of (3.15) by $K(x, t)/r(x, t)$ to get

$$\frac{K(x, t)}{r(x, t)} \frac{M'(t)}{M(t)} = K(x, t) - \theta^*(x, t).$$

Integrating the above over in $x \in \Omega$ and using (3.18), we get

$$\overline{K/r}(t) \frac{M'(t)}{M(t)} = \overline{K}(t) - M(t),$$

which is equivalent to (3.5).

Then, defining $\tilde{K}(x, t) = \theta^*(x, t)/M(t)$, we deduce from (3.15) that

$$(3.19) \quad \frac{M'(t)}{M(t)} = r(x, t) \left(1 - \frac{M(t) \tilde{K}(x, t)}{K(x, t)} \right),$$

which is equivalent to (3.3).

Finally, (3.19) implies $r(x, t) > M'(t)/M(t)$, which implies that (3.9) holds. \square

COROLLARY 3.8. *Let $\theta^*(x, t)$ be a positive solution of the single-species problem (2.1). Suppose θ^* is an IFD, i.e.,*

$$r(x, t) \left(1 - \frac{\theta^*(x, t)}{K(x, t)} \right) \quad \text{depends on } t \text{ only.}$$

Then $\theta^(x, t) = M(t) \tilde{K}(x, t)$ and (3.9) holds, where the T -periodic functions $M(t)$ and $\tilde{K}(x, t)$ are uniquely determined by $r(x, t)$ and $K(x, t)$, via (3.5) and (3.3), respectively.*

3.3. Sufficient condition for existence of an IFD strategy.

THEOREM 3.9. *Let $r(x, t), K(x, t)$ be given, and let $M(t), \tilde{K}(x, t)$ be given, respectively, by (3.7) and (3.3) in terms of $r(x, t)$ and $K(x, t)$. Suppose (3.9) holds. Then for each $\mu(x, t) > 0$ there exists a suitable $\tilde{P}(x, t)$ such that the corresponding positive periodic solution $\theta^*(x, t)$ is an IFD. In fact, $\theta^*(x, t) = M(t) \tilde{K}(x, t)$.*

Proof of Theorem 3.9. Fix $r(x, t)$, $K(x, t)$, and $\mu(x, t)$, and let $M(t)$ and $\tilde{K}(x, t)$ be given, respectively, by (3.7) and (3.3). Since (3.9) holds, Lemma 3.2 says that the function $\theta^*(x, t) = M(t)\tilde{K}(x, t)$ defines an IFD.

Next, we define $\tilde{P}^*(x, t)$ in terms of $\mu(x, t)$, as in [7, equation (8)]:

$$(3.20) \quad \tilde{P}^*(x, t) = \frac{1}{\tilde{K}(x, t)} \left[\mu \nabla \tilde{K}(x, t) - \nabla q \right],$$

where, for each t , $q(x, t)$ is the unique solution to

$$\Delta q = \frac{\partial \tilde{K}}{\partial t} \quad \text{in } \Omega, \quad \text{and} \quad n \cdot \nabla q = 0 \quad \text{on } \partial\Omega.$$

The function q is well-defined for each t , since we have $\int_{\Omega} \frac{\partial \tilde{K}}{\partial t}(x, t) dx = 0$ for all t , according to (3.4).

CLAIM 3.10. *The unique time-periodic solution corresponding to the dispersal strategy (μ, \tilde{P}^*) is given by $\theta^*(x, t) = M(t)\tilde{K}(x, t)$; i.e., it is the unique positive solution to*

$$(3.21) \quad \frac{\partial \theta^*}{\partial t} = \nabla \cdot [\mu \nabla \theta^* - \theta^* \tilde{P}^*] + r(x, t)\theta^* \left[1 - \frac{\theta^*(x, t)}{K(x, t)} \right] \quad \text{in } \Omega \times [0, T],$$

$$(3.22) \quad n \cdot [\mu \nabla \theta^* - \theta^* \tilde{P}^*] = 0 \quad \text{on } \partial\Omega \times [0, T],$$

$$(3.23) \quad \theta^*(x, 0) = \theta^*(x, T) \quad \text{in } \Omega.$$

To show (3.23), we first observe that $M(t)$ is T -periodic by Lemma 3.1. Thus $\tilde{K}(x, t)$ is also T -periodic in t by (3.3). Since $\theta^*(x, t) = M(t)\tilde{K}(x, t)$, we deduce (3.23).

Next, we show (3.22).

$$\begin{aligned} n \cdot [\mu \nabla \theta^* - \theta^* \tilde{P}^*] &= M(t)n \cdot [\mu \nabla \tilde{K} - \tilde{K} \tilde{P}^*] \\ &= M(t) \left[\mu(n \cdot \nabla \tilde{K}) - \tilde{K}(n \cdot \tilde{P}^*) \right] \\ &= M(t) \left[\mu(n \cdot \nabla \tilde{K}) - \tilde{K} \left(\frac{n}{\tilde{K}} \right) \cdot (\mu \nabla \tilde{K} - \nabla q) \right] \\ &= M(t)(n \cdot \nabla q) = 0, \end{aligned}$$

where the third equality follows by taking the scalar product of both sides of (3.20) with the outer normal vector n , and the last equality follows from the fact that q satisfies the Neumann boundary condition on $\partial\Omega$.

Before going further, we multiply both sides of (3.20) by \tilde{K} and take divergence of both sides to obtain

$$(3.24) \quad \nabla \cdot (\tilde{K} \tilde{P}^*) = \nabla \cdot (\mu \nabla \tilde{K} - \nabla q) = \nabla \cdot (\mu \nabla \tilde{K}) - \frac{\partial \tilde{K}}{\partial t}.$$

Now we proceed to show (3.21):

$$\begin{aligned} &\frac{\partial \theta^*}{\partial t} - \nabla \cdot [\mu \nabla \theta^* - \theta^* \tilde{P}^*] \\ &= \frac{\partial}{\partial t} (M(t)\tilde{K}(x, t)) - \nabla \cdot [\mu \nabla (M(t)\tilde{K}(x, t)) - (M(t)\tilde{K}(x, t))\tilde{P}^*(x, t)] \\ &= \tilde{K}(x, t)M'(t) + M(t) \left\{ \frac{\partial \tilde{K}}{\partial t}(x, t) - \nabla \cdot [\mu \nabla \tilde{K}(x, t) - \tilde{K}(x, t)\tilde{P}^*(x, t)] \right\} \\ &= \tilde{K}(x, t)M'(t), \end{aligned}$$

where we used (3.24) in the last equality. Taking (3.10) into account,

$$\frac{\partial \theta^*}{\partial t} - \nabla \cdot [\mu \nabla \theta^* - \theta^* \vec{P}^*] = r \tilde{K} M \left(1 - \frac{\theta^*}{K} \right).$$

This proves (3.21). The uniqueness of θ^* is standard [32]. \square

4. An IFD is necessary and sufficient for ESS and NIS. We consider the following class of two-species competition models in the spatially heterogeneous and temporally periodic setting:

$$(4.1) \quad \begin{cases} \frac{\partial u}{\partial t} = \nabla \cdot [\mu(x, t) \nabla u - u \vec{P}(x, t)] + r(x, t) u \left(1 - \frac{u+v}{K(x, t)} \right) & \text{in } \Omega \times (0, \infty), \\ \frac{\partial v}{\partial t} = \nabla \cdot [\nu(x, t) \nabla v - v \vec{Q}(x, t)] + r(x, t) v \left(1 - \frac{u+v}{K(x, t)} \right) & \text{in } \Omega \times (0, \infty), \\ n \cdot [\mu(t, x) \nabla u + u \vec{P}(x, t)] = 0 & \text{on } \partial\Omega \times (0, \infty), \\ n \cdot [\nu(t, x) \nabla v + v \vec{Q}(x, t)] = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

where the functions μ, ν, r, K are positive, smooth, T -periodic in t , the vector fields \vec{P}, \vec{Q} are smooth and T -periodic in t , and n denotes the outer unit normal vector on $\partial\Omega$. The no-flux boundary conditions say that there is no net movement into or out of the domain. Note that, as in [30], the two species are assumed to be identical except for their dispersal strategies.

We note that the competition system (4.1) has one trivial periodic solution, $(0, 0)$, and two semitrivial periodic solutions, $(\theta^*, 0)$ and $(0, v^*)$, where θ^* is the unique positive periodic solution of (2.1), and v^* is the unique positive solution to

$$(4.2) \quad \begin{cases} \frac{\partial v^*}{\partial t} = \nabla \cdot [\nu(x, t) \nabla v^* - v^* \vec{Q}(x, t)] + r(x, t) v^* \left(1 - \frac{v^*}{K(x, t)} \right) & \text{in } \Omega \times [0, T], \\ n \cdot [\nu(x, t) \nabla v^* - v^* \vec{Q}(x, t)] = 0 & \text{on } \partial\Omega \times [0, T], \\ v^*(x, 0) = v^*(x, T) & \text{in } \Omega. \end{cases}$$

There are two main results in this section. The first one is to show that, for the competition model (4.1), the dispersal strategies which generate IFD always dominate the strategies which do not. That is, the dispersal strategies which generate IFD are both ESS and NIS.

THEOREM 4.1. *Let (u, v) be a solution of the competition model (4.1) with nonnegative, nontrivial initial data. Suppose*

(C) θ^* is an IFD and v^* is not an IFD,

where IFD is defined in the sense of Definition 2.1. Then the semitrivial periodic solution $(\theta^*, 0)$ is globally asymptotically stable among all nontrivial nonnegative initial data, i.e.,

$$\|(u(\cdot, t), v(\cdot, t)) - (\theta^*(\cdot, 0), 0)\|_{C(\bar{\Omega})} \rightarrow 0 \quad \text{as } t \rightarrow \infty.$$

Theorem 4.1 is proved in subsection 4.1.

Our second result says that the condition θ^* being an IFD in Theorem 4.1 is sharp.

THEOREM 4.2. *Let $(\theta^*(x, t), 0)$ be a T -periodic solution of (4.1). If $\theta^*(x, t)$ is not IFD, then there exists (ν, \vec{Q}) such that a second species with diffusion rate $\nu > 0$ and advection rate $\vec{Q}(x, t)$ can invade when rare; i.e., the $(\theta^*(x, t), 0)$ is unstable in (4.1).*

Proof. Recall that $F(x, t) = r(x, t)(1 - \frac{\theta^*(x, t)}{K(x, t)})$. Suppose $\theta^*(x, t)$ is not IFD. We claim that

$$(4.3) \quad \int_0^T \sup_{x \in \Omega} F(x, t) dt > 0.$$

Indeed, if we integrate (2.1) over Ω , then

$$\frac{d}{dt} \int_{\Omega} \theta^*(x, t) dx = \int_{\Omega} F(x, t)\theta^*(x, t) dx < \left(\sup_{x \in \Omega} F(x, t) \right) \int_{\Omega} \theta^*(x, t) dx,$$

where the latter equality is strict as $F(x, t)$ is not independent of x . If we divide the above by $\int_{\Omega} \theta^*(x, t) dx$, then

$$\frac{d}{dt} \log \left(\int_{\Omega} \theta^*(x, t) dx \right) < \sup_{x \in \Omega} F(x, t).$$

Integrating over $[0, T]$ and using the periodicity of $\theta(x, t)$, we obtain (4.3).

By (4.3) and the latter part of (2.9), one can choose a smooth, T -periodic curve $\gamma : \mathbb{R} \rightarrow \text{Int } \Omega$ such that

$$(4.4) \quad \int_0^T F(\gamma(t), t) dt > 0.$$

Now, let ν be a positive constant and define

$$(4.5) \quad \vec{Q}_{\alpha}(x, t) = \alpha(\gamma(t) - x),$$

where α is a constant to be specified later. It suffices to show that the principal eigenvalue λ_1 of the linear periodic-parabolic problem

$$(4.6) \quad \begin{cases} \frac{d\varphi}{dt} = \nabla \cdot [\nu \nabla \varphi - \varphi \vec{Q}_{\alpha}(x, t)] + F(x, t)\varphi + \lambda_1 \varphi & \text{in } \Omega \times [0, T], \\ n \cdot [\nabla \varphi - \varphi \vec{Q}_{\alpha}(x, t)] = 0 & \text{on } \partial\Omega \times [0, T], \\ \varphi(x, 0) = \varphi(x, T) & \text{in } \Omega \end{cases}$$

is negative. We proceed by considering the adjoint problem, for which the principal eigenvalue λ_1 is the same:

$$(4.7) \quad \begin{cases} \frac{d\phi}{dt} = \nu \Delta \phi + \nabla \phi \cdot \vec{Q}_{\alpha}(x, T - t) + F(x, T - t)\phi + \lambda_1 \phi & \text{in } \Omega \times [0, T], \\ n \cdot \nabla \phi = 0 & \text{on } \partial\Omega \times [0, T], \\ \phi(x, 0) = \phi(x, T) & \text{in } \Omega, \end{cases}$$

where we used the fact that ν is constant. By taking $m(x, t) = -\frac{1}{2}|x - \gamma(T - t)|^2$, Remark A.2 in the appendix shows the hypotheses of Proposition A.1 in the appendix are met, and thereby that result may be employed to show that

$$\limsup_{\alpha \rightarrow \infty} \lambda_1 \leq -\frac{1}{T} \int_0^T F(\gamma(T - t), T - t) dt = -\frac{1}{T} \int_0^T F(\gamma(t), t) dt.$$

Since the last term on the right-hand side is negative (by (4.4)), we have proved that the new species can indeed invade the non-IFD $\theta^*(x, t)$ when rare. \square

Remark 4.3. Let $N \geq 2$ and let $\tilde{u} = (\tilde{u}_1, \dots, \tilde{u}_N)$ be a stable T -periodic solution of the N -species competition system (3.13). Then the above can be applied to show the instability of $(\tilde{u}, 0)$ in the extended $(N + 1)$ -species competition model, with an additional species with a suitable dispersal strategy.

Remark 4.4. For environments where (3.9) does not hold, it is proved in Theorem 3.6 that no T -periodic solutions can achieve IFD. In such a case, the proof of Theorem 4.2 says that no T -periodic solution consisting of any number of species can be an ESS.

Remark 4.5. When the number of species is less than or equal to two, then the corresponding model generates a monotone dynamical system [60], in which any attractor is necessarily T -periodic. Hence, Theorem 4.2 says that, in the case where (3.9) does not hold, any ecological attractor that is ESS must not be periodic in time and must consist of at least three species.

4.1. Proof of Theorem 4.1. In this subsection, we prove Theorem 4.1 by transforming the question into the context of [7] and then adapting the arguments therein.

Proof of Theorem 4.1. By Corollary 3.8, we deduce that (3.9) holds and

$$(4.8) \quad \theta^*(x, t) = M(t)\tilde{K}(x, t) \quad \text{and} \quad v^*(x, t) \neq M(t)\tilde{K}(x, t).$$

The idea is to transform the system into one that is similar to [7] and adapt the arguments therein. For this purpose, write

$$(u(x, t), v(x, t)) = M(t)(U(x, t), V(x, t))$$

so that by (3.3), (U, V) satisfies

$$(4.9) \quad \begin{cases} \frac{\partial U}{\partial t} = \nabla \cdot [\mu(x, t)\nabla U - U\tilde{P}(x, t)] + \hat{r}(x, t)U \left(\tilde{K}(x, t) - U - V \right) & \text{in } \Omega \times (0, \infty), \\ \frac{\partial V}{\partial t} = \nabla \cdot [\nu(x, t)\nabla V - V\tilde{Q}(x, t)] + \hat{r}(x, t)V \left(\tilde{K}(x, t) - U - V \right) & \text{in } \Omega \times (0, \infty), \\ n \cdot [\mu(t, x)\nabla U - U\tilde{P}(x, t)] = 0 & \text{on } \partial\Omega \times (0, \infty), \\ n \cdot [\nu(t, x)\nabla V - V\tilde{Q}(x, t)] = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

where $\hat{r}(x, t) = \frac{r(x, t)M(t)}{K(x, t)}$ and $\tilde{K}(x, t)$ is given by (3.3). By noting that $(\theta^*(x, t), 0) = (M(t)\tilde{K}(x, t), 0)$ and $(0, v^*(x, t))$ are semitrivial T -periodic solutions of (4.1), we deduce that $(\tilde{K}(x, t), 0)$ and $(0, V^*(x, t)) = (0, v^*(x, t)/M(t))$ are the corresponding semitrivial T -periodic solutions of the transformed system (4.9).

Substituting $(\tilde{K}(x, t), 0)$ into the first equation of (4.9), we obtain

$$(4.10) \quad \frac{\partial \tilde{K}}{\partial t} = \nabla \cdot [\mu\nabla \tilde{K} - \tilde{K}\tilde{P}] \quad \text{in } \Omega \times [0, T].$$

It remains to show that $(\tilde{K}(x, t), 0)$ is a globally asymptotically stable solution of (4.9).

Step 1. We claim that (4.9) has no componentwise positive periodic solutions (i.e., (U, V) such that $U > 0$ and $V > 0$). To this end, let (U, V) be a componentwise nonnegative periodic solution of (4.9) (i.e., $U \geq 0$ and $V \geq 0$). Assume $U \not\equiv 0$; then by the strong maximum principle we have $U > 0$ in $\Omega \times [0, T]$. It remains to show that $V(x, t) \equiv 0$.

Multiply the first equation of (4.9) by $\frac{\tilde{K}(x,t)}{U(x,t)}$, then multiply (4.10) by $\log U$ and add the two to get

$$\begin{aligned} \frac{\partial}{\partial t}(\tilde{K} \log U) &= \frac{\partial \tilde{K}}{\partial t} \log U + \frac{\tilde{K}}{U} \frac{\partial U}{\partial t} \\ &= \frac{\tilde{K}}{U} \nabla \cdot [\mu \nabla U - U \vec{P}] + \log U \nabla \cdot [\mu \nabla \tilde{K} - \tilde{K} \vec{P}] + \hat{r} \tilde{K} (\tilde{K} - U - V). \end{aligned}$$

Integrate by parts over Ω , then integrate in $[0, T]$. We get

$$\begin{aligned} (4.11) \quad 0 &= \iiint \left\{ - \left[\frac{\nabla \tilde{K}}{U} - \frac{\tilde{K} \nabla U}{U^2} \right] \cdot [\mu \nabla U - U \vec{P}] - \frac{\nabla U}{U} \cdot [\mu \nabla \tilde{K} - \tilde{K} \vec{P}] + \hat{r} \tilde{K} (\tilde{K} - U - V) \right\} dx dt \\ &= \iint \left\{ \mu \tilde{K} \frac{|\nabla U|^2}{U^2} - 2\mu \frac{\nabla \tilde{K} \cdot \nabla U}{U} + \nabla \tilde{K} \cdot \vec{P} + \hat{r} \tilde{K} (\tilde{K} - U - V) \right\} dx dt \\ &= \iint \left\{ \mu \tilde{K} \left| \frac{\nabla U}{U} - \frac{\nabla \tilde{K}}{\tilde{K}} \right|^2 - \mu \frac{|\nabla \tilde{K}|^2}{\tilde{K}} + \nabla \tilde{K} \cdot \vec{P} + \hat{r} \tilde{K} (\tilde{K} - U - V) \right\} dx dt. \end{aligned}$$

Next, we claim the following identity concerning $\tilde{K}(x, t)$ and $P(x, t)$ (see also [7, pp. 73-74]):

$$(4.12) \quad \iint \left[-\mu \frac{|\nabla \tilde{K}|^2}{\tilde{K}} + \nabla \tilde{K} \cdot \vec{P} \right] dx dt = 0.$$

Indeed,

$$\begin{aligned} \int_{\Omega} \left[-\mu \frac{|\nabla \tilde{K}|^2}{\tilde{K}} + \nabla \tilde{K} \cdot \vec{P} \right] dx &= - \int_{\Omega} (\nabla \log \tilde{K}) \cdot [\mu \nabla \tilde{K} - \tilde{K} \vec{P}] dx \\ &= \int_{\Omega} \frac{\partial \tilde{K}}{\partial t} \log \tilde{K} dx \\ &= \int_{\Omega} \frac{\partial}{\partial t} (\tilde{K} \log \tilde{K} - \tilde{K}) dx, \end{aligned}$$

where the first and third equalities follow by simply rewriting the integrands; the second equality follows by multiplying both sides of (4.10) by $\log \tilde{K}$ and integrating by parts. Integrating in $t \in [0, T]$, we obtain (4.12).

Substituting (4.12) into (4.11), we deduce that

$$(4.13) \quad 0 = \iint \left\{ \mu \tilde{K} \left| \frac{\nabla U}{U} - \frac{\nabla \tilde{K}}{\tilde{K}} \right|^2 + \hat{r} \tilde{K} (\tilde{K} - U - V) \right\} dx dt.$$

Furthermore, we may integrate the first and second equations of (4.9) over $\Omega \times [0, T]$. Then

$$(4.14) \quad \iint \hat{r} U (\tilde{K} - U - V) dx dt = 0 = \iint \hat{r} V (\tilde{K} - U - V) dx dt.$$

Combining (4.13) and (4.14), we have

$$(4.15) \quad 0 = \iint \left\{ \mu \tilde{K} \left| \frac{\nabla U}{U} - \frac{\nabla \tilde{K}}{\tilde{K}} \right|^2 + \hat{r}(\tilde{K} - U - V)^2 \right\} dx dt.$$

Therefore,

$$(4.16) \quad U(x, t) + V(x, t) \equiv \tilde{K}(x, t),$$

and there exists a T -periodic function $0 \leq c(t) \leq 1$ such that

$$(4.17) \quad U(x, t) = c(t)\tilde{K}(x, t) \quad \text{in } \Omega \times [0, T].$$

Substituting (4.16) and (4.17) into the first equation of (4.9) and comparing it with (4.10), we deduce that $c(t) = c_0$ for some constant $c_0 \in [0, 1]$. Since both U and V are positive, we have $c_0 \in (0, 1)$. Hence, we must have $V(x, t) = (1 - c_0)\tilde{K}(x, t)$ for some $c_0 \in (0, 1)$. Substituting that into the second equation of (4.9), we deduce that $\tilde{K}(x, t)$ is a positive, T -periodic solution of

$$\begin{cases} \frac{\partial \tilde{K}}{\partial t} = \nabla \cdot [\nu \nabla \tilde{K} - \tilde{K} \vec{Q}] = 0 & \text{in } \Omega \times [0, T], \\ n \cdot [\nu \nabla \tilde{K} - \tilde{K} \vec{Q}] = 0 & \text{on } \partial\Omega \times [0, T]. \end{cases}$$

This implies, by way of (3.10), that

$$\begin{aligned} \frac{\partial}{\partial t}(M\tilde{K}) - \nabla \cdot [\nu \nabla(M\tilde{K}) - (M\tilde{K})\vec{Q}] &= M'(t)\tilde{K}(x, t) \\ &= r(x, t)M(t)\tilde{K}(x, t) \left(1 - \frac{M(t)\tilde{K}(x, t)}{K} \right) \end{aligned}$$

and that $n \cdot [\nu \nabla(M\tilde{K}) - (M\tilde{K})\vec{Q}] = 0$ on $\partial\Omega \times [0, T]$. By uniqueness of positive solution to (4.2), this means $v^*(x, t) = M(t)\tilde{K}(x, t)$. This is in contradiction with (4.8). Hence we conclude that there exists no positive periodic solution (U, V) to (4.9).

Step 2. We prove that the T -periodic solution $(0, V^*)$ of (4.9) is repelling. That is, for solutions (U, V) with nonnegative, nontrivial initial data, $\|(U, V)(\cdot, t) - (0, V^*)(\cdot, t)\| \not\rightarrow 0$.

It suffices to show that $(0, V^*)$ is linearly unstable. (See, e.g., [46, Theorem 1.3].) To this end, let σ_1 be the principal eigenvalue of the following periodic-parabolic eigenvalue problem (see, e.g., [32] for the spectral theory of linear periodic-parabolic operators):

$$(4.18) \quad \begin{cases} \frac{\partial}{\partial t} \Psi = \nabla \cdot [\mu \nabla \Psi - \Psi \vec{P}] + \hat{r}(x, t) [\tilde{K}(x, t) - V^*(x, t)] \Psi + \sigma_1 \Psi & \text{for } x \in \Omega, t \in [0, T], \\ n \cdot [\mu \nabla \Psi - \Psi \vec{P}] = 0 & \text{for } x \in \partial\Omega, t \in [0, T], \\ \Psi(x, 0) = \Psi(x, T) & \text{for } x \in \Omega, \end{cases}$$

where $V^*(x, t) = v^*(x, t)/M(t)$ is the unique positive periodic solution of

$$(4.19) \quad \begin{cases} \frac{\partial}{\partial t} V^* = \nabla \cdot [\nu \nabla V^* - V^* \vec{Q}] + \hat{r}V^*(\tilde{K} - V^*) & \text{in } \Omega \times [0, T], \\ n \cdot [\nu \nabla V^* - V^* \vec{Q}] = 0 & \text{on } \partial\Omega \times [0, T]. \end{cases}$$

By arguing as in Step 1, we obtain

$$0 = \iint \left\{ \mu \tilde{K} \left| \frac{\nabla \Psi}{\Psi} - \frac{\nabla \tilde{K}}{\tilde{K}} \right|^2 - \mu \frac{|\nabla \tilde{K}|^2}{\tilde{K}} + \nabla \tilde{K} \cdot \vec{P} + \hat{r} \tilde{K} (\tilde{K} - V^*) + \tilde{K} \sigma_1 \right\} dx dt.$$

Using the identity (4.12), we deduce that

$$(4.20) \quad 0 = \iint \left\{ \mu \tilde{K} \left| \frac{\nabla \Psi}{\Psi} - \frac{\nabla \tilde{K}}{\tilde{K}} \right|^2 + \hat{r} \tilde{K} (\tilde{K} - V^*) + \tilde{K} \sigma_1 \right\} dx dt.$$

Furthermore, we may integrate (4.19) over $\Omega \times [0, T]$ to obtain

$$(4.21) \quad \iint \hat{r} V^* (\tilde{K} - V^*) dx dt = 0.$$

Subtracting (4.21) from (4.20), we obtain

$$0 = \iint \left\{ \mu \tilde{K} \left| \frac{\nabla \Psi}{\Psi} - \frac{\nabla \tilde{K}}{\tilde{K}} \right|^2 + \hat{r} (\tilde{K} - V^*)^2 + \tilde{K} \sigma_1 \right\} dx dt.$$

Hence $\sigma_1 \leq 0$. We claim that $\sigma_1 < 0$. Indeed, suppose to the contrary that $\sigma_1 = 0$. Then $V^* = \tilde{K}$ and thus $v^* = M(t)V^*(x, t) = M(t)\tilde{K}(x, t)$, which is impossible in view of (4.8). Hence $\sigma_1 < 0$, i.e., $(0, v^*)$ is linearly unstable.

Step 3. We prove that the trivial solution $(0, 0)$ of (4.9) is also repelling. That is, for solutions (U, V) with nonnegative, nontrivial initial data, $\|(U, V)(\cdot, t)\| \not\rightarrow 0$.

The instability of $(0, 0)$ can be proved by repeating Step 2 line by line, while setting $V^* \equiv 0$. We omit the details.

Step 4. Conclude with the theory of monotone dynamical systems.

By [7, section 3], system (4.9) defines a monotone dynamical system. By Step 1, we may invoke [33, Theorem A(c)] (see also [46, Theorem 1.3]) to deduce that any internal trajectory of (4.9) converges to either $(\tilde{K}, 0)$ or $(0, V^*)$. By Step 2, the possibility $(U, V) \rightarrow (0, V^*)$ is ruled out. Thus $(U, V) \rightarrow (\tilde{K}, 0)$. That is, the T -periodic solution $(\tilde{K}, 0)$ of (4.9) is globally asymptotically stable. This is equivalent to the global asymptotic stability of the T -periodic solution $(\theta^*, 0)$ of (4.1). \square

5. Conclusions. Our results extend those of [5, 7, 9] to more general forms of logistic-type models and to situations where the total amount of resources available in the environment can vary periodically in time. Specifically, we extend the idea of fitness associated with a specific location in space to account for the full path that an organism takes in space and time over a periodic, or seasonal, cycle, and we extend the mathematical formulation of an ideal free distribution to general time-periodic environments. We find that, as in many other cases, populations using dispersal strategies that can produce a (generalized) ideal free distribution have a competitive advantage relative to populations using strategies that do not produce an ideal free distribution. From the biological point of view, a reason to specifically consider the periodic case is that conditions on our planet are approximately periodic, and periodic migrations are common and important, so they are a natural focus for ecological theory and have attracted much interest from biologists. From the mathematical point of view, the periodic case is the obvious next step after the static case, which remains

mathematically tractable. We refer the reader to [37] for related discussions for an invasibility criterion for populations with general time dependence.

There are a number of biological conclusions that can be drawn from the results of our analysis. First, a sufficient and necessary criterion (see (3.9)) for the existence of such a generalized ideal free distribution is obtained. The criterion is a statement on the environment (local intrinsic growth rate $r(x, t)$ and local carrying capacity $K(x, t)$) only. While such a generalized ideal free distribution is possible in quite general time-periodic environments, there exist certain environments where it is impossible for a single species—or for that matter, any coalition of species—to achieve ideal free distribution. In the latter case, one can envision a never-ending dynamic succession of the community of species in the evolutionary timescale. Namely, starting with any group of interacting species which have already reached some stable pattern in the ecological timescale, there is always the possibility that a novel mutation arises (or a foreign invasive species arrives) and destabilizes the configuration. Such an instability may cause the community to become larger (addition of one more species) or smaller (one or more species become extinct). In either case, the whole community will then approach a different stable ecological configuration, until the next destabilizing mutation/invasion takes place.

An interesting observation is that a mathematical definition of fitness associated with a movement strategy for organisms in time-periodic environments requires consideration of the specific paths individuals take through space and time, not just the spatiotemporal distribution of the population that the strategy produces. In a related but different context, it was shown in [52] that the effectiveness of a protection zone depends on the details of its path through space and time during a periodic cycle, where in the static case there are no such geometric restrictions. Also, in [50] the asymptotic behavior of the periodic-parabolic eigenvalue is also connected with some periodic cycle in the associated kinetic system. These are only a few data points, but they suggest a possible feature that may distinguish periodic-parabolic models from elliptic models. It may be that to extend results in the elliptic case that depend on local conditions in space to the periodic case will often require that the condition hold on or in a neighborhood of an entire path connecting the beginning and end of a periodic cycle. That would be consistent with our conclusions about the need for nonlocal information in optimal dispersal in time-periodic environments. Related ideas are discussed in [52].

Key features of populations that have an ideal free distribution are that individuals optimize fitness; for populations with negative density dependence the area of occupying region increases with population size; densities of populations at steady state track habitat quality; and at steady state fitness is approximately constant among individuals. These are all testable predictions of many models for the ideal free distribution, including ours. There has been considerable empirical study of the ideal free distribution, or the ideal free distribution with costs [61], which considers the effects of factors other than resource uptake that affect fitness. Studies typically look for fitness equalization or optimization [28, 31], matching of population density with habitat quality or resource availability [18, 55, 59, 62], or some combination of those [35, 48, 47]. The studies [35, 48, 47] were done on *Daphnia magna* in a water column, which perform a periodic diel vertical migration between regions near the surface and regions near the bottom of the water column. These empirical studies support the idea that some populations, including those in periodic environments, approximately follow some version of the ideal free distribution. The methods used in these studies in principle could be adapted to further study systems, including some with periodic

variation in time. Our results provide a way to theoretically characterize what an ideal free distribution should look like in a general periodic environment and display movement strategies that a population could use to achieve it. Recently, a study of blue whales [1] showed that they can accurately track the locations of what amounts to a multiyear average of roughly periodic, but somewhat stochastic, resources during the course of a year. A particularly interesting finding of [1] is that blue whales use memory to achieve resource matching. In temporally static but spatially varying environments it is possible for a population to achieve an ideal free distribution by using purely local information on environmental gradients [5, 9] or habitat quality [40] to track resources. The results of [7] and their extensions in this paper to more general and realistic periodic models, which allow for seasonal variation in the total amount of resources available in the environment, show that the realization of an ideal free distribution typically requires some use of nonlocal information in space and time. In general environments the nonlocal information must be processed in a complex way, but it is plausible that blue whales could use memory to do that, since they are intelligent and long lived. In any case, our results show that a species possessing the ability to use memory or other means to process nonlocal information in dispersal has a distinct selective advantage in a temporally periodic environment. See [22] for some evidence that organisms can and do use nonlocal information in deciding how to move. However, [35, 48, 47] found evidence of effective resource matching by *D. magna* in periodic environments. This raises the question of how such a simple organism as *D. magna* can manage to do this as a possible topic for further research. More broadly, our work suggests that there should be additional theoretical and empirical study of how organisms can approximate an ideal free distribution under realistic assumptions about the limitations of their cognitive and dispersal abilities.

Appendix A. Asymptotic behavior of the principal eigenvalue. Consider the principal eigenvalue λ_1 of

$$(A.1) \quad \begin{cases} \frac{d\varphi}{dt} = \mu\Delta\varphi + \alpha\nabla m(x, t) \cdot \nabla\varphi + V(x, t)\varphi + \lambda_1\varphi & \text{in } \Omega \times [0, T], \\ n \cdot \nabla\varphi = 0 & \text{on } \partial\Omega \times [0, T], \\ \varphi(x, 0) = \varphi(x, T) & \text{in } \Omega, \end{cases}$$

where ∇ is the gradient operator with respect to the spatial variable x , α is a positive constant, $m \in C^2(\bar{\Omega} \times [0, T])$, and $V \in C(\bar{\Omega} \times [0, T])$. We will follow the idea in [49, Propositions 2.1 and 2.2] to prove the following result.

PROPOSITION A.1. *Suppose there exist a smooth, T -periodic curve $\gamma : \mathbb{R} \rightarrow \text{Int } \Omega$ and a set U which is open relative to $\bar{\Omega} \times [0, T]$ such that*

- (i) $\{(\gamma(t), t) : t \in [0, T]\} \subset U \subset \text{Int } \Omega \times [0, T]$;
- (ii) $m(x, t) < m(\gamma(t), t)$ if $(x, t) \in U$ and $x \neq \gamma(t)$;
- (iii) $|\nabla m(x, t)| > 0$ if $(x, t) \in U$ and $x \neq \gamma(t)$.

Then

$$(A.2) \quad \limsup_{\alpha \rightarrow \infty} \lambda_1 \leq -\frac{1}{T} \int_0^T V(\gamma(t), t) dt.$$

Remark A.2. Suppose $\gamma(t)$ is a smooth, T -periodic curve such that $\nabla^2 m(\gamma(t), t)$ is negative definite for each $t \in [0, T]$. Then the hypotheses (i)–(iii) can be verified.

Proof. By a rescaling in the x variable, we may assume $\mu = 1$. We also assume, without loss of generality, that

$$(A.3) \quad m(\gamma(t), t) \equiv 0 \quad \text{and} \quad V(\gamma(t), t) dt \equiv 0.$$

These can be achieved if we replace $m(x, t)$ by $m(x, t) - m(\gamma(t), t)$, $V(x, t)$ by $V(x, t) - V(\gamma(t), t)$, $\varphi(x, t)$ by $\varphi(x, t) \exp(\frac{t}{T} \int_0^T V(\gamma(s), s) ds - \int_0^t V(\gamma(s), s) ds)$, and λ_1 by $\lambda_1 + \frac{1}{T} \int_0^T V(\gamma(t), t) dt$.

The goal is to show that $\limsup_{\alpha \rightarrow \infty} \lambda_1 < \varepsilon$ for each $\varepsilon > 0$. By [49, Proposition A.1], it suffices to construct a nonnegative, nontrivial subsolution $\underline{\varphi}$, such that

$$(A.4) \quad \frac{d\underline{\varphi}}{dt} \leq \Delta \underline{\varphi} + \alpha \nabla m(x, t) \cdot \nabla \underline{\varphi} + V(x, t) \underline{\varphi} + \varepsilon \underline{\varphi} \quad \text{in } \Omega \times [0, T],$$

$$(A.5) \quad n \cdot \nabla \underline{\varphi} = 0 \quad \text{on } \partial\Omega \times [0, T],$$

$$(A.6) \quad \varphi(x, 0) = \varphi(x, T) \quad \text{in } \Omega.$$

We now fix $\varepsilon > 0$ hereafter and construct $\underline{\varphi}$. By the strictness of the spatial local maximum point of m at $x = \gamma(t)$, we can choose $a_0 < 0$ such that $m(x, t) \leq a_0$ on ∂U . By hypotheses (i) and (ii), we can choose $a \in (a_0, 0)$ small enough such that

$$(A.7) \quad |V(x, t)| < \frac{\varepsilon}{2} \quad \text{in } \{(x, t) \in U : m(x, t) > a\}.$$

Next, fix $b = a/2$. Then $a < b < 0$ and, by virtue of hypothesis (iii) and compactness,

$$(A.8) \quad \inf |\nabla m| > 0 \quad \text{with the infimum taken over } \{(x, t) \in U : a \leq m(x, t) \leq b\}.$$

Next, fix $\delta > 0$ small such that

$$(A.9) \quad \delta(\|\partial_t m\|_{L^\infty(\Omega \times [0, T])} + \|\Delta m\|_{L^\infty(\Omega \times [0, T])}) < \frac{\varepsilon}{2}$$

and choose a smooth function $g : \mathbb{R} \rightarrow \mathbb{R}$ such that

$$(A.10) \quad g'(s) > 0 \text{ for } s \in \mathbb{R}, \quad g(a) = 0, \quad \text{and} \quad g(s) = 1 + \delta(s - b) \text{ for } s \in [b, 0].$$

Now, define

$$\underline{\varphi}(x, t) = \begin{cases} \max\{g(m(x, t)), 0\} & \text{in } U, \\ 0 & \text{otherwise.} \end{cases}$$

Since $m(x, t) \leq a_0$ on ∂U , it also satisfies $m(x, t) < a$ in a neighborhood of ∂U . Hence $\underline{\varphi}$ is continuous in $\bar{\Omega} \times [0, T]$ and satisfies (A.4) in an open set containing the complement of U . Also, since $\underline{\varphi}(x, t)$ is T -periodic (since $m(x, t)$ is) and is compactly supported in the interior of U , it is clear that (A.5) and (A.6) hold. It remains to show that (A.4) holds in U .

For $(x, t) \in U$, the function $\underline{\varphi}$ can be written as

$$\underline{\varphi}(x, t) = \max\{g(m(x, t)), 0\} = \begin{cases} g(m(x, t)) & \text{when } m(x, t) > a, \\ 0 & \text{when } m(x, t) \leq a. \end{cases}$$

It is enough to verify that $g(m(x, t))$ satisfies (A.4) in $\{(x, t) \in U : m(x, t) > a\}$ in the classical sense. We argue differently for the two regions

$$\{(x, t) \in U : m(x, t) > b\} \quad \text{and} \quad \{(x, t) \in U : a < m(x, t) \leq b\}.$$

In the first case $\underline{\varphi}(x, t) = 1 + \delta(m(x, t) - b)$, $\underline{\varphi}(x, t) \geq 1$, and

$$\begin{aligned} & \frac{d\underline{\varphi}}{dt} - \Delta \underline{\varphi} - \alpha \nabla m(x, t) \cdot \nabla \underline{\varphi} - (V(x, t) + \varepsilon) \underline{\varphi} \\ &= \delta(\partial_t m - \Delta m - \alpha |\nabla m|^2) - (V(x, t) + \varepsilon)[1 + \delta(m - b)] \\ &\leq \delta(|\partial_t m| + |\Delta m|) - \frac{\varepsilon}{2} < 0, \end{aligned}$$

where we used (A.7) for the second-to-last inequality, and (A.9) for the last inequality. In the latter case, we have $a < m(x, t) \leq b$, and for α sufficient large,

$$\begin{aligned} & \frac{d\varphi}{dt} - \Delta\varphi - \alpha \nabla m(x, t) \cdot \nabla\varphi - (V(x, t) + \varepsilon)\varphi \\ &= -g'(m) \left[-\partial_t m + \Delta m + \left(\frac{g''(m)}{g'(m)} + \alpha \right) |\nabla m|^2 \right] - (V(x, t) + \varepsilon)g(m) \\ &\leq -g'(m) \left[-\|\partial_t m\|_\infty - \|\Delta m\|_\infty + \left(-\left\| \frac{g''}{g'} \right\|_\infty + \alpha \right) \inf |\nabla m|^2 \right], \end{aligned}$$

where we used (A.7) and that $g(m)$, $g'(m)$ are both positive. Note that the infimum of $|\nabla m|$, which is taken over the set $\{(x, t) \in U : a < m(x, t) \leq b\}$, is a positive real number by (A.8). Hence, by taking α sufficiently large, we deduce that the first part of (A.4) holds in $\{(x, t) : a < m(x, t) \leq b\}$. Having verified that φ is a nontrivial, nonnegative subsolution, we apply [49, Proposition A.1] to deduce that $\limsup_{\alpha \rightarrow \infty} \lambda_1 < \varepsilon$. Since $\varepsilon > 0$ is arbitrarily, the proof is finished. \square

Appendix B. Generalized IFD in relation to pathwise fitness. We provide a proof for (2.9), which relates the notion of pathwise fitness with the generalized IFD in the sense of Definition 2.1.

LEMMA B.1. *Let $F(x, t) \in C(\bar{\Omega} \times [0, T])$. Then*

$$(B.1) \quad \int_0^T \inf_{x \in \Omega} F(x, t) dt = \inf_{\gamma} \int_0^T F(\gamma(t), t) dt,$$

where the infimum is taken over the family of all smooth, T -periodic paths.

Remark B.2. By replacing F by $-F$, we show that

$$(B.2) \quad \int_0^T \sup_{x \in \Omega} F(x, t) dt = \sup_{\gamma} \int_0^T F(\gamma(t), t) dt,$$

where the supremum is taken over the family of all smooth, T -periodic paths.

Remark B.3. Since $\int_0^T F(\gamma(t), t) dt \geq \int_0^T \inf_{x \in \Omega} F(x, t) dt$ for any $\gamma \in C([0, T]; \Omega)$, we can replace the family in taking the infimum in (B.1) (resp., supremum in (B.2)) by (i) all smooth paths, (ii) all continuous, T -periodic paths, or (iii) all continuous paths.

Proof. Since it is clear that

$$(B.3) \quad \int_0^T \inf_{x \in \Omega} F(x, t) dt \leq \inf_{\gamma} \int_0^T F(\gamma(t), t) dt,$$

it remains to prove the reverse inequality. Let $\varepsilon > 0$ be given. Choose $m \in \mathbb{N}$ such that

$$(B.4) \quad |F(x, t) - F(x, s)| < \varepsilon \quad \text{if } x \in \bar{\Omega} \text{ and } |t - s| < T/m.$$

Denote $t_i = \frac{i}{m}T$ for $0 \leq i \leq m$, and choose $(x'_i, t'_i) \in \Omega \times [t_i, t_{i+1}]$ ($i = 0, \dots, m - 1$) so that $F(x_i, t_i) < \inf_{\Omega \times [t_i, t_{i+1}]} F + \varepsilon$. Next, define the piecewise constant path γ_1 by

$$(B.5) \quad \gamma_1(t) = x'_i \quad \text{for } t \in [t_i, t_{i+1}), \quad i = 0, \dots, m - 1,$$

and let $\gamma_2(t)$ be a smooth, T -periodic path such that

$$(B.6) \quad \gamma_2(t) = x'_i \quad \text{for } t \in [t_i, t_{i+1} - \varepsilon/m], \quad i = 0, \dots, m-1.$$

Then by the uniform boundedness of F , we have

$$(B.7) \quad \int_0^T |F(\gamma_1(t), t) - F(\gamma_2(t), t)| dt \leq 2\varepsilon \|F\|_\infty.$$

Hence,

$$\begin{aligned} \int_0^T \inf_{x \in \Omega} F(x, t) dt &\geq \frac{T}{m} \sum_{i=0}^{m-1} \inf_{\Omega \times [t_i, t_{i+1}]} F \\ &\geq \frac{T}{m} \sum_{i=0}^{m-1} [F(x'_i, t'_i) - \varepsilon] \\ &\geq \int_0^T [F(\gamma_1(t), t) - 2\varepsilon] dt \\ &\geq \int_0^T F(\gamma_2(t), t) dt - 2\varepsilon(T + \|F\|_\infty), \end{aligned}$$

where the second inequality follows from the construction of $(x'_i, t'_i) \in \Omega \times [t_i, t_{i+1}]$, the third inequality follows from (B.4), and the last inequality follows from (B.7). Thus,

$$\int_0^T \inf_{\Omega} F(x, t) dt \geq \inf_{\gamma} \int_0^T F(\gamma(t), t) dt - 2\varepsilon(T + \|F\|_\infty).$$

Letting $\varepsilon \rightarrow 0$ and combining with (A.2), we prove (A.1). \square

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