

The Ideal Free Distribution: Theory and Engineering Application

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Abstract—We extend the theory of the “ideal free distribution” (IFD) from theoretical ecology by providing methods to analytically find the distribution for a relatively general class of “suitability” functions. We show that the resulting IFD is a Nash equilibrium and an evolutionarily stable strategy (ESS). Moreover, we show that for a certain cost function it is a global optimum point. We introduce the “replicator dynamics” for the IFD and show that we provide an allocation strategy that is guaranteed to achieve the IFD. Finally, we show how this allocation strategy can achieve an IFD for a multizone temperature control problem that corresponds to achieving the maximum uniform temperature on a grid under a multivariable saturation constraint.

Index Terms—Dynamic resource allocation, evolutionarily stable strategy (ESS), ideal free distribution (IFD), replicator dynamics, temperature control.

I. INTRODUCTION

THE CONCEPT of ideal free distribution (IFD) was originally introduced in [1]. For many years, this concept has been used to analyze how animals distribute themselves across different habitats. These habitats have different characteristics (e.g., one habitat might have a higher nutrient input rate than another), but animals tend to reach an equilibrium point where each has the same correlate of fitness (e.g., consumption rate). The term “ideal” means that the animals can perfectly sense the quality of all habitats and seek to maximize the suitability of the habitat they are in, and the term “free” means that the animals can go to any habitat. In [2] and [3], the authors survey the various extensions to the IFD (e.g., the interference model [4] and standing crop idea [5]), and overview the experimental biological evidence that supports these models.

The IFD is studied here for a general class of correlates of fitness called suitability functions. This general class of suitability functions covers the ones studied in [6] and [7] for the “continuous-input” model, and also includes the case of “interference” [4], [7], [8]. We also study a suitability function studied in [1]. For these suitability functions, we prove the equivalence of the habitat [6], [7] and input matching rules [4], [9], an equivalence only previously recognized to hold for one special class of suitability functions [2], [4]. We introduce

the concept of an individual animal with a fitness and explain the type of equivalences that hold between habitat suitability and individual animal fitness equalization. Then, we show that the treatment of a more general class of suitability functions allows us to characterize and analyze the “ideal dominance distribution” (IDD) [1], something that has not been done in the literature to date [3]. Next, we explain how the IFD is a Nash equilibrium and an evolutionarily stable strategy (ESS) [10] for the case of a “game against the field” [11] for our expanded set of suitability functions. This means that in a large population of animals, whose mean population strategy is an IFD, no mutant animal strategy can invade the population. While this means that the IFD is locally optimal in a game-theoretic sense (i.e., unilateral strategy deviations by a single animal are not profitable for that animal), here we show that the IFD possesses much stronger optimality properties. We show how to model a group of animals all simultaneously seeking to maximize their fitness as a “minimax” optimization problem. For this problem, we prove that the IFD is a global optimum point. This means that even if an arbitrary number of animals deviate so that the distribution is not an IFD, then there can be an arbitrary number of animals who need to change strategies to maximize their fitness. Moreover, it means that there is no other animal distribution where all the animals can simultaneously maximize their fitness. Our results bear some relationships to the work in [12], but here we consider a different (and more generic) class of suitability functions, and a “nonlinear” game against the field. Finally, we study how evolutionary dynamics can represent the animal allocation process over long time periods. In particular, we introduce the “replicator dynamics” [13] for the animal distribution “population game” [14], [15] and show how it relates to a steepest descent allocation strategy. For this model, natural selection according to differential fitness is the mechanism underlying the animal allocation and animal strategy mutations are represented by perturbations in the population “strategy mix” [14]. We show that the IFD is an equilibrium of the replicator dynamics, and via Lyapunov stability analysis show that the IFD is asymptotically stable for our general class of suitability functions (thereby extending earlier such analysis [13]–[15]). This means that the population will recover from perturbations (mutations) off the IFD equilibrium and the population’s strategy mix dynamics eliminate mutants that are different from the IFD so that evolution leads to the maintenance of an IFD strategy. We show one case where the IFD is exponentially stable so that mutant rejection is fast, and relate the size of the population to the rate of rejection of mutant strategies.

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In the last section of the paper, we use the theory to solve a challenging engineering problem that involves achieving temperature control for multiple zones of a planar temperature grid, in spite of limited current available to drive the heaters and significant ambient and interzone effects. This problem can be seen as a distributed multivariable “dynamic resource allocation” problem because we want to split some quantity (current or voltage) that we have a limited amount of, and dedicate appropriate proportions of it to optimize some quantity of interest (quality of regulation). The allocations are inputs to a dynamical system and its response determines the quality of the allocation. The control goal could be a standard regulation or tracking objective (e.g., making all zones have the same given temperature), or a nontraditional objective like reaching the maximum uniform temperature across the entire grid. Control goals like these arise in the context of a variety of commercial applications (e.g., building temperature control) industrial systems. For instance, in semiconductor processing, one challenge is to achieve a uniform temperature on a plate [16]. Others [17] study distributed control of wafer temperature via multizone rapid thermal processing systems. In related work, the authors of [18] describe a multizone space heating system that maintains a desired temperature in different zones. Another application where the type of multizone temperature control that we study is very important is in personal computers. In [19], the author describes several current strategies used to solve this problem. In addition to such strategies, several other methods are currently available for distributed control design when set-point regulation or tracking is the objective. For instance, in [20] the authors show how systems with a spatial interconnection topology can be controlled using conditions that can be expressed as linear matrix inequalities.

Unlike the work outlined above, we seek to confront the problem of the allocation of a limited amount of current (a multivariable saturation nonlinearity) in order to achieve a maximum uniform temperature on a planar grid, which is a true dynamic resource allocation problem. Dynamic resource allocation problems are found in a variety of applications beyond temperature control and are currently one of the most important challenges in the control systems area [21]. Current work on allocation for dynamical systems has its roots in the extensive literature that focuses on solving “static” resource allocation problems in optimization theory [22]. Unfortunately, such methods do not directly apply to a dynamic resource allocation problem like the one we are confronting since they neither consider feedback-based allocation nor simultaneous constraints involving differential equations, equalities, and inequalities. An excellent example of innovative work in resource allocation for dynamical systems is found in [23] where the authors define a model for an air-jet system that describes the relationship between macro and microlevel forces, and derive dynamic allocations that can be mapped to, and configured for, different levels in a control hierarchy. Three other examples of dynamic resource allocation challenges are provided in [24], one for scheduling, one for temperature control, and the other for levitating balls in tubes (a university educational experiment). Here, we show how to apply the IFD strategy described in Section V to simultaneously satisfy current limitations and

try to minimize energy use for a version of the planar temperature control problem in [24]. We provide data from an experimental testbed to demonstrate the dynamical behavior and effectiveness of the method, particularly for achieving disturbance rejection. In this way, we show one case where the IFD theoretical framework we establish in this paper can be used to provide a methodology to design strategies for dynamic resource allocation. Due to the generic nature of the theory we developed in this paper it is likely that other applications can follow (e.g., for other applications in dynamic resource allocation see [24], or for potential uses of the IFD in other engineering applications see [25] and [26]).

II. IFD

Suppose that there is a set $H = \{1, \dots, N\}$ of N disjoint habitats in an environment that are indexed by $i = 1, \dots, N$. Let the continuous variable $x_i(t) \in \mathbb{R}_+$ be the amount of animals in the i th habitat at time $t \geq 0$, where $\mathbb{R}_+ = [0, \infty)$. Let $x = [x_1, \dots, x_N]^T \in \mathbb{R}_+^N$. Suppose that $\sum_{j=1}^N x_j = P$, where $P > 0$ is a constant for all time t , i.e., the amount of animals in the environment is constant. We say that a habitat i is truncated if $x_i = 0$, and is inhabited if $x_i > 0$.

A. General Class of Suitability Functions

Suppose that $b_i \geq 0$, is a constant that we sometimes interpret as a fixed number of resident animals in the i th habitat, and $c_i > 0$ is a constant associated with the i th habitat. Assume that $\sum_{j=1}^N a_j > 0$ and $a_i \geq 0$ for all $i = 1, \dots, N$. Let $H^* = \{i \in H : a_i > 0\}$ so $j \in H - H^*$ have $a_j = 0$. Let $m > 0$ be a constant. Let s_i be the suitability function for the i th habitat, with

$$s_i = \frac{a_i}{(c_i x_i + b_i)^m} \quad (1)$$

(if we had let $s_i = b_i - c_i x_i$ all the key theoretical results of this paper still hold). In the literature, the most common function that has been used to describe the “continuous-input model” [2], [3] is a function that assumes that $b_i = 0$ and $c_i = m = 1$, so therefore

$$s_i = \frac{a_i}{x_i}. \quad (2)$$

Then, if a_i is in nutrients per second, a_i/x_i is each animal’s consumption rate at habitat i . This suitability is typically assumed to be a correlate of Darwinian fitness so sometimes it is called the fitness of an animal at habitat i . In this case, it is said that animals distribute in a way that they all achieve equal fitness. Below, in Section II-D, we will derive an explicit relationship between habitat suitability and individual animal fitness since strictly speaking these two are different. In any case, the IFD is achieved via a sequential allocation process that places more (fewer) animals in higher (lower, respectively) suitability habitats until the suitability functions and fitnesses equalize at the IFD. That is, the IFD is achieved via a process where each animal simultaneously maximizes its own fitness.

Another popular suitability function found in the literature is the one that describes the “interference model” [4], [7], [8]. For it, in (1), let $c_i = 1$ and $b_i = 0$. Therefore

$$s_i = \frac{a_i}{x_i^m}. \quad (3)$$

Notice that in the case of (3), if we use the fact that at the IFD all the habitats will end up with the same suitability, then we can transform the interference model into a suitability function that looks like the standard one in (2) by taking the m th root on the right-hand side of (3). In this case, we will end up with a suitability function of the form $s_i = a_i^{1/m}/x_i$. The animals will achieve an IFD, but they will not be able to determine precisely the quality of each habitat if they do not know m .

Since (1) is more general than the ones in (2) and (3), our analysis is based on (1). The analysis starts by studying the habitat and input matching rules [4], [6], [7], [9]. Then, we define the IDD, and finally, we define the idea of individual animal fitness equalization that will be useful for the game-theoretic and optimality analysis of the IFD.

B. Habitat and Input Matching Rules

The “habitat matching rule” [6], [7] says that at the IFD, the animals will distribute so that for each $i, j \in H^*$

$$a_i(c_j x_j + b_j)^m = a_j(c_i x_i + b_i)^m. \quad (4)$$

Since all the terms in (4) are positive, we can write this equation as $a_i^{1/m}(c_j x_j + b_j) = a_j^{1/m}(c_i x_i + b_i)$. If we assume that c_i is a scaling factor, and that b_i is the number of fixed animals in the i th habitat, we can say that what we have is the relative proportion of animals between two different habitats should be equal to some scaled relative proportion of the quality between the same habitats. Equation (4) can also be written as $a_j^{1/m}/(c_j x_j + b_j) = a_i^{1/m}/(c_i x_i + b_i)$. Therefore, for the rest of our analysis, we assume that the suitability function in (1) is written as

$$s_i = \frac{a_i^{\frac{1}{m}}}{c_i x_i + b_i}. \quad (5)$$

For (2), the habitat matching rule simply says that nutrient consumption rates are equal at all habitats.

Another approach to characterize the IFD is to use the “input matching rule” [4], [9] which says the animals distribute so that for all $i \in H^*$

$$\frac{c_i x_i + b_i}{\sum_{j=1}^N c_j x_j + b_j} = \frac{a_i^{\frac{1}{m}}}{\sum_{j=1}^N a_j^{\frac{1}{m}}}. \quad (6)$$

This equation can be written as $a_i^{1/m}/(c_i x_i + b_i) = \sum_{j=1}^N a_j^{1/m}/(\sum_{j=1}^N c_j x_j + b_j)$. Notice that for (2), what we obtain is that the overall consumption rate in the environment, characterized by the right-hand side of this equation (with $c_i = m = 1$ and $b_i = 0$) has to be equal to the consumption rate in any single habitat. The IFD is achieved via a sequential allocation process that places more animals in habitats that

have $s_i > \sum_{j=1}^N a_j / \sum_{j=1}^N x_j$, which lowers the suitability of habitat i for each animal there and raises the suitability of other habitats for animals there. Note that (2) is also equivalent to $s_i^{-1} = x_i/a_i = \sum_{j=1}^N x_j / \sum_{j=1}^N a_j$, for $i \in H^*$. The right-hand side of this equation is the total number of animals in the environment divided by the total number of nutrients arriving per second. At the IFD, the animals are distributed so that no matter which habitat they are at, they get the same amount of nutrients. In this case, we can view the IFD as being achieved via the sequential allocation of animals to habitats with $s_i^{-1} < \sum_{j=1}^N x_j / \sum_{j=1}^N a_j$.

Since (4) and (6) are going to be used extensively in our analysis, we provide a proof of their equivalence in the next theorem (proofs of all theorems are in the Appendix).

Theorem 2.1: Assume that $\sum_{i=1}^N x_i = P > 0$, $\sum_{i=1}^N a_i^{1/m} > 0$, $c_i, m > 0$, and $a_i, b_i \geq 0$ for $i = 1, \dots, N$. The habitat and input matching rules are equivalent characterizations of the IFD in that for a given set of a_i, b_i, c_i, m , the x_i are the same for either rule.

C. Ideal Free and Dominance Distributions

The IDD concept introduced in [1] comes from a type of relaxation of the “free” assumption of the IFD. The basic idea is that, assuming that all individuals are not equally aggressive, if there are new individuals arriving, then it will be more difficult for these “unsettled” individuals to access any habitat dominated by current residents. Thus, the unsettled individuals will end up in habitats that might not optimize their fitness compared to the case where they were the first arrivals.

The IDD can be interpreted via sequential settling of species of animals at IFDs. Suppose that we have \bar{N} species who are arriving sequentially into the environment. We assume that the index $k = 1, \dots, \bar{N}$, represents the arrival and settling at the IFD for each of these species. Let $i = 1, \dots, N$, be each of the N habitats that can be chosen for the distribution of each species. Let a_i^k be the input rate for habitat i when the species k is settling. Let x_i^k be the number of animals of species k at habitat i . Then, x_i^{k-1} is the fixed number of individuals that settled down in habitat i , where $x_i^0 = 0$ (i.e., only the first species will distribute in such a way that there is no interference with animals that are already settled in a particular habitat). Let $c_i^k > 0$ and $m^k > 0$ be constants associated with the k th species. Let P^k be the total number of animals associated with the k th species. For each species arrival the individuals want to settle down in the best available habitat by maximizing fitness. The suitability function that each species uses to determine which is the best habitat, is defined as

$$s_i^k = \frac{(a_i^k)^{\frac{1}{m^k}}}{c_i^k x_i^k + x_i^{k-1}} \quad (7)$$

with the constraint $\sum_{j=1}^N x_j^k = P^k$ for all k . Equation (7) defines a nonlinear difference equation for the distribution of subsequent species. If $P^k > 0$ is such that $P = \sum_{k=1}^{\bar{N}} P^k \rightarrow \infty$ as \bar{N} and $k \rightarrow \infty$ then for some finite $k' \geq 0$ no habitat will be

truncated. Since the parameter m skews the distribution it will change the k' such that truncation first disappears in an IDD.

The question that arises is: can we know the final value for each species in any habitat? Notice that (7) is similar to (5), with a slight change in the variables. Thus, the distribution of the individuals will be given by the IFD for this specific case. The next theorem shows how to find the distribution representing the IFD for the suitability functions as defined in (5) [or (7)]. It gives a solution for the IFD for a general class of suitability functions (not available in the literature) and a solution to (7) (when for each species k , we have that $x_i^{k-1} = b_i$) so that the IDD can be found for any number of species \bar{N} that sequentially arrive at the environment.

Theorem 2.2: For $i = 1, \dots, N$, the point

$$x_i^* = \frac{\frac{1}{c_i} P + \frac{1}{c_i} \sum_{j=1}^N \frac{b_j}{c_j} - \frac{b_i}{c_i} \sum_{j=1}^N \frac{a_j^{\frac{1}{m}}}{c_j}}{\sum_{j=1}^N \frac{a_j^{\frac{1}{m}}}{c_j}} \quad (8)$$

is the IFD for the suitability function defined in (5), whenever P satisfies

$$P \geq \max_{i=1, \dots, N} \left\{ \frac{b_i}{a_i^{\frac{1}{m}}} \sum_{j=1}^N \frac{a_j^{\frac{1}{m}}}{c_j} - \sum_{j=1}^N \frac{b_j}{c_j} \right\}. \quad (9)$$

If (9) is not satisfied, and without (significant) loss of generality, we assume that $a_1^{1/m}/b_1 > \dots > a_N^{1/m}/b_N$, the IFD is given by

$$x_i^* = \begin{cases} \frac{\frac{1}{c_i} P + \frac{1}{c_i} \sum_{j=1}^{k^*} \frac{b_j}{c_j} - \frac{b_i}{c_i} \sum_{j=1}^{k^*} \frac{a_j^{\frac{1}{m}}}{c_j}}{\sum_{j=1}^{k^*} \frac{a_j^{\frac{1}{m}}}{c_j}}, & i = 1, \dots, k^* \\ 0, & i = k^* + 1, \dots, N \end{cases} \quad (10)$$

where

$$k^* = \arg \max \left\{ k : \frac{b_k}{a_k^{\frac{1}{m}}} < \frac{P + \sum_{j=1}^N \frac{b_j}{c_j}}{\sum_{j=1}^N \frac{a_j^{\frac{1}{m}}}{c_j}} \right\}. \quad (11)$$

Notice that whenever (9) is satisfied with strict inequality $x_i^* > 0$, which implies that all the habitats end up inhabited. Also, notice that k^* is given by analyzing the values of the suitability functions when $x_i = 0$. It is clear that if P is big enough, then the right-hand side of the inequality in (11) becomes almost 0, and hence all habitats will end up inhabited.

D. Individual Animal Fitness Equalization

Normally, the number of habitats N , the $a_i, b_i, c_i, m, i = 1, \dots, N$, and $P > 0$ are given. Then, the x_i must be found that achieve the IFD via (6). Problems with existence of the IFD can arise, however, if x_i is the number of animals since in that case it is natural to assume that x_i is discrete. For example, assume that $x_i \in \{0, 1, \dots\}$. In this case, the IFD may not exist (e.g., if $P = 7, N = 2, m = 1, a_1 = 0.1, b_1 = b_2 = 0, c_1 = c_2 = 1$ and $a_2 = 0.2$, then (6) cannot be satisfied). But, if the $P, a_i,$

$b_i, c_i, m,$ and N have appropriate values, (6) can be satisfied. The standard approach to cope with this problem is to assume that there is a large enough number of animals so that it is a good approximation to consider x_i to vary continuously. We will take this same approach so we are assured that an IFD exists. But, with x_i continuous, we lose the ability to distinguish between individual animals. In this framework it is, however, still possible to introduce a limited notion of an individual. This will allow us to assign each individual a fitness and then clearly relate equalization of habitat suitabilities to equalization of individual animal fitnesses. Moreover, our concept of an individual is critical to modeling the IFD as a game between many individuals in Section III-A, showing how individuals' fitness maximization objective leads to an IFD, and relating this to optimality formulations for the IFD.

To introduce the concept of an individual, assume that each animal is identical and represented by some arbitrarily small $\epsilon_x > 0$ so that there is an arbitrarily large (integer) number $n > 0$ of animals in the environment, where $n\epsilon_x = P$, and $b_i = \bar{b}_i\epsilon_x$, with $\bar{b}_i \geq 0$ being the integer fixed number of resident animals in the i th habitat. Then, if $n_i \geq 0$ is the (integer) number of animals at habitat i , $\sum_{j=1}^N n_j = n$, $x_i = n_i\epsilon_x$, and the IFD in (6) is achieved when for all $i = 1, \dots, N$

$$\frac{\epsilon_x(c_i n_i + \bar{b}_i)}{\sum_{j=1}^N \epsilon_x(c_j n_j + \bar{b}_j)} = \frac{a_i^{\frac{1}{m}}}{\sum_{j=1}^N a_j^{\frac{1}{m}}} \quad (12)$$

which has been another interpretation of the IFD in the literature (e.g., in [1] and [3]) for the case $b_i = 0, c_i = m = 1$. Notice that for an arbitrary P and b_i , in order to ensure the existence of the IFD, we need to have an arbitrarily small positive value ϵ_x .

Given the concept of an individual animal $\epsilon_x > 0$ at habitat $i, i = 1, \dots, N$, we define this animal's fitness as $f(i) = a_i^{1/m}/(c_i n_i + \bar{b}_i)$. In the case when $b_i = 0, c_i = m = 1$, if a_i is nutrients per second, $f(i)$ is the number of nutrients per second that an animal gets at habitat i . This choice is consistent with the results in [7], which show other ways to relate fitness and suitability. Notice that

$$f(i) = \frac{a_i^{\frac{1}{m}}}{c_i n_i + \bar{b}_i} = \epsilon_x \frac{a_i^{\frac{1}{m}}}{c_i x_i + b_i}. \quad (13)$$

Notice that if we use the suitability function in (2), we have $f(i) = a_i/n_i = \epsilon_x s_i$, so that individual animal fitness is indeed a correlate of habitat suitability. Clearly, however, even though they are linearly related, habitat suitability is not the same as individual animal fitness. Moreover, if $a_i, b_i, c_i > 0$ and $x_i > 0, i = 1, \dots, N$, then equalization of habitat suitability (i.e., $s_i = s_j, i, j = 1, \dots, N$) is equivalent to equalization of animal fitness (i.e., $f(i) = f(j), i, j = 1, \dots, N$). The equivalence characterized by Theorem 2.1 holds for the fitness of all individuals at any habitat $j \in H^*$.

III. GAME-THEORETIC AND OPTIMALITY PROPERTIES OF THE IFD

In this section, first we define the basic concepts of evolutionary game theory in order to prove that the IFD is indeed an ESS. Then, in order to extend this result, we model the IFD achievement as solving an optimization problem, and we prove that the IFD is a global optimum point.

A. Nash Equilibria and Evolutionarily Stable Strategies

In this and the next section, to use a game-theoretic perspective, we view each “player” as an individual animal that makes strategy choices to maximize its payoff, which is fitness. A Nash equilibrium is a set of animal strategy choices such that any unilateral deviation by any animal from its strategy choice will not be better for that animal. The standard definition for an ESS is a strategy such that no “mutant” can invade a population of members (“incumbents”) who use this strategy [10]. The classical ESS idea is based on a two-player game where incumbents either play other incumbents or mutants (and vice versa). These players are drawn from an infinite population. There is an extension of this ESS concept that is called a “game against the field” where the success of each individual does not depend on a single opponent, but instead depends on the strategies of all other members of the population (see [11, p. 23]).

Let $f(\bar{x}, P_{\bar{y}})$ be the fitness of a single \bar{x} -strategist in a population (set) of \bar{y} -strategists that we denote by $P_{\bar{y}}$. We will say that \bar{x} is an ESS if both of the following two conditions hold [11].

- 1) For all $\bar{y} \neq \bar{x}$

$$f(\bar{y}, P_{\bar{x}}) \leq f(\bar{x}, P_{\bar{x}}). \quad (14)$$

- 2) For any $\bar{y} \neq \bar{x}$, if $f(\bar{y}, P_{\bar{x}}) = f(\bar{x}, P_{\bar{x}})$, then for a small $q > 0$

$$f(\bar{y}, P_{\bar{y}_q}) < f(\bar{x}, P_{\bar{y}_q}) \quad (15)$$

where $f(\bar{y}, P_{\bar{y}_q})$ is defined as the fitness of a \bar{y} -strategist in a population consisting of individuals playing the strategy $\bar{y}_q = q\bar{y} + (1 - q)\bar{x}$.

The first condition means that \bar{x} is a Nash equilibrium, since no mutant strategy \bar{y} does better than the incumbent strategy \bar{x} , and usually this condition is called the “equilibrium condition” [14]. The second condition states that if the mutant strategy \bar{y} does as well as the incumbent strategy \bar{x} , then the mutant strategy does not do as well as the incumbent strategy when they play against a population formed from both the incumbent and the mutant strategies. This is a variation of what is known as the “stability condition” [14].

B. Game-Theoretic Characteristics of the IFD

In this section, we characterize the relationships between equilibria in games and the IFD. In a game-theoretic interpretation of the animal distribution problem each animal has

N pure strategies corresponding to choosing habitat i , $i = 1, \dots, N$. Each animal can only reside in one and only one habitat. Hence, each animal ϵ_x has a strategy of the form $\bar{x} = [0, \dots, \epsilon_x, \dots, 0]^T$, where ϵ_x is in the i th position. These strategies can be interpreted as pure strategies of a polymorphic population [14]. The meaning of “ $\bar{y} \neq \bar{x}$ ” for (14) and (15) is that \bar{y} can correspond to placement of ϵ_x in any habitat $j \neq i$. In the next theorem, $P_{\bar{x}}$ for (14) is any population such that all individuals play a strategy so that the IFD defined by (6) is satisfied. Clearly, in this case, the strategies of individuals in $P_{\bar{x}}$ are not the same since the animals must play different strategies to achieve the IFD.

Theorem 3.1: If x_i is a continuous variable with $\epsilon_x > 0$ representing an animal, then the x_i , $i = 1, \dots, N$, given by the IFD in (6) are the result of animals using a (strict) Nash equilibrium strategy and hence an ESS.

The game-theoretic model is developed from the perspective of the individual animals. Theorem 3.1 shows that if each individual uses a strategy that maximizes its own fitness, they will achieve an IFD, which is an ESS, and hence a Nash strategy. Due to the equivalence of individual fitness equalization and habitat suitability equalization, Theorem 3.1 implies that choices at the individual level lead to habitat suitability equalization across the entire environment. The Nash equilibrium is often called an “optimal” strategy since no animal can do better by deviating from the strategy. The only allowed deviations from the IFD in the game-theoretic model of animal distribution problem correspond to shifting ϵ_x from one habitat to another and this is consistent with the assumption that animals can adopt one of N pure strategies. This fits with the ESS concept above since this corresponds to a single “rare” mutation in a population. Clearly, if there are certain types of simultaneous deviations of animals (e.g., by swapping habitats via simultaneous mutations), the strict Nash can also be maintained; however, such deviations would require coordination and this is not possible since we are inherently considering a competitive game-theoretic framework via the Nash concept, and hence also the ESS. In the next section, we will, however, reconsider this assumption.

Finally, we note that while in [11] and other papers it has been pointed out that the IFD is an ESS, this is to our knowledge the first formal proof of this fact. The value of the formal proof lies in the treatment of fitness, and it clearly connects individual fitness maximization to habitat-level suitability equalization. The proof shows that the IFD is a strict Nash equilibrium so some would consider the animal distribution game to be unique since most games do not have strict Nash equilibria [15]. Moreover, the proof shows that the IFD of the animal distribution population game is what is called a “local ESS” in [14].

C. Optimality of the IFD

In this section, we show how optimization models can represent the animal distribution game and how the IFD is a global optimum point for such a model. Recall that the animal distribution game assumes that all animals in the population seek to simultaneously maximize their fitness. Assume that a_i , b_i , $c_i > 0$ and $x_i \geq 0$, $i = 1, \dots, N$. An optimization model for

the animal distribution game is one where the minimum fitness is maximized. In other words

$$\begin{aligned} & \max \min \left\{ \epsilon_x \frac{a_1^{\frac{1}{m}}}{(c_1 x_1 + b_1)}, \dots, \epsilon_x \frac{a_N^{\frac{1}{m}}}{(c_N x_N + b_N)} \right\} \\ & \text{subject to } \sum_{j=1}^N x_j = P \\ & \quad x_i \geq 0, \quad i = 1, \dots, N. \end{aligned} \quad (16)$$

The constraints demand that the population size stays constant and that the number of animals at each habitat is non-negative. The terms $\epsilon_x (a_i^{1/m} / (c_i x_i + b_i))$ are the fitnesses for any animal that chooses habitat i , $i = 1, \dots, N$. Consider a single individual $\epsilon_x > 0$. If this animal is at habitat i and $f(i) < f(j)$, $j \neq i$, then it can move to habitat j (i.e., change strategies). The “max min” represents that multiple animals simultaneously shift strategies to improve their fitness since at least some animals with lowest fitness shift habitats (and if $f(i) = f(j)$ for some i and j the min can be achieved at multiple habitats).

The following theorem shows that the animals choose the IFD in order to maximize their fitness when everybody else is trying to do the same.

Theorem 3.2: The point $x^* = [x_1^*, \dots, x_N^*]^T$, such that for all $i = 1, \dots, N$, [with x_i^* defined in (10) and (11)] is a unique global maximum point that solves the optimization problem in (16) that represents that each animal simultaneously chooses a habitat to maximize its own fitness.

The value of Theorem 3.2 is that it shows that the IFD is a global optimum point for the animal distribution problem. The game-theoretic setting of Section III-B only illustrated local optimality in the Nash sense. Theorem 3.2 shows that any number of simultaneous perturbations from the IFD result in possibly many animals incurring a degradation in fitness. Hence, an arbitrary number of mutants cannot invade the population. This idea will be studied further in Section IV.

IV. EVOLUTIONARY ALLOCATION DYNAMICS FOR IFD ACHIEVEMENT

In this section, we consider animal allocation dynamics from evolutionary and decision-making perspectives. We focus on defining allocation dynamics that guarantee the achievement of an IFD.

A. Replicator Dynamics Model

The replicator dynamics are a simple model of how selection via differential fitness affects the proportions of animals using different strategies [14], [15]. Here, building on the game-theoretic formulation in Section III, we show how equilibria of one class of replicator dynamics are related to the IFD. These are not the standard replicator dynamics that are developed based on random pairings of two individuals in what is called a “linear game.” Here, we extend such standard formulations in

[13] and [14] to represent our game against the field, which is classified as a nonlinear game.

Recall that each animal has N pure strategies, which correspond to choosing which habitat to live in for its entire life, and that the number of animals is constant and $\sum_{j=1}^N x_j = P$ for some $P > 0$ and all $t \geq 0$. Let $p_i = x_i / \sum_{j=1}^N x_j$ represent the fraction of individuals in a population of animals playing pure strategy i , $i = 1, \dots, N$. Clearly $p_i(t) \geq 0$ and $\sum_{j=1}^N p_j = 1$ for all $t \geq 0$. The vector $p = [p_1, \dots, p_N]^T$ is the “population state,” which represents the strategy mix of the population [14]. Clearly, $p(t) \in \Delta$ for all $t \geq 0$, where $\Delta = \{p(t) \in \mathbb{R}_+^N : \sum_{i=1}^N p_i(t) = 1\}$ is the “constraint set” (simplex) that defines a subset of the state space. The vector $x(t) = [x_1, \dots, x_N]^T$ lies in the simplex Δ_x , where $\Delta_x = \{x(t) \in \mathbb{R}_+^N : \sum_{i=1}^N x_i = P\}$.

The replicator dynamics assume continuously mixed generations and are given by

$$\begin{aligned} \frac{\dot{p}_i}{p_i} &= \beta_i [\{\text{fitness of animals that play } i \in H\} \\ &\quad - \{\text{average fitness in population}\}] \end{aligned} \quad (17)$$

where $\beta_i > 0$ are proportionality constants. The left-hand side of (17) is the normalized rate of increase in the population share playing strategy i . The right-hand side of (17) indicates that if i -strategists are more successful (less successful) than the average, their population share will increase (decrease, respectively).

The replicator dynamics generally describe the evolution of the state of the population p . Note, however, in the case where the players only have pure strategies $i \in H$, the mean population strategy $p = \sum_{i=1}^N p_i e_i$, where $e_i = [0, \dots, 1, \dots, 0]^T$ (a vector with a 1 in the i th position), represents the pure strategy $i \in H$. This means that the population state is the mean population strategy. Hence, we can think of the replicator dynamics as representing the evolution of the IFD strategy by the process of natural selection.

In this specific case, we have defined the fitness of animals that play $i \in H$ in (17) at time t as (13), and the average fitness (of a randomly selected individual from the population) is $\bar{f} = \sum_{j=1}^N p_j f(j)$. Hence, the replicator dynamics are

$$\dot{p}_i = \beta_i p_i (f(i) - \bar{f}) \quad (18)$$

or

$$\dot{p}_i = \beta_i \epsilon_x p_i \left(\frac{a_i^{\frac{1}{m}}}{c_i P p_i + b_i} - \sum_{j=1}^N \frac{p_j a_j^{\frac{1}{m}}}{c_j P p_j + b_j} \right) \quad (19)$$

with $\beta_i > 0$ for all $i = 1, \dots, N$, when $p(0) \in \Delta$. Notice that $f(i) - \bar{f}$ measures the deviation from the IFD as quantified by the habitat matching rule (after some mathematical manipulation). The replicator dynamics for our population game are in the form of “monotone selection dynamics” [14]. The monotone selection dynamics in [14, p. 88] show what is essential to set up a replicator dynamics so that Δ is invariant. Notice that when s_i is defined as in (2), the average payoff \bar{f} is constant.

B. Constraint Set Invariance for the Replicator Dynamics

First, we specify conditions under which (19) can be satisfied at the same time that the constraints $\sum_{j=1}^N p_j = 1$ and $p_i \geq 0$, $i = 1, \dots, N$ are satisfied. This is essential since we are only interested in solutions to (19) that satisfy the appropriate constraints.

Theorem 4.1: The system in (19) satisfies the constraint $p(t) \in \Delta$, for all $t \geq 0$ if and only if $\beta_i = \beta_j$, $i, j = 1, \dots, N$, and $p(0) \in \Delta$.

This shows that the rate of increase or decrease in proportions of the strategies must be the same in order for the ordinary differential equation describing the replicator dynamics to satisfy the constraints of $\sum_{j=1}^N p_j = 1$, $p_i \geq 0$, $i = 1, \dots, N$. A special case of this result is the following theorem, which is from [14].

Theorem 4.2: If $\beta_i = \beta_j = \beta$ for all $i, j = 1, \dots, N$, and $p(0) \in \Delta$, then $p \in \Delta$ for all $t \geq 0$ [i.e., Δ is invariant with respect to (18)].

To ensure that the constraint set Δ is satisfied in all that follows, we assume that $\beta_i = \beta_j$.

C. Stability Analysis of the IFD

First, we need to find the equilibrium point in (19). We assume in the following analysis that P in (9) is satisfied with strict inequality, which implies that $p_i > 0$. It also implies that the equilibrium point is strictly inside the simplex Δ , i.e., in $\Delta - \partial\Delta$. If we let p_i^* be the equilibrium point, we get for any i, j that $a_i^{1/m}/(c_i P p_i^* + b_i) = a_j^{1/m}/(c_j P p_j^* + b_j)$, which is the habitat matching rule in (4) but in p -coordinates. In Theorem 2.2, we have shown that this point is given by (8).

Note that, for (2), when we try to find this equilibrium point, if $p_i \neq 0$ the solution would be $f(i) = \bar{f}$, which means that the consumption rate in each habitat i has to be equal to the overall consumption rate (in this case, this one is described by \bar{f}) at the IFD equilibrium. Otherwise, the strategy mix of the population will continue to change.

Theorem 4.3: For the replicator dynamics in (19), the IFD equilibrium given by $p^* = x^*/P$ [where x^* is defined in (8)] is asymptotically stable, with region of asymptotic stability $\Delta - \partial\Delta$.

Theorem 4.3 is a “semiglobal” result, which means that if the population state perturbs from the IFD to a point within some set, then the population state will return to the IFD. Note that under the game-theoretic interpretation, only a special type of perturbation is allowed: perturbations correspond to a single animal $\epsilon_x > 0$ switching to another strategy where ϵ_x is arbitrarily small. Theorem 4.3 includes this strategy perturbation as a special case; so, it applies to the game-theoretic setting. What does it mean for the population state to “return” to the IFD? If any animal switches habitats, then the mechanisms of reproduction via differential fitness will always shift the animal distribution back to the IFD. The shift of animal ϵ_x will result in more deaths in its new habitat and correspondingly more births in the habitat it shifted from.

In [13] and [14], it was shown that any ESS for a two-player game must be an asymptotically stable equilibrium in the

replicator dynamics defined for that type of game, but that there could exist asymptotically stable equilibria that are not ESS. For our replicator dynamics for the game against the field, the above results show that there is one unique equilibrium strictly inside the simplex, which this equilibrium is the IFD (which we showed was an ESS in Section III), and that the IFD is asymptotically stable [or exponentially stable for the standard suitability function in (2)].

D. Allocation Dynamics: Gradient Optimization Perspective

Related work has been done via the study of the Shahshahani gradient [14] and for linear games in [12].

Consider the cost function $J = (1/2) \sum_{i=1}^N ((x_i/P) - (x_i^*/P))^2$, where x_i^* is defined in (8), and $\sum_{j=1}^N x_j = P$. Note that J measures the deviation off the IFD defined by (6). The following theorem shows that minimization of this J , results in an IFD.

Theorem 4.4: The point x_i^* in (8) is a global minimizer for the constrained optimization problem defined as

$$\begin{aligned} \text{minimize} \quad & J = \frac{1}{2} \sum_{i=1}^N \left(\frac{x_i}{P} - \frac{x_i^*}{P} \right)^2 \\ \text{subject to} \quad & \sum_{j=1}^N x_j = P \\ & x_i > 0, \quad i = 1, \dots, N \end{aligned} \quad (20)$$

where x_i^* is defined in (8), when P is satisfied with strict inequality in (9).

Next, suppose that a steepest descent method is used in animal reallocation so that

$$\dot{x}_i = -\lambda P \frac{\partial J}{\partial x_i} \quad (21)$$

where $\lambda > 0$ is a “step-size” parameter. Note that if we let $b_i = 0$ and choose $\lambda = \beta \epsilon_x \sum_{j=1}^N (a_j^{1/m}/c_j)$, (21) is

$$\dot{x}_i = - \left(\beta \epsilon_x \sum_{j=1}^N \frac{a_j^{1/m}}{c_j} \right) \left(\frac{x_i}{P} - \frac{\frac{a_i^{1/m}}{c_i}}{\sum_{j=1}^N \frac{a_j^{1/m}}{c_j}} \right). \quad (22)$$

These allocation dynamics are equivalent to the replicator dynamics in (19). If in (18) we take $f(i) = \epsilon_x (a_i^{1/m}/c_i x_i)$, then the replicator dynamics in (19) are the same as in (22). Hence, we know that the constraint $\sum_{j=1}^N x_j = P$ is met for all $t \geq 0$. Moreover, for the optimal allocation dynamics the following result holds.

Theorem 4.5: The optimal allocation dynamics in (22) have the IFD as an equilibrium and it has a region of exponential stability given by $\Delta_x - \partial\Delta_x$.

Hence, the allocation strategy will not get “stuck” and will result in a distribution of effort that converges to the

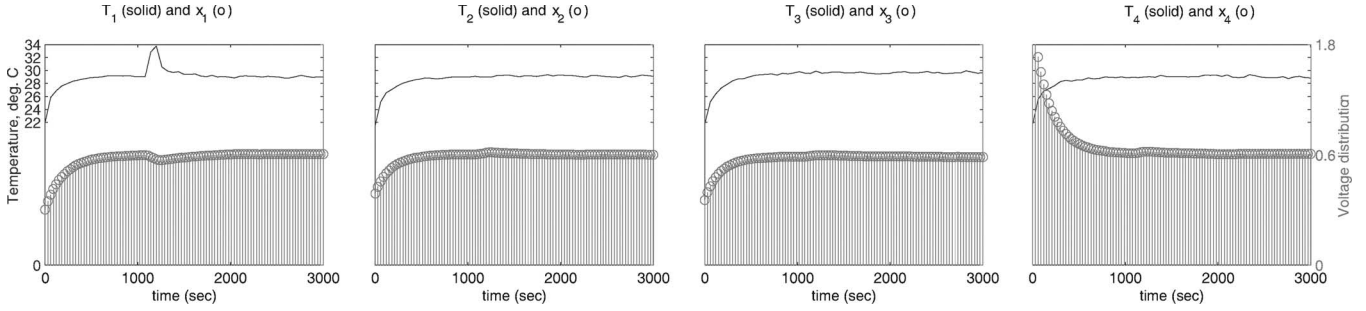


Fig. 1. Temperatures in four zones of the multizone temperature control experiment. The plot represents the temperature in each of the zones (left axis), and the distribution of the x_i (right axis).

IFD. Convergence is achieved independent of where the effort distribution starts. Equation (21) and the proof illustrate that if P is small (big), we will have a faster (slower) convergence rate. Also, notice that there is a critical difference compared to the strict Nash equilibrium and replicator dynamics viewpoint. Perturbations for the game-theoretic formulation are due to a single animal $\epsilon_x > 0$ switching habitats, and the replicator dynamics are built upon that perspective. With the optimal allocation perspective, any perturbation is allowed (i.e., any initial condition corresponding to the initial animal effort distribution must be possible), even ones that are not small perturbations $\epsilon_x > 0$.

V. MULTIZONE TEMPERATURE CONTROL APPLICATION

Here, to illustrate the theoretical results shown in the previous sections, we consider a multizone temperature control problem that has a voltage saturation constraint [24]. The experiment consists of $N = 4$ zones, where each zone consists of one lamp with voltage input $v_i(t)$ and one sensor that provides the temperature $T_i(t)$, $t \geq 0$. The idea of this experiment is to use the replicator dynamics in (19) to reach a maximum uniform temperature in each of the zones (it is important to note that this is not a standard tracking problem since the maximum achievable temperature is not known). The controller is implemented using a dSPACE DS1104 data acquisition card.

Equation (19) has two main variables: The proportion of the number of animals in habitat i , p_i , and the arrival rate a_i for the i th habitat. In the previous analysis, the a_i values were positive constants, however, these arrival rates could vary with time. Suppose we define each arrival rate to be the inverse of the temperature sensed in each zone, so that for $i = 1, \dots, N$, $a_i(t) = 1/T_i(t)$. Since $T_i(t) > 0$, $a_i(t) > 0$ for all i . Next, let $x_i(t) = p_i(t)P = v_i(t)$, where $\sum_{j=1}^N v_j(t) = P$ is the total amount of voltage that can be applied to all zones. For our lamps, $v_i(t) \geq 0$, $t \geq 0$, and this fits with the assumptions on $x_i(t)$ in the theory. For a given $v_i(0)$, the replicator dynamics indicate how to redistribute voltage, depending on $a_i(t)$. Here, the temperature will change due to ambient and interzone influences, and the replicator dynamics will persistently and dynamically redistribute the constrained amount of voltage. Will it do this in a way to try to achieve the maximum uniform temperature? The results below seem to illustrate that it will. Why? Because, it will allocate more voltage to the minimum temperature at

each time step. It will tend to force the lowest (minimum) temperatures to rise faster than the higher temperatures.

While we expect that the temperature in each of the zones will be the same after some time, there are certain features of the physical experiment that conspire against us achieving this goal. One problem is the physical location of the lamps and the sensors. Since we are working with breadboards, it is difficult to have the same sensor-lamp, interlamp, and intersensor distances for all the zones, and hence the interzone effects are different for each zone. The second problem is the sensors. We calibrate one sensor and then we pick three others that provide temperatures close to it before construction. Next, there is sensor noise. If all the sensors were the same, and there was no noise, after a period of time the same temperature would be achieved in each of the zones.

The results are shown in Fig. 1. This figure shows the first 50 min of the experiment. At the beginning, the experiment was at 22 °C, and as we can see, practically all the zones were around this temperature. The temperature in each of the zones starts to increase according to the voltage that we allocate to each of the lamps. The idea is to distribute 3.5 V across the zones. We assume that these 3.5 V are equivalent to P . The initial conditions are $x_1(0) = 0.44$, $x_2(0) = 0.57$, $x_3(0) = 0.51$, and $x_4(0) = 1.98$. All the units are in volts. At 18 min, we add a disturbance to the grid. This disturbance consists of turning on a lamp that is close to the first temperature zone, and leaving it on for 2 min. As we can see in Fig. 1, the first zone drastically increases its temperature, but at the same time there is a reallocation of the resource (voltage) across the four zones. We can see then that all the zones but the first one start to have more voltage and that occurs until the disturbance finishes. The final temperature in the grid is practically the same (29 °C), ± 1 °C. In this case, it is clear that we do not reach a unique equilibrium point described by the input matching rule due to ambient and interzone influences. However, as we can see in Fig. 1, the final values allocated are $x_1(3000) = 0.88$, $x_2(3000) = 0.88$, $x_3(3000) = 0.86$, and $x_4(3000) = 0.88$. However, using our previous analysis the final values should be $x_1^* = 0.88$, $x_2^* = 0.87$, $x_3^* = 0.86$, and $x_4^* = 0.89$, which as we can see are relatively close to what we have in the experiment. Notice that the only computations needed to implement the control are those for the computation of (19), using $a_i = 1/T_i$, and with $\epsilon_x = c_i = m = b_i = \beta = 1$. Clearly, the computational complexity is not a concern for this application.

VI. CONCLUSION

We have analyzed the IFD for a general class of suitability functions. We have proven that the habitat and input matching rules are equivalent for this general case. We also proved that the IFD is indeed an ESS for the general case. Since this last concept only provides local results, we state a constrained optimization problem where we prove that the IFD is a global optimum point. Finally, from an evolutionary time perspective, we set up the replicator dynamics and show that the IFD is an asymptotically stable equilibrium point. An interesting characteristic for this case is that under some constraints, a gradient optimization perspective leads us to the same replicator dynamics. Finally, in order to provide more insight on why these allocation dynamics are useful from an engineering perspective, we applied the approach to the multizone temperature control problem. Using the replicator dynamics ideas, we showed how in spite of limiting the input voltage, we can manage to have a uniform temperature in each of four temperature zones. A future direction is to evaluate the relative advantages and disadvantages of other control-theoretic approaches for solving dynamic resource allocation problems such as the multizone temperature control problem studied here.

APPENDIX

A. Proof of Theorem 2.1

For (4) \Rightarrow (6) note that $(c_i x_i + b_i) \sum_{j=1}^N a_j^{1/m} = a_i^{1/m} \times \sum_{j=1}^N (c_j x_j + b_j)$, which clearly is (6). For (6) \Rightarrow (4), for all $i = 1, \dots, N$, $a_i^{1/m}/(c_i x_i + b_i) = \sum_{j=1}^N a_j^{1/m} / \sum_{j=1}^N (c_j x_j + b_j) = C$, where C is a constant, so for all i, j , (4) holds.

B. Proof of Theorem 2.2

From (4), $(a_i^{1/m}/c_i)(x_j^* + (b_j/c_j)) = (a_j^{1/m}/c_j)(x_i^* + (b_i/c_i))$. Therefore

$$\frac{a_i^{1/m}}{c_i} \sum_{j=1}^N \left(x_j^* + \frac{b_j}{c_j} \right) = \left(x_i^* + \frac{b_i}{c_i} \right) \sum_{j=1}^N \frac{a_j^{1/m}}{c_j} \quad (23)$$

with $\sum_{j=1}^N x_j^* = P$, we obtain (8). The constraint on P in (9) is obtained by using $x_i^* \geq 0$. In the case when $P > 0$, without (9) necessarily holding, the analysis changes. Since we need to satisfy the constraint that $x_i \geq 0$, and using the fact that $a_i^{1/m}/c_i > 0$, for some $i = 1, \dots, N$, for $x_i > 0$

$$\frac{a_i^{1/m}}{b_i} > \sigma = \frac{\sum_{j=1}^N \frac{a_j^{1/m}}{c_j}}{P + \sum_{j=1}^N \frac{b_j}{c_j}}. \quad (24)$$

Since $a_1^{1/m}/b_1 > \dots > a_N^{1/m}/b_N$, if we let k^* be the largest index k for which $a_k^{1/m}/b_k > \sigma$, k^* is given by (11). Then, if $i \in \{k^* + 1, k^* + 2, \dots, N\}$, (24) is not satisfied, and since $c_i > 0$, this equation can be written as $((a_i^{1/m}/c_i)P + (a_i^{1/m}/c_i) \sum_{j=1}^N (b_j/c_j) - (b_i/c_i) \sum_{j=1}^N (a_j^{1/m}/c_j)) / \sum_{j=1}^N \times$

$(a_j^{1/m}/c_j) \leq 0$. The left-hand side of this inequality is the same x_i^* in (8). However, we have assumed that $x_i^* \geq 0$, therefore $x_i^* = 0$ for $i \in \{k^* + 1, \dots, N\}$. Hence, we will have $N - k^*$ truncated habitats, which implies that $\sum_{j=1}^N x_j^* = \sum_{j=1}^{k^*} x_j^* = P$. Therefore, instead of taking the sum over all habitats in (23), we need to consider only those habitats that are inhabited, i.e., we need to take the sum over k^* habitats. Then, $(a_i^{1/m}/c_i) \sum_{j=1}^{k^*} (x_j^* + (b_j/c_j)) = (x_i^* + (b_i/c_i)) \sum_{j=1}^{k^*} (a_j^{1/m}/c_j)$. Using the fact that $\sum_{j=1}^{k^*} x_j^* = P$, and the same ideas as before, we obtain that the IFD for the suitability function in (5) is given by (10) and (11).

C. Proof of Theorem 3.1

Let \bar{x} represent a strategy choice by animal ϵ_x such that all other animals make strategy choices such that the IFD defined by (6) holds. From the habitat matching rule, we know that for any j such that $a_j = 0$, $x_j = 0$. Therefore, \bar{x} will only correspond to strategy (habitat) choices $i \in H^*$ where $a_i > 0$ and $x_i > 0$. Let $P_{\bar{x}}$ represent the population with individuals all playing strategies such that the IFD is achieved. It is impossible to know which habitat $i \in H^*$ player ϵ_x will choose since the IFD can be achieved for any strategy choice $i \in H^*$ provided the other animals adopt the appropriate strategies. In Theorem 2.1, we have shown that the habitat matching rule is satisfied and it is given by (6), which in terms of fitness is equivalent to (13). Hence, for any $i \in H^*$

$$f(\bar{x}, P_{\bar{x}}) = f(i) = \epsilon_x \frac{a_i^{1/m}}{(c_i x_i + b_i)} = \epsilon_x \frac{a_j^{1/m}}{(c_j x_j + b_j)} = f(j) \quad (25)$$

for all $i, j \in H^*$. Suppose that the animal ϵ_x makes a unilateral deviation to strategy $\bar{y} \neq \bar{x}$ that corresponds to choosing habitat $j \neq i$, $j \in H$ (the animal could choose j such that $a_j = 0$). Then, $f(\bar{y}, P_{\bar{x}}) = \epsilon_x (a_j^{1/m}/(c_j(x_j + \epsilon_x) + b_j))$, and if $j \in H - H^*$, $a_j = 0$, $f(\bar{y}, P_{\bar{x}}) = 0$. In either case, by monotonicity and from (25), $f(\bar{y}, P_{\bar{x}}) < f(\bar{x}, P_{\bar{x}})$. Hence, the IFD is a strict Nash equilibrium and hence an ESS.

D. Proof of Theorem 3.2

Note that (16) is equivalent to the optimization problem

$$\begin{aligned} & \max \quad z \\ & \text{subject to} \quad \sum_{j=1}^N x_j = P \\ & \quad \quad \quad x_i \geq 0, \quad i = 1, \dots, N \\ & \quad \quad \quad \epsilon_x \frac{\frac{a_i^{1/m}}{c_i}}{x_i + \frac{b_i}{c_i}} \geq z, \quad i = 1, \dots, N \end{aligned} \quad (26)$$

where we have introduced the new variable $z \in \mathbb{R}$, $z > 0$. If we combine the constraints, we obtain that for each

$i = 1, \dots, N$, $\epsilon_x((a_i^{1/m}/c_i)/z) \geq x_i + (b_i/c_i) > 0$, since $z > 0$. Adding all the terms across the N habitats, we obtain that $z \leq \epsilon_x((\sum_{j=1}^N (a_j^{1/m}/c_j))/(P + \sum_{j=1}^N (b_j/c_j)))$. Therefore, (26) is equivalent to

$$\begin{aligned} \max \quad & z \\ \text{subject to} \quad & z \leq \epsilon_x \frac{\sum_{j=1}^N \frac{a_j^{1/m}}{c_j}}{P + \sum_{j=1}^N \frac{b_j}{c_j}}. \end{aligned}$$

In this case, the maximum is unique and equal to $z^* = \epsilon_x(\sum_{j=1}^N (a_j^{1/m}/c_j)/(P + \sum_{j=1}^N (b_j/c_j)))$. Hence, for $i = 1, \dots, N$, the x_i^* are any values that satisfy the constraints of (26) and such that

$$x_i^* \leq \frac{\frac{a_i^{1/m}}{c_i} P + \frac{a_i^{1/m}}{c_i} \sum_{j=1}^N \frac{b_j}{c_j} - \frac{b_i}{c_i} \sum_{j=1}^N \frac{a_j^{1/m}}{c_j}}{\sum_{j=1}^N \frac{a_j^{1/m}}{c_j}}. \quad (27)$$

We have then two cases. For the “<” option, adding all the terms across the N habitats, we obtain a contradiction (i.e., the total population size is less than P). Therefore, the “=” option in (27) must hold. Using the same ideas as in the proof of Theorem 2.2, we can show that the IFD for the suitability function in (5) is given by (10) and (11).

E. Proof of Theorem 4.1

For (\implies), since by hypothesis the sum of the p_i is equal to 1 for all $t \geq 0$, and $p_i(0) \geq 0$ for all i , then $p(0) \in \Delta$. For the $N = 2$ case

$$\begin{aligned} \dot{p}_1 &= \beta_1 \epsilon_x \left(\frac{a_1^{1/m} p_1 (1 - p_1)}{(c_1 P p_1 + b_1)} - \frac{a_2^{1/m} p_1 (1 - p_1)}{(c_2 P p_2 + b_2)} \right) \\ \dot{p}_2 &= \beta_2 \epsilon_x \left(\frac{a_2^{1/m} (1 - p_1) (1 - (1 - p_1))}{(c_2 P p_2 + b_2)} - \frac{a_1^{1/m} p_1 (1 - p_1)}{(c_1 P p_1 + b_1)} \right). \end{aligned}$$

Since $\sum_{j=1}^N p_j = 1$, $\sum_{j=1}^N \dot{p}_j = 0$. Hence, $\beta_1 = \beta_2$. Next, we assume that $\beta = \beta_i = \beta_j$ for all $i, j = 1, \dots, N$, and prove that it also holds for $N + 1$. Note that

$$\begin{aligned} 0 &= \sum_{i=1}^N \beta_i p_i \frac{a_i^{1/m}}{(c_i P p_i + b_i)} - \sum_{i=1}^N \beta_i p_i \sum_{j=1}^{N+1} \frac{p_j a_j^{1/m}}{(c_j P p_j + b_j)} \\ &+ \beta_{N+1} \frac{a_{N+1}^{1/m} p_{N+1}}{(c_{N+1} P p_{N+1} + b_{N+1})} - \beta_{N+1} p_{N+1} \sum_{j=1}^{N+1} \frac{p_j a_j^{1/m}}{(c_j P p_j + b_j)}. \end{aligned}$$

Using $\sum_{i=1}^{N+1} p_i = 1$, and $\beta_i = \beta$ for all $i = 1, \dots, N$, by hypothesis, we obtain that $\beta = \beta_{N+1}$.

For (\impliedby), since $\beta_i = \beta_j$, then $\sum_{i=1}^N \dot{p}_i = \epsilon_x(\sum_{i=1}^N \beta_i p_i f(i) - \sum_{i=1}^N \beta_i p_i \bar{f}) = 0$. But, if we take the integral with respect to time, for $t \geq 0$, $\int_0^t \sum_{i=1}^N \dot{p}_i(\tau) d\tau = 0$, or $\sum_{i=1}^N p_i(t) - \sum_{i=1}^N p_i(0) = 0$. But, by hypothesis, the sum of all the initial conditions has to be equal to 1, then we get that for all $t \geq 0$ $\sum_{i=1}^N p_i(t) = 1$. Since by hypothesis $p(0) \in \Delta$, we can conclude that $p \in \Delta$ for all $t \geq 0$.

F. Proof of Theorem 4.3

Using the Lyapunov function

$$V = - \sum_{i=1}^N p_i^* \ln \left(\frac{p_i}{p_i^*} \right). \quad (28)$$

In information theory, this function is called the relative entropy function or Kullback–Leibler distance [15]. It has the property that $0 \ln(0/p_i) = 0 \ln(0/0) = 0$, and $p_i^* \ln(p_i^*/0) = +\infty$. It has been proven that V is a valid Lyapunov function candidate (e.g., see [15]). The derivative of V along the trajectories in (18), is $\dot{V} = - \sum_{i=1}^N p_i^* (1/p_i) (p_i (f(i) - \bar{f}))$. Since $\sum_{j=1}^N p_j^* = 1$

$$\begin{aligned} \dot{V} &= - \sum_{i=1}^N p_i^* f(i) + \bar{f} \sum_{i=1}^N p_i^* \\ &= - \sum_{i=1}^N p_i^* f(i) + \sum_{i=1}^N p_i f(i) \\ &= \sum_{i=1}^N f(i) (p_i - p_i^*). \end{aligned} \quad (29)$$

In order to show that \dot{V} is nonpositive, we will prove that the maximum value of \dot{V} in (29) is equal to 0. For that, we let $f(i)$ be as in (13) and we solve the optimization problem

$$\max \quad J = \dot{V} = \sum_{i=1}^N \epsilon_x \left(\frac{\frac{a_i^{1/m}}{c_i}}{P p_i + \frac{b_i}{c_i}} (p_i - p_i^*) \right)$$

$$\begin{aligned} \text{subject to} \quad & \sum_{j=1}^N p_j = 1 \\ & p_i > 0 \text{ for all } i = 1, \dots, N. \end{aligned}$$

Using Lagrange multiplier theory, the Jacobian $\nabla J = [\partial J / \partial p_1, \partial J / \partial p_2, \dots, \partial J / \partial p_N]^\top$, where $\partial J / \partial p_i = \epsilon_x(a_i^{1/m}/c_i)$

$(Pp_i^* + (b_i/c_i))/(Pp_i + (b_i/c_i))^2$. Since the inequality constraint $p_i > 0$ is inactive, for $i = 1, \dots, N$

$$\epsilon_x \frac{\left(\frac{1}{c_i}\right)^2 \left(P + \sum_{j=1}^N \frac{b_j}{c_j}\right)}{\left(P\bar{p}_i^* + \frac{b_i}{c_i}\right)^2 \sum_{j=1}^N \frac{a_j^m}{c_j}} + \lambda^* = 0 \quad (30)$$

where $\bar{p}^* = [\bar{p}_1^*, \dots, \bar{p}_N^*]^\top$ is the regular point for the optimization problem, and λ^* is the Lagrange multiplier. From (30), for any $i, j = 1, \dots, N$, $(a_i^{1/m}/c_i) \sum_{j=1}^N (P\bar{p}_j^* + (b_j/c_j)) = (P\bar{p}_i^* + (b_i/c_i)) \sum_{j=1}^N (a_j^{1/m}/c_j)$. After solving the above equation for \bar{p}_i^* , we obtain a scaled version of (8), i.e., $\bar{p}_i^* = x_i^*/P = p_i^*$. In order to see if it is a global or a local maximum, we need to check the Hessian $\nabla^2 J$. We have that

$$\frac{\partial^2 J}{\partial p_i^2} = -\epsilon_x \frac{2P \left(\frac{1}{c_i}\right)^2 \left(P + \sum_{j=1}^N \frac{b_j}{c_j}\right)}{\left(Pp_i + \frac{b_i}{c_i}\right)^3 \sum_{j=1}^N \frac{a_j^m}{c_j}} < 0$$

and $\frac{\partial^2 J}{\partial p_i \partial p_j} = 0$. Hence, $\nabla^2 J$ is negative definite, which implies that \bar{p}^* is indeed a global maximum. Therefore, the maximum value of J is $\max J = 0$. Since $\dot{V} < 0$ for all $p_i \neq p_i^*$, and $\dot{V} = 0$ if $p_i = p_i^*$, the IFD is (uniformly) asymptotically stable.

Notice that \dot{V} in (29) is negative, except when it is equal to the equilibrium point. The previous analysis showed that whenever we are inside the simplex (i.e., when $p \in \Delta - \partial\Delta$) the Lyapunov function satisfied all the previous conditions. Therefore, the region of asymptotic stability is $\Delta - \partial\Delta$.

G. Proof of Theorem 4.4

We want to minimize J , subject to $h(x) = \sum_{i=1}^N x_i - P$, and $g_i(x) = x_i$, $i = 1, \dots, N$ where the g_i constraints are inactive. We have $\partial J/\partial x_i = 1/P((x_i/P) - (x_i^*/P))$, and $\nabla h(x) = [1, \dots, 1]^\top$. Also, $\nabla^2 J(x) = (1/P^2)I_{N \times N}$, where $I_{N \times N}$ is the identity matrix $N \times N$. Equation $P > 0$, and satisfies with strict inequality (9), $\nabla^2 J(x)$ is positive definite. Using the fact that the constraint is inactive, we have for all $i = 1, \dots, N$ that $1/P((\bar{x}_i^*/P) - (x_i^*/P)) + \lambda^* = 0$, where λ^* is the Lagrange multiplier, and \bar{x}_i^* is the optimum point. Rearranging, we have for any k, w , $\bar{x}_k^* - \bar{x}_w^* = x_k^* - x_w^*$. In terms of k only, we will have $N - 1$ of these equations. If we add all these equations, we get that $\bar{x}_k^*(N - 1) - \sum_{j=1, j \neq k}^N \bar{x}_j^* = x_k^*(N - 1) - \sum_{j=1, j \neq k}^N x_j^*$, which is equal to (8). It is clear that $\bar{x}_i^* > 0$ since P is assumed to satisfy (9) with strict inequality. However, J is defined over $\Delta_x - \partial\Delta_x$, and its Hessian is positive definite, which implies that the cost function is convex on $\Delta_x - \partial\Delta_x$. Therefore, the point in (8) is a global minimum for the cost function J defined in (20), subject to $\sum_{j=1}^N x_j = P$, with $x_i > 0$ for all $i = 1, \dots, N$.

H. Proof of Theorem 4.5

Equation (22) is equivalent to (19) for the case when $b_i = 0$ for all $i = 1, \dots, N$. We know that the IFD defined by (8) is an equilibrium point whenever $P > 0$ and it is unique, and that $\Delta_x - \partial\Delta_x$ is invariant in x generated by (22). Let $e_i = p_i - ((a_i^{1/m}/c_i)/\sum_{j=1}^N (a_j^{1/m}/c_j))$. Since a_i, c_i , and m are positive, we have that $\dot{e}_i = \dot{p}_i = -((\beta\epsilon_x/P)\sum_{j=1}^N (a_j^{1/m}/c_j))e_i$. Taking the Lyapunov function $V_i = (1/2)e_i^2$, then $\dot{V}_i = -((\beta\epsilon_x/P)\sum_{j=1}^N (a_j^{1/m}/c_j))e_i^2(t)$, which implies that the IFD equilibrium is (uniformly) exponentially stable.

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