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The ideal free distribution: A review and synthesis of the game-theoretic perspective

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Abstract

The Ideal Free Distribution (IFD), introduced by Fretwell and Lucas in [Fretwell, D.S., Lucas, H.L., 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19, 16–32] to predict how a single species will distribute itself among several patches, is often cited as an example of an evolutionarily stable strategy (ESS). By defining the strategies and payoffs for habitat selection, this article puts the IFD concept in a more general game-theoretic setting of the "habitat selection game". Within this game-theoretic framework, the article focuses on recent progress in the following directions: (1) studying evolutionarily stable dispersal rates and corresponding dispersal dynamics; (2) extending the concept when population numbers are not fixed but undergo population dynamics; (3) generalizing the IFD to multiple species.

For a single species, the article briefly reviews existing results. It also develops a new perspective for Parker's matching principle, showing that this can be viewed as the IFD of the habitat selection game that models consumer behavior in several resource patches and analyzing complications involved when the model includes resource dynamics as well. For two species, the article first demonstrates that the connection between IFD and ESS is now more delicate by pointing out pitfalls that arise when applying several existing game-theoretic approaches to these habitat selection games. However, by providing a new detailed analysis of dispersal dynamics for predator–prey or competitive interactions in two habitats, it also pinpoints one approach that shows much promise in this general setting, the so-called "two-species ESS". The consequences of this concept are shown to be related to recent studies of population dynamics combined with individual dispersal and are explored for more species or more patches.

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1. Introduction

Understanding the spatial distribution of animals is one of the ultimate goals of ecology (Morris, 2003). The problem is not simple as species distribution is not only a function of the quality of the environment but also of the species distribution itself. The relationship between environmental productivity and species richness is complicated by the fact that habitat selection depends on interactions among animals. These interactions can take many forms (e.g., predator-prey, competition, or social type) that are used either singly or in combination to model complex ecological systems. Thus, abiotic factors related to the quality of the environment cannot by themselves completely explain species distribution.

One of the basic concepts that considers frequencydependent animal distribution of a single species is that of the Ideal Free Distribution (Fretwell and Lucas, 1970). The original theoretical concept of the IFD (Fretwell and Lucas, 1970) was derived under the following assumptions: resources are distributed in discrete habitats (also called patches); animals are equal competitors for resources and their number does not change; animals are free to settle in any patch and there

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is no cost to move between patches; they have complete knowledge (i.e. they are ideal or omniscient) of the resource quality of each patch and this quality does not change in time; individual animal resource intake rate decreases with increased consumer (i.e. animal) numbers in the patch. Many of these assumptions were relaxed in subsequent articles (for reviews see, for example, Milinski (1988), Kacelnik et al. (1992), Milinski and Parker (1991), Weber (1998) and Morris (2003)). There has also been a heated debate on whether or not observed animal distributions conform to the IFD (Kennedy and Gray, 1993; Gray and Kennedy, 1994b; Milinski, 1994) and to misconceptions in the use of the IFD (Tregenza, 1994). Recently, some strong support for the IFD in a natural setting was observed (Haugen et al., 2006; Morris, 2006).

With more than 450 articles returned when searching the Web of Science for "Ideal Free Distribution", it might seem that there is little or nothing to be added to the concept itself. However, we do not think so, as we believe a lot of confusion related to the IFD arises because the concept itself is still underdeveloped. A striking illustration of this fact is that, although most authors refer to the single-species IFD as an example of an Evolutionarily Stable Strategy (Parker, 1978, 1984; Morris, 1994),¹ this seems to be proved only recently (Cressman and Křivan, 2006). This is perhaps because the original definition of the IFD by Fretwell and Lucas (1970) is equivalent to the Nash equilibrium (NE) concept of a corresponding game, but it does not guarantee that the equilibrium is stable with respect to other patch selection strategies. However, the ESS stability of the IFD is crucial since one cannot expect to get consistent empirical observations of the IFD if it is not stable since there would then always be some random perturbations that drive the animal distribution away from the IFD. That is, if the IFD were not stable, then its usefulness for ecology would be negligible. In this article we review and synthesize various conceptual studies on the IFD from the game-theoretical point of view, with an emphasis on stability of the IFD.

We split this article into two parts. The first part (Section 2) focuses on the IFD for a single species, which is the original setting of the Fretwell and Lucas (1970) article. The second part (Section 3) is related to two-species IFD. We also suggest some future directions in which theoretical research on the IFD should focus.

2. Single-species IFD

2.1. The IFD as a game-theoretical concept

One of the basic models that aims to describe the spatial distribution of a single species was developed by Fretwell and Lucas (1970). These authors assumed that animals are free to move between several patches, the travel time is negligible, each individual knows perfectly the quality (or suitability) of all patches and all individuals have the same competitive abilities.

Assuming that these patches differ in their basic suitability (i.e. their quality when unoccupied by any consumers), they predicted that the best patch will always be occupied. They also assumed that a patch's quality and the species' density there determined individual fitness (which, in game-theoretic terms, is equated to individual payoff). Let us order the patches so that the first patch has a higher basic quality than the second patch and so on. Following the method and terminology of Fretwell and Lucas (1970), consider H habitat patches with suitabilities (i.e. individual payoffs)

$$V_i = B_i - h_i(m_i). \tag{1}$$

Here B_i is the basic suitability, m_i is the animal density in patch i, and h_i is an increasing function that is 0 when patch i is unoccupied. In particular, $B_1 > \cdots > B_H$.

As the density of individuals in patch 1 increases, individual payoff there will decrease and, at a certain critical density, patch 2 will have the same payoff. Then, for a higher population density, both patches will be occupied and the payoff in either patch will be the same. For yet higher species densities, the third patch will give the same payoff and it will be occupied too. Thus, all occupied patches provide the same payoff and no unoccupied patch has a higher payoff. This distribution was termed the Ideal Free Distribution. In other words, if the first ℓ patches are occupied at the IFD, then

$$V_1 = \cdots = V_\ell$$

and $V_{\ell} \geq B_{\ell+1} > \cdots > B_H$.

Fretwell and Lucas (1970) showed that, for each positive total population size M, there will be a unique IFD. This result also arises since the IFD is a NE of the single-species "habitat selection game" (Section 2.1.1) and since this game has exactly one NE.

Thus, when the population distribution is at its IFD $p^* =$ (p_1^*, \ldots, p_H^*) , no other individual strategy can achieve a higher payoff. However, this concept does not address the question of whether the population distribution will return to the IFD after a perturbation to p^* . That is, the IFD definition as a NE *a priori* lacks a stability property. A concept of stability for the NE was introduced in the biological context later on by Maynard Smith and Price (1973) (see also Maynard Smith (1982)) under the term Evolutionarily Stable Strategy. The ESS, besides being a NE, must also be stable with respect to rare mutant strategies in the sense that these strategies cannot spread in a population consisting of a few mutants together with a resident population where all individuals play the ESS. To avoid confusion of stability with respect to some explicit dynamics that we discuss in the following sections, we call this the ESS stability type. For playing-the-field models, p^* is an ESS if it satisfies (Maynard Smith, 1982; Hofbauer and Sigmund, 1998)

$$p \cdot V(p) < p^* \cdot V(p) \tag{2}$$

for all $p \in \Delta^H$ sufficiently close (but not equal) to p^* . Cressman et al. (2004) and Cressman and Křivan (2006) prove that inequality (2) holds for all $p \neq p^*$ in every habitat selection game (where animal payoffs in every patch decrease

¹ We remark that the concept of the IFD was introduced before the ESS was conceived by Maynard Smith and Price (1973).



Fig. 1. Panel A plots mean payoff \overline{V} as a function of distribution p_1 and overall number of individuals M for a two-patch model with linear payoff $(V_i = r_i(1 - \frac{p_i M}{K_i}), i = 1, 2)$. The thick curve corresponds to the IFD, while the thin solid curve corresponds to the distribution along which the mean payoff maximizes. Panel B shows that along the IFD the fitness in both patches is the same (solid line) for all M when both patches are occupied. On the other hand, for the strategy that maximizes the mean payoff, the patch specific payoffs are different (the two dashed lines correspond to payoffs in the two patches). Parameters used in simulations: $r_1 = 1$, $r_2 = 2$, $K_1 = 20$, $K_2 = 10$.

as the density of the patch increases). That is, the IFD is not only a NE, it is an ESS.

When V_i is linear, the payoff in patch *i* becomes $V_i(p) = r_i(1 - p_iM/K_i)$. That is, per capita fitness in each patch has the form of a logistic equation. In this important special case, payoffs can be interpreted as resulting from random pairwise interactions between individuals. The payoff a_{ij} to individual using pure strategy *i* against pure strategy *j* can then be taken as the intrinsic growth rate r_i if $i \neq j$ and $r_i(1 - M/K_i)$ if i = j. These payoffs form the entries of the $H \times H$ payoff matrix with the expected payoff of an individual with strategy *p* against an individual with strategy p' given by $\sum_{i,j=1}^{H} p_i a_{ij} p'_j$ (in particular, $V_i(p) = \sum_{j=1}^{H} a_{ij} p_j$). From the matrix structure, an algorithm exists for determining NE and ESS in general matrix games (Haigh, 1975; Abakuks, 1980) and for the specific habitat selection game (Křivan and Sirot, 2002) where it produces the IFD. For instance, for the case of two patches with *M* large enough that both patches are occupied, the IFD is given by

$$p_1^* = \frac{r_2 K_1}{r_1 K_2 + r_2 K_1} + \frac{K_1 K_2 (r_1 - r_2)}{(r_1 K_2 + r_2 K_1)M}$$
(3)

and of course $p_2^* = 1 - p_1^*$.

For readers unfamiliar with the NE concept, it is important to emphasize here that the IFD is very different from maximization of the mean animal payoff $\overline{V} = p \cdot V(p)$ (Brown, 1998). As an example, when the IFD is given by (3), the strategy that maximizes the mean payoff is given by $p_1 = \frac{r_2K_1}{r_1K_2+r_2K_1} + \frac{K_1K_2(r_1-r_2)}{2(r_1K_2+r_2K_1)M}$, provided this number is between 0 and 1. Thus, $p_1 = p_1^*$ if and only if $r_1 = r_2$. Fig. 1 shows that, while the latter strategy is never worse than the IFD, individuals using it obtain lower payoffs in one patch than in the other patch which makes this strategy such as the IFD. It seems that in the ecological literature these two different approaches are not always clearly distinguished (cf. Figure 2 in Morris (2003)).

2.1.1. Single-species habitat selection game

To describe habitat selection as a game, we must specify the set of (pure) strategies and the payoff functions associated with each of these strategies. Each player (i.e. animal) chooses among *H* pure strategies, where strategy *i* corresponds to the animal spending all of its time in habitat *i*. To each pure strategy, there is a payoff function $V_i : \Delta^H \to \mathbf{R}$ that is given through (1) as

$$V_i(p) = B_i - h_i(p_i M).$$
(4)

 V_i is a decreasing function of p_i . Here M is the fixed positive total population size and Δ^H is the (H-1) dimensional strategy simplex $\{p = (p_1, \ldots, p_H) \mid \sum p_i = 1 \text{ and } p_i \ge 0 \text{ for all } 1 \le i \le H\}$ that serves a dual purpose in evolutionary game theory. It is used to denote the set of population distributions (also called population states) but can also refer to an individual's mixed strategy (i. e., an individual using strategy p spends a proportion p_i of its time in habitat i).

This set of pure strategies combined with their payoff functions constitutes a single population game (Sandholm, 2007) which we call the habitat selection game. Unless each V_i is a linear function, the habitat selection game cannot be viewed as a two-player game where animals compete in random pairwise contests. Instead, it is known in the biological literature as a "playing-the-field" game (Maynard Smith, 1982) (which has also been called "scrambles", Parker, 1984).

The concept of a NE was introduced for *n*-player games by the Nobel prize winner J.F. Nash (Nash, 1951). For a single population game, $p^* \in \Delta^H$ is a NE if

$$p \cdot V(p^*) \le p^* \cdot V(p^*)$$

for all $p \in \Delta^{H}$. Here $p \cdot V(p^{*}) \equiv \sum_{i=1}^{H} p_{i}V_{i}(p^{*})$ is the payoff to an individual using strategy p when the population distribution is at the NE p^{*} . Thus, $p^{*} \cdot V(p^{*})$ is the average individual payoff (i.e. mean payoff) of the population. The linearity of this inequality in the components of p_{i} implies $V_{i}(p^{*}) = V_{j}(p^{*})$ for all $p_{i}^{*}p_{j}^{*} > 0$ and $V_{i}(p^{*}) \leq V_{j}(p^{*})$ if $p_{i}^{*} = 0$ and $p_{j}^{*} > 0$. That is, the IFD definition is equivalent to that of a NE. Cressman and Křivan (2006, Appendix B) show that the habitat selection game has a unique NE when the payoff in each patch is a decreasing function of population density there.

2.2. Parker's matching rule, resource dynamics

The IFD concept as a game between individuals does not consider any population dynamics whatsoever. Instead, it assumes that patch payoff decreases with increasing number of animals without specifying the mechanism leading to this negative relation. The payoff is related to competition between animals. Either animals scramble for food resources or mate (also called exploitative or scramble competition), or they compete for space and territories (called contest competition or interference). The original concept of the IFD assumes that each patch is characterized by its individual payoff V_i which decreases as more animals settle in this patch (Section 2.1.1). Although this payoff can implicitly capture the resource dynamics (e.g., by assuming that resource dynamics are fast with respect to consumer dynamics so that resources quickly equilibrate with each consumer density), it does not describe resource dynamics explicitly and is therefore more directly related to the concept of contest competition than scramble competition.

Parker (1978) derived, under particular assumptions, an IFD that is called the "input matching" principle. There has been a lot of confusion in the literature (see discussion in Gray and Kennedy (1994a) and Milinski (1994)) as often the matching principle was identified with the IFD. However, this is not so. because the matching principle is only an IFD for a particular payoff function choice, while the IFD is a general concept that applies for any payoff function satisfying the general assumptions given by Fretwell and Lucas (1970). In particular, Parker (1978) assumed that resource input rates are constant and all resources in all patches are consumed immediately when they enter the system and so there is no standing crop. This leads to a particularly simple definition of animal payoff in a patch as the ratio of the resource input rate divided by the number of individuals there. The matching principle then states that animals distribute themselves so that their density in each patch is proportional to the rate with which resources arrive into the patch $p_i/p_i = r_i/r_i$ (see Section 2.2.1) and all patches will be occupied (as the consumer density in a patch decreases, payoff $r_i/(p_i M)$ tends to infinity). This concept successfully predicts the distribution of house flies that arrive at a cow patch where they immediately mate (Parker, 1978, 1984; Blanckenhorn et al., 2000), or of fish that are fed at two feeders in a tank (Milinski, 1979, 1988; Berec et al., 2006). However, it has also been inappropriately applied to many other empirical

systems where resources form a standing crop (for a review see Tregenza (1994)).

Although the matching principle does not consider any resource dynamics (because resources are assumed to be immediately consumed), Section 2.2.1 shows that even if resources are not immediately consumed and they exist at positive densities in the system, a matching principle still holds (Lessells, 1995; Křivan, 2003). In particular, if resource densities R_i converge to an equilibrium R_i^* , the corresponding matching principle reads $p_i/p_j = r_i(R_i^*)/r_j(R_j^*)$ (see Section 2.2.1). In contrast to the fixed input rates of the preceding paragraph, not all patches need to be occupied now. For instance, when consumer densities are low, their payoff at the resource equilibrium in one patch may be higher than the payoff in the other patch and all consumers will occupy one patch only at the IFD Křivan (2003).

2.2.1. Parker's matching principle for a single species

If resources $(R_i, i = 1, ..., H)$ undergo population dynamics, their densities can be described by the system of differential equations (Lessells, 1995)

$$\frac{dR_i}{dt} = r_i(R_i) - f_i(R_i)p_iM \tag{5}$$

where r_i and f_i are the resource growth rate and the individual consumption rate (i.e. the functional response) of consumers, respectively, as functions of the resource level R_i in patch *i*. As before, p_i is the proportion of consumers in patch *i* and *M* is the (fixed) consumer density.

Let us assume that consumer payoff in any occupied patch is equal to the individual consumption rate (i.e. $V_i = f_i(R_i)$), that each patch has a resource carrying capacity K_i (i.e. $r_i(K_i) = 0$) and that the resource dynamics converges to an equilibrium R_i^* in each patch. Then, in each occupied patch, R_i^* is a decreasing function of consumer density in the patch. This follows from the identity

$$\frac{\partial (r_i(R_i) - f_i(R_i)p_iM)}{\partial R_i}\frac{dR_i}{dp_i} + \frac{\partial (r_i(R_i) - f_i(R_i)p_iM)}{\partial p_i} = 0$$

combined with the facts that $\frac{\partial (r_i(R_i) - f_i(R_i)p_iM)}{\partial R_i}$ is negative at the stable equilibrium and $\frac{\partial (r_i(R_i) - f_i(R_i)p_iM)}{\partial p_i} = -f_i(R_i)M$ is also negative (these expressions are evaluated at the equilibrium, i.e., $R_i = R_i^*$). Moreover, since the resource level R_i^* decreases as p_i increases, individual consumer payoff in patch *i* is a decreasing function of p_i . That is, the consumers are playing a habitat selection game according to Section 2.1.1. Since $V_i = f_i(R_i^*) = r_i(R_i^*)/(p_i^*M)$ at equilibrium, the IFD of this habitat selection game is a $p^* \in \Delta^H$ such that $r_i(R_i^*)/(p_i^*M) = r_j(R_j^*)/(p_j^*M) = V^*$ for all occupied patches *i* and *j*. Furthermore, individual consumer payoff in any unoccupied patch *k* is $V_k = f_k(K_k) \leq V^*$. In particular, at the equilibrium,

$$\frac{p_i^*}{p_j^*} = \frac{r_i(R_i^*)}{r_j(R_j^*)}$$

for those patches that are occupied, which is a generalized Parker's matching law (Lessells, 1995).

2.3. Dispersal dynamics

Although the IFD is assumed to be the ultimate outcome of animal dispersal, there is no explicit dispersal process associated with this concept. In biological applications of game theory, an explicit game dynamics was introduced by Taylor and Jonker (1978). These dynamics, known as the "replicator equation" describe the changing proportion of various phenotypes in an exponentially growing population. These authors proved that a dynamically stable equilibrium (the "stability" here means (local) asymptotic stability of the equilibrium with respect to the replicator equation) must be a NE and that an ESS is a stable equilibrium. These results form part of what is now called the Folk Theorem of Evolutionary Game Theory (Cressman, 2003). They also showed that there are evolutionary games that have stable (with respect to the replicator equation) NE that are not ESS. This clearly shows that the ESS stability concept of Section 2.1 can differ from the dynamic stability concept once explicit rules (e.g., the replicator equation) for dispersal are given. However, for the single-species habitat selection game, the IFD is the only NE and it is also an ESS. Thus, the Folk Theorem implies that the IFD is the only stable equilibrium of the replicator equation.

Unfortunately, the replicator equation is not a realistic dynamics for dispersal between patches. In particular, under this dynamics, patches which are empty are never colonized. This led Cressman and Křivan (2006) to consider the following wider class of dispersal dynamics for habitat selection models (and study the dynamic stability of the IFD under them). Suppose the dispersal process is described by

$$\frac{dp}{dt} = I(p)p - p \tag{6}$$

where I(p) is the $H \times H$ dispersal matrix that describes the probability of dispersal between patches (i.e. $I_{ij}(p)$ is the probability an individual from patch *j* disperses to patch *i* in unit time).²

An equivalent formulation of Eq. (6) in terms of patch densities $m = (m_1, \ldots, m_H)$ that distinguishes between immigration and emigration is

$$\frac{dm_i}{dt} = \sum_{j=1}^H I_{ij}(m)m_j - \sum_{j=1}^H I_{ji}(m)m_i = \sum_{j=1}^H I_{ij}(m)m_j - m_i.$$

Here the first term in the summation describes immigration to patch i and the second term describes emigration from patch i. The dispersal process will then depend on the properties of the dispersal matrix (i.e. on the particular dispersal rules chosen). The remainder of this section considers two such classes of dynamics.

2.3.1. Best and better response dynamics

First, consider dispersal under the assumption that "...each individual will go to the habitat of highest suitability" (Fretwell

and Lucas, 1970, p. 22). Since their ideal animals move directly without cost to the patch with the highest payoff, the corresponding dispersal matrix is $I_{ij}(p) = 1$ if patch *i* is the only patch with highest payoff and $V_j(p) < V_i(p)$. The dispersal dynamics (6) exhibiting such ideal movement are called the best response dynamics. These actually become a differential inclusion (Section 2.3.1.1 below; Hofbauer and Sigmund, 1998) when there is more than one patch with the highest payoff.³ Clearly, the best response dynamics satisfy the following two conditions:

- (i) animals never disperse to patches with lower payoff,
- (ii) from every occupied patch some animals always disperse to a patch with the highest payoff.

However, the two conditions are also satisfied by animals who do not know the payoffs in all patches and so cannot be ideal. In particular, this is the case if animals scan patches at random and switch to the sampled patch only when their payoff increases. Such locally myopic dispersal rules are biologically much more plausible than the best response dynamics.

By showing that $W(p) = \max_{1 \le i \le H} V_i(p)$ is a strictly decreasing Lyapunov function along trajectories of (6) with a global minimum at the IFD p^* , Cressman and Křivan (2006, Appendix B) proved the IFD is globally asymptotically stable for any dispersal dynamics (6) satisfying (i) and (ii). This shows that dispersal rules based on local patch knowledge are sufficient to achieve the IFD or, to rephrase, the IFD can be established by animals who do not have a global knowledge of the environment and so do not always exhibit ideal movement.

Interestingly, Fretwell and Lucas (1970, later on p. 22) already alluded to the fact that the IFD could be achieved by animals who do not move directly to the best patch as long as their non-ideal movement is to a patch with higher payoff. Thus, the class of dynamics that satisfies conditions (i) and (ii) is quite natural for habitat selection games but, as far as we know, has not been given a name in the literature. We propose this class be called the "better response dynamics" as animal movement is always towards patches with higher payoff.⁴

Fig. 2A shows dispersal dynamics describing animal distribution among three patches in the probability triangle Δ^3 (i.e. $p_1 + p_2 + p_3 = 1$) for three initial animal distributions that

² We set $I_{ii}(p) = 1 - \sum_{j=1, j \neq i}^{H} I_{ji}(p)$ so that I(p) is a stochastic matrix whose column sums are all equal to one. In particular, we assume the time unit to be small enough so that $I_{ii} \ge 0$.

³ These best response dynamics can also be multiplied by a positive constant (to reflect the time scale of moving to the best patch) without affecting the final outcome of the dispersal process. In the above discussion, it is implicitly assumed that there are solutions to the dispersal dynamics (6) for each initial population distribution p (i.e. a trajectory starting at p that satisfies (6) and is defined for all positive t). Mathematically, this requires either some continuity assumption on the vector field I(p) - p or, in the case of differential inclusions, an assumption on the continuity of the set-valued map I(p) - p (e.g., see the set BR(p) in Section 2.3.1.1). Thus, strictly speaking, our dispersal dynamics refer to those for which solutions exist for each initial population.

⁴ In hindsight, a more descriptive name for the best response dynamics for the habitat selection game is "ideal movement dynamics" in that they are based on the Fretwell and Lucas (1970) assumption of ideal free animals. Similarly, alternative phrases such as "monotone movement dynamics" may be more descriptive than better response dynamics for habitat selection games. Furthermore, trajectories of these dynamics are "monotone" for the differential inclusion in the sense of Aubin and Cellina (1984, p. 181). Instead, we will use best (and better) response dynamics in keeping with game-theoretic terminology.



Fig. 2. Three trajectories for distribution dynamics in a three-patch environment. Panel A shows the best response dynamics at a fixed population density (M = 10) when $V_i(p_i M) = r_i(1 - p_i M/K_i)$. Trajectories converge to the IFD ($p_1^* = 0.50$, $p_2^* = 0.35$, $p_3^* = 0.15$) at M = 10. Panels B and C show combined dispersal and population dynamics described by model (9). Panel B shows the case where population dynamics are fast when compared with dispersal dynamics ($\nu = 0.001$) and panel C shows the opposite case where population dynamics are slow when compared with dispersal dynamics ($\nu = 0.001$) and panel C shows the opposite case where population dynamics are slow when compared with dispersal dynamics ($\nu = 10$). In both cases, trajectories converge to the IFD ($p_1^* = 0.37$, $p_2^* = 0.33$, $p_3^* = 0.30$ and M = 27) corresponding to the patch carrying capacities. The trajectories are shown in a probability simplex phase space (p_1 , p_2 , p_3) where $0 \le p_i \le 1$ and $p_1 + p_2 + p_3 = 1$. The vertices of the triangle correspond to the pure strategies where all individuals occupy one patch only. Along the sides of the triangle, one patch is not occupied. Other parameters used in simulations: $r_1 = 1$, $r_2 = 0.8$, $r_3 = 0.6$, $K_1 = 10$, $K_2 = 9$, $K_3 = 8$.

correspond to the situations in which, initially, only one patch is occupied. In this case the dispersal dynamics are described by the best response dynamics (Section 2.3.1.1). We observe, according to our prediction, that trajectories converge to the IFD (shown as the solid dot in Fig. 2A). Let us consider the trajectory with initially all animals in patch 1 (which is the trajectory that starts at the left lower corner in Fig. 2A). Initially, patch 2 is the most profitable patch and animals disperse from patch 1 to patch 2 only. As animal payoff in patch 2 decreases, at a certain time instant patch 3 becomes as profitable as patch 2. From then on, animals disperse from patch 1 to the other two patches in such a way that the payoff in patch 2 and patch 3 is the same (and higher than it is in patch 1).

If all patches are occupied at the IFD, the population reaches this IFD after some finite time and remains at this distribution even though animal dispersal between these equal payoff patches continues. Specifically, the dispersal rates are then equal to $I_{ij}(p^*) = p_i^*$ (Cressman and Křivan, 2006). These rates (or the same positive multiple of them) are called "balanced dispersal rates" by Holt (1985) (see also McPeek and Holt (1992), Padrón and Trevisan (2006) and DeAngelis et al. (2007)) who shows that constant balanced dispersal rates (i.e. $I_{ij}(p) = p_i^*$ for all $p \in \Delta^H$) when total population size is at carrying capacity cannot be invaded by mutants using different constant dispersal rates under the combined population-dispersal dynamics (see Section 2.4). It is tempting to call these "evolutionarily stable" dispersal rates but we think it is inappropriate to use the term ESS in this sense since the terminology would then depend on the specified dynamics (see the discussion at the end of Section 2.3.2). From our perspective, the IFD is an ESS since it satisfies the static payoff comparisons (2) of the habitat selection game introduced in Section 2.1. Its biological relevance is then bolstered by its dynamic stability under many different models of dispersal dynamics.

Fig. 2A also shows another common characteristic of trajectories when the dispersal process (6) is a better response dynamics with continued dispersal between patches with the

highest payoff; namely, their sharp corners when they reach lines where two patches have the same highest payoff (shown as dashed lines in Fig. 2A). In what follows we call these lines equal payoff lines. The sharp corners result from dispersal rates that are discontinuous functions of animal distribution along the equal payoff lines. In other words, if two (or more) patches have the same highest payoff, then either there is no dispersal between these patches (in which case these dispersal rates are zero along the equal payoff line), or dispersal rates change abruptly when animal distributions vary from one side of this line to the other while animals still disperse. That is, if animals never disperse to a patch with a lower payoff (e.g., when they are ideal) it is not possible that dispersal rates are continuous functions of species distribution and animals still disperse between patches with the same highest payoffs.

2.3.1.1. Best response dynamics. Under Fretwell and Lucas (1970) assumptions, animals are ideal in the sense that they know perfectly their environment and they move to one of the patches with the highest payoff. If $V_i(p)$ is the animal payoff in patch *i* when the proportion of animals in this patch is p_i , then this type of dynamics is also called "the best response dynamics" (Hofbauer, 1995; Hofbauer and Sigmund, 1998) and it is described by a differential inclusion

$$\frac{dp}{dt} \in BR(p) - p \tag{7}$$

where BR(p) is the set of best response strategies to the current distribution $p = (p_1, ..., p_H)$. That is, BR(p) is defined as the set of those patches where the animal payoff maximizes. If such a patch is defined uniquely (i.e., $V_i(p) > V_k(p)$ for any patch k different from patch i), then the set BR(p) is a vector of zeros except at the *i*th position where it is 1. That is, BR(p) - p is the vector field for the differential equation in this case. If there is more than one patch with the same maximal payoff, then $BR(p) = \{(u_1, ..., u_H) \in \Delta^H | u_1V_1(p) + \cdots + u_HV_H(p) \ge$ $\hat{v}_1V_1(p) + \cdots + \hat{v}_HV_H(p)$ for all $(\hat{v}_1, ..., \hat{v}_H) \in \Delta^H\}$. Thus, if dispersal matrix I(p) is such that all entries in the *i*th row are equal to the *i*th component of the best response u_i , then the dispersal dynamics (6) become the best response dynamics (7). Since $V_i(p)$ are continuous functions of p, solutions for (6) exist for all positive time although these trajectories may not be unique for a given initial condition. A typical example of the best response dynamics for three patches is shown in Fig. 2A where we set $V_i(p) = r_i(1 - p_iM/K_i)$. Since these payoff functions are linear in p, best response trajectories are piecewise linear curves consisting of straight line segments in the direction of the current best response if this is unique (Hofbauer, 1995; Hofbauer and Sigmund, 1998). When two patches currently have the highest payoff in a three-patch system, the trajectory moves along the equal payoff line at a rate that can be calculated explicitly (Appendix C, Cressman and Křivan, 2006).

2.3.2. Suboptimal dispersal

Better response dynamics assume that animals never make a wrong decision as to where to disperse in that they never disperse to a patch with a lower payoff. This is often unrealistic (Hugie and Grand, 1998), in which case it is more plausible to assume that the non-ideal movement of animals also includes suboptimal dispersal from patches with higher payoffs to patches with lower payoffs. Several authors (e.g., Sutherland (1983), Abrahams (1986), Houston et al. (1995), Hugie and Grand (1998), Briggs and Hoopes (2004) and Křivan (in press)) have investigated theoretically dispersal dynamics where the two conditions (i) and (ii) are replaced by

- (i)' the dispersal rates between any two patches are positive,
- (ii) the dispersal rate is a continuous function of animal distribution,
- (iii)' the probability of dispersal from one patch to another patch increases as the payoff in the new patch increases and decreases as the payoff in the current patch increases.

Notice that, with some suboptimal (e.g., random) dispersal, continuity of the dispersal matrix no longer implies that there cannot be any dispersal between patches with the same payoff. Hugie and Grand (1998) showed that, for two patches, conditions (i) –(iii) imply there is an equilibrium of the dispersal process which is stable with respect to dispersal dynamics (6). This result has been extended to any number of patches by Cressman and Křivan (2006). However, due to condition (i), there may be some random dispersal which shifts the equilibrium of model (6) off the IFD, causing fewer animals to be in the better patch than predicted by the IFD. That is, dispersal models satisfying conditions (i) –(iii) are examples under which the ESS of the habitat selection game is often not dynamically stable. Such "undermatching" when animals underuse better patches and overuse poorer patches was observed in many experiments (for a review see Kennedy and Gray (1993)). For two patches, the extent of undermatching increases as the degree of random animal movement in the population increases. Thus, the difference between the predicted IFD and the observed animal distribution can be used as a measure of random dispersal versus better response dispersal in animal movement between patches.

The results of the preceding paragraph show there is a fundamental difference between the evolutionary stability of the IFD and dynamic stability of the IFD with respect to dispersal dynamics described by model (6). As discussed above, the evolutionary stability of the IFD refers to its gametheoretic properties. On the other hand, dynamic stability of the IFD refers to stability with respect to the dispersal process. The IFD is dynamically stable for the intuitive class of better response dynamics of Section 2.3.1 but not for all possible dispersal dynamics (i.e. those modeling non-ideal animal movement satisfying conditions (i) -(iii)). Thus, ESS stability is independent of the particular dispersal process and so the result of dispersal can often be predicted without explicitly describing the dispersal process itself (a major goal of evolutionary game theory; Maynard Smith, 1982). Moreover, for single-species habitat selection, the NE is unique and automatically an ESS. Thus, the IFD, NE and ESS concepts are identical for these models. As we will see in Section 3, this is no longer true for two-species models because there will be distributions that are NE but not ESS stable. We argue there that such a distribution cannot be called an IFD.

2.4. The single-species IFD as a population concept

Although the IFD is assumed to result from animal dispersal between habitats, the IFD can be reached solely due to demographic changes without any dispersal as noted by Cressman and Křivan (2006). To see this, assume that per capita density-dependent population growth (i.e. individual fitness) in each patch is directly proportional to the decreasing payoff function in that patch, which is the usual assumption that links behavioral and population ecology. That is,

$$\frac{dm_i}{dt} = m_i V_i(m_i) \tag{8}$$

where m_i is population density in patch *i*.⁵ Moreover, assume that there exists a single carrying capacity in each patch to which the population density converges. For example, the classical logistic population growth satisfies these assumptions. At these carrying capacities, the overall population neither increases or decreases and so the average payoff is equal zero. All patches that were initially occupied stay occupied at the equilibrium because the animal fitness would be positive in any patch where the population was decreasing to zero. Since better patches support higher number of individuals, fitness in all occupied patches is the same and equal to zero at the population equilibrium. That is, if all patches are initially occupied, then the IFD is achieved at the population equilibrium without any dispersal between patches. Furthermore, the global asymptotic stability of this IFD is an immediate consequence of the negative density dependence of $V_i(m_i)$ in (8).

The dispersal effect can now be added to dynamics (8) by including parameter v that characterizes the relative time scale

⁵ Notice that, in this section, V_i is no longer a function of p since the total population size M is now changing. Instead, V_i is written as a function of $m_i = p_i M$.

between the population and dispersal processes. The combined population-dispersal dynamics are then

$$\frac{dm_i}{dt} = m_i V_i(m_i) + \nu \left(\sum_{j=1}^H I_{ij}(m)m_j - m_i\right).$$
(9)

For v = 0, we revert to the model of no dispersal given by (8) whereas, for large values of v, dispersal acts very quickly by driving the population to its equilibrium distribution for current total population size. The population distribution then tracks the changes in total population size until the population size reaches its equilibrium. For any positive values of v, Cressman and Křivan (2006) assert that population densities in this combined model still converge to habitat carrying capacities provided the dispersal process is based on best/better response dynamics that drive the population distribution to the IFD for each fixed population size.⁶

The convergence of the combined population-dispersal dynamics to the IFD is documented in Fig. 2B and C. We remark that without any dispersal (i.e. when $\nu = 0$ in model (9)), the three trajectories in these panels would never leave the vertices of the triangle because the initial distributions are such that only one patch is occupied. Because there is a small amount of dispersal in Fig. 2B ($\nu = 0.001$), all patches will eventually be occupied. However, because only a small proportion of animals disperse, it takes a relatively long time before it is clearly seen in the figure that the two patches that were originally unoccupied have animals in them. In panel C (v = 10), all three trajectories converge quickly to the IFD at the initial population density and then follow the IFD animal distribution as a function of the overall population abundance until they reach the IFD corresponding to the patches' carrying capacities. The solid dot in panels B and C shows the IFD at this population equilibrium.

In summary, for the single-species habitat selection game, we see that the game-theoretic IFD/ESS concept is relevant for the combined population-dispersal process (and not only for the distribution dynamics at fixed population size which is the usual situation for evolutionary game theory). As we will see, this result is no longer true for two-species habitat selection games.

2.5. Both resource and consumers undergo population dynamics

In the previous section, we modeled consumer population dynamics without explicitly considering resource dynamics. In fact, such models assume that resource equilibrates very quickly with current consumer numbers. This assumption leads to decreasing per capita consumer growth rates with increasing density (e.g., logistic growth) in each patch. On the contrary, Parker's matching law considers resource dynamics while total consumer population numbers are assumed to be fixed. This is reasonable when the time scale for the resource dynamics is much shorter than the consumer life span, or when consumer numbers are relatively stable due to such effects as alternative resources (Polis and Hurd, 1996).

In this section, we briefly consider the game-theoretic consequences of a two-patch model where both resources and consumers undergo population dynamics, but only consumers are adaptive foragers and so may disperse between patches. Specifically, suppose that the resources R_i in patch *i* as well as consumers undergo population dynamics described by the classical Lotka–Volterra predator–prey two-patch model. Then

$$\begin{aligned} \frac{dR_1}{dt} &= R_1(r_1 - \lambda_1 u_1 M), \\ \frac{dR_2}{dt} &= R_2(r_2 - \lambda_2 u_2 M), \\ \frac{dM}{dt} &= (e_1 \lambda_1 R_1 - d_1) u_1 M + (e_2 \lambda_2 R_2 - d_2) u_2 M \end{aligned}$$

where r_i and d_i are the instantaneous per capita growth rate of prey and mortality rate of predators in patch *i*, respectively, and u_i ($u_1 + u_2 = 1$) denotes the probability that a predator will be in patch *i*. In particular, there is a linear functional response of consumers to the resource levels in each patch (cf. (5)). Furthermore, the individual payoff $e_i\lambda_i R_i - d_i$ to consumers in patch *i* depends only indirectly on consumer density there through current resource levels.

Křivan (1997) considered the situation where the consumers move instantaneously to the patch with the highest payoff (i.e. $u_1 = 1$ when $e_1 \lambda_1 R_1 - d_1 > e_2 \lambda_2 R_2 - d_2$ and $u_1 = 0$ when $e_1 \lambda_1 R_1 - d_1 < e_2 \lambda_2 R_2 - d_2$). In this case, the consumer distribution between the two patches track their IFD for current resource levels. In fact, consumers then drive the resource to levels where consumer fitness is the same in both patches (i.e. as t increases, R_1 and R_2 are such that $e_1\lambda_1R_1 - d_1$ approaches $e_2\lambda_2R_2 - d_2$). From the result of Section 2.4, one might expect this two-patch predator-prey system restricted to the invariant planar surface where $e_1\lambda_1R_1$ $d_1 = e_2 \lambda_2 R_2 - d_2$ to evolve to the consumer population equilibrium $M = r_1/\lambda_1 + r_2/\lambda_2$ at resource level R_i = $d_i/(e_i\lambda_i)$ in patch *i*. However, as shown by Křivan (1997) (see also Fig. 1A in Křivan and Eisner (2006)), the resource and consumer densities actually fluctuate indefinitely along closed Lotka-Volterra orbits around this (neutrally stable) equilibrium.⁷ It is clear that along such an orbit individual consumer payoff in patch *i* will periodically fluctuate, i.e., it will not satisfy the condition imposed by Fretwell and Lucas that payoffs decrease with increasing population densities. Thus, interspecific effects between consumers and resources

⁶ This result follows from the fact that $W(p, M) = \max_{1 \le i \le H} V_i(p_i M)$ is then strictly decreasing if it is positive and $w(p, M) = \min_{1 \le i \le H} \{V_i(p_i M) | p_i > 0\}$ is strictly increasing if it is negative. For instance, if W(p, M) is positive and attains this value only in patch *i*, (9) implies that $\sum_{j=1}^{H} I_{ij}(m)m_j - m_i \ge 0$ with strict inequality if $m_j \ne 0$ for some $j \ne i$. Furthermore, (9) implies $m_i(t)$ is increasing and so $W = V_i(m_i)$ is decreasing. Combined with the analogous result for *w*, we see that *W* and *w* both converge to 0 and this is the IFD at population equilibrium.

⁷ An ecologically interesting observation is that the same system where consumer preferences for either patch are fixed (and different from $u_i = r_i/(\lambda_i M)$) is impermanent in the sense that one resource is always outcompeted by the other resource due to strong apparent competition (Holt, 1984).

cannot be ignored, a motivation for the two-species analysis of Section $3.^{8}$

This example also clearly shows that consumer aggregation in patches with the highest payoffs can promote species coexistence without promoting species stability. Furthermore, Holt (1984) proved that optimal habitat selection by consumers decouples the resources in different patches (even when prey growth rate is density dependent). This is because the number of consumers found in any given patch exactly reflects the productivity of that patch (i.e. at the equilibrium of the above model, $m_i = u_i M = r_i / \lambda_i$ exactly as if there was no consumer movement between patches).

Numerical analysis shows that a similar model where the linear functional response is replaced by the Holling type II functional response (i.e. $f_i(R_i) = \lambda_i R_i/(1 + h_i\lambda_i R_i)$ in (5) where h_i is the predator handling time of the resource in patch *i*) also promotes species coexistence. As the handling time increases, the population eventually undergoes chaotic fluctuations (Křivan and Eisner, 2006). Related results of Fryxell and Lundberg (1997), where a more gradual movement to a less profitable patch) is assumed, also support this prediction (see also similar models reviewed in Bolker et al. (2003)).

3. Two-species IFD

As species do interact, it is important to understand what is the analogue of the single-species IFD for two and more species. As we will see, this is not as straightforward as in Section 2, even for the two-species systems considered here. First, let us define the (two-species) habitat selection game.⁹ For this, we need to describe the individuals' strategies and their payoff functions.

Let *M* and *N* be the fixed positive population sizes of species one and two respectively. Individuals in both species have the same set of *H* pure strategies but their payoff functions (which depend on the distributions *p* and *q* of species one and two respectively among the *H* patches) differ. That is, we have a (two-species) population game (Sandholm, 2007) with V_i and W_i as the payoff functions in patch *i* of species one and two respectively. Moreover, V_i and W_i depend only on the pair (p_i, q_i) of proportions of species one and two in habitat *i*.

At a minimum, the IFD must satisfy the analogue of the single-species definition; namely, the payoffs for all individuals of species one (respectively, species two) in any patch occupied by this species must be the same and at least as high as the individual payoff for any unoccupied patch of species one (respectively, species two). (Otherwise, there would be an

incentive for individuals to move to another patch.) That is, if (p^*, q^*) is an IFD, we require

$$V_{i}(p^{*}, q^{*}) = V_{j}(p^{*}, q^{*}) \ge V_{k}(p^{*}, q^{*})$$

if $p_{i}^{*}p_{j}^{*} > 0$ and $p_{k}^{*} = 0$
 $W_{i}(p^{*}, q^{*}) = W_{j}(p^{*}, q^{*}) \ge W_{k}(p^{*}, q^{*})$
if $q_{i}^{*}q_{i}^{*} > 0$ and $q_{k}^{*} = 0$.

It is straightforward to show that this is equivalent to the requirement

$$p \cdot V(p^*, q^*) \le p^* \cdot V(p^*, q^*) \text{ and} q \cdot W(p^*, q^*) \le q^* \cdot W(p^*, q^*)$$
(10)

for all $(p,q) \in \Delta^H \times \Delta^H$. These latter inequalities are the definition that the pair of (mixed) strategies (p^*, q^*) is a NE of the habitat selection game. Alternatively, a NE is a distribution (p^*, q^*) whereby p^* is a single-species IFD for species one given that species two is distributed at q^* and q^* is a single-species IFD for species two given that species one is distributed at p^* .

These NE of the habitat selection game have been called by several other names in the literature such as "joint IFD" (e.g., Křivan and Sirot (2002), Focardi et al. (2003) and Morris (2004)) and "candidate IFD" (Abrams et al., 2007). In fact, several authors (e.g., Auslander et al. (1978), van Baalen and Sabelis (1993), Křivan (1997), Brown (1998), van Baalen and Sabelis (1999) and Abrams (2007)) define the IFD as a NE. However, Cressman et al. (2004) and Cressman and Křivan (2006) show conclusively that this is not appropriate since such an IFD definition does not imply any analogue of the singlespecies ESS stability condition (2). For these reasons, we prefer to continue using the game-theoretic terminology for the NE and reserve the term IFD to only use in its unmodified form as a NE that satisfies further stability properties.

The "correct" stability condition for the IFD is most clear for the two-patch competitive systems of the following section. We develop the game-theoretic perspective of the IFD condition for such systems in Section 3.3 after discussing issues that already arise for two-patch predator–prey systems in Section 3.2.

3.1. The two-patch habitat selection game for two competitive species

We assume that the two species compete in each patch. By this, we mean that individual payoff in patch i (i = 1, 2) is a decreasing function of the density of conspecifics and heterospecifics in this patch. For example, if individual payoff is linear in these densities, the payoff functions in patch i may then be written in the Lotka–Volterra form (Křivan and Sirot, 2002; Cressman et al., 2004)

$$V_i(p,q) = r_i \left(1 - \frac{p_i M}{K_i} - \frac{\alpha_i q_i N}{K_i} \right)$$

$$W_i(p,q) = s_i \left(1 - \frac{q_i N}{L_i} - \frac{\beta_i p_i M}{L_i} \right).$$
(11)

Here, positive parameters α_i (respectively, β_i), are interspecific competition coefficients, r_i (respectively, s_i) are the intrinsic

 $^{^{8}}$ In Section 3, we consider the related two-patch predator–prey model where both consumers (predators) and resources (prey) disperse between patches. In Section 3.2, the total density of predators and of prey is fixed (i.e. there is only dispersal between patches). In Section 3.6, we also discuss such models combined with population dynamics.

⁹ For the remainder of this section, it will be understood that phrases such as "habitat selection game", "NE", "IFD" and "ESS" refer to the two-species concepts unless otherwise indicated.



Fig. 3. Nash equilibria for two competing species. Only in panel A is the interior NE an IFD (i.e. an ESS). In panel B there are two other boundary NE that are IFDs since they are both ESSs (the NE at the lower right vertex is actually a strict NE). Panel C shows the case where the two equal payoff lines coincide and infinitely many NE exist, each one being a weak ESS. The dashed and dotted lines are the equal payoff lines for species 1 and species 2, respectively. NE are shown as circles (either empty or filled). The IFDs are the filled circles in panels A and B.

per capita population growth rates and K_i (respectively L_i) are the environmental carrying capacities. All these parameters are assumed to be patch specific.

The NE structure of the two-patch habitat selection game relies heavily on the analysis of the two equal payoff lines, one for each species. The equal payoff line for species one is defined to be those $(p,q) \in \Delta^2 \times \Delta^2$ for which $V_1(p,q) =$ $V_2(p,q)$. Similarly, the equal payoff line for species two satisfies $W_1(p,q) = W_2(p,q)$. Since payoffs are linear functions and since $p_2 = 1 - p_1$ and $q_2 = 1 - q_1$, these are lines in the coordinates p_1 and q_1 as indicated in Fig. 3. If the two equal payoff lines do not intersect in the unit square of Fig. 3, the two species cannot coexist in both patches at a NE. This means that at least one species will reside in a single habitat only. If only one species (say, species one) is entirely in its higher payoff patch, then species two will distribute itself according to the single-species IFD conditional on species one being in its single patch. That is, there is then exactly one NE, which must automatically be on the boundary of the unit square (see Figure 2 in Křivan and Sirot (2002)).

Fig. 3 shows more interesting cases; namely, where the two equal payoff lines intersect inside the unit square. Notice that, in all cases, both equal payoff lines must have negative slopes.¹⁰ Points of intersection in the unit square of the equal payoff lines are automatically NE. A point on the boundary of the unit square is a NE if and only if all nearby boundary arrows, as well as all nearby interior arrows corresponding to the species that is only present in one patch at the NE, are directed towards it. The arrows are used to indicate which patch has the higher payoff in a given region (a horizontal arrow to the right means patch one has higher payoff for species one whereas a downward arrow means patch two has the higher payoff for species two). Thus, the circles (both empty and filled) in Fig. 3 give all NE.

¹⁰ If p_1 and q_1 both increase, then V_1 decreases and V_2 increases and so payoffs to species one in patches 1 and 2 can no longer be equal.



Fig. 4. The best response dynamics for the two-patch competitive systems with a unique interior NE. Trajectories are shown as solid curves and the vector field is shown as short arrows. In panel A ($\alpha_1 = 0.1, \alpha_2 = 0.1, \beta_1 = 0.9, \beta_2 = 0.9$), the animal distribution that corresponds to the interior NE is also an IFD, while in panel B ($\alpha_1 = 0.8, \alpha_2 = 0.8, \beta_1 = 4, \beta_2 = 4$) the interior NE is unstable and there are two boundary IFDs. Other parameters: $K_1 = 15, K_2 = 10, L_1 = 12, L_2 = 10, r_1 = 1, r_2 = 1, s_1 = 1, s_2 = 1, M = 3, N = 3, \nu = 2, \xi = 1$.

Notice that the coincident equal payoff lines in panel C consists entirely of empty circles.

The central issue for us is which, if any, NE is stable, either in the ESS sense or dynamically stable under some class of dispersal dynamics. We postpone discussing ESS stability until Section 3.3 and begin our analysis here with the best response dynamics.

The single-species dispersal dynamics (6) can be easily generalized for two (or more) species. These dispersal dynamics, at fixed population densities M and N of the two species, are described by a system of equations

$$\frac{dp}{dt} = v(I(p,q)p - p)$$

$$\frac{dq}{dt} = \xi(J(p,q)q - q)$$
(12)

where $p = (p_1, \ldots, p_H)$ and $q = (q_1, \ldots, q_H)$ are distributions of species one and two, respectively, and I and J are dispersal matrices. As before, the entries of these dispersal matrices describe the transition probabilities that an animal moves from one patch to another patch in a unit of time. For instance, under the ideal movement modeled by the best response dynamics, $I_{ii}(p,q) = 1$ if patch *i* is the only patch with the highest payoff for species one and otherwise $I_{ii}(p,q) = 0$. Because the time unit can be different for each species (e.g., due to differences in speed of movement), we introduce positive parameters ν and ξ to reflect different time scales. Thus, dispersal dynamics are defined by some specific dispersal rules given by transition matrices I and J and by time scales ν and ξ . For example, transition matrices can correspond to the best (respectively, better) response dynamics. In this case, we call (12), for all possible positive choices of ν and ξ , the class of best (respectively, better) response dynamics. We remark that the scaling constants do not influence the position of equal payoff lines, but they may influence stability of the dispersal equilibrium of model (12).

The trajectories of best response dynamics all evolve in the direction of the arrows given in Fig. 3 (cf. the vector field in Fig. 4). From Figs. 3 and 4, it is clear that the equal payoff lines play a similar role for these dispersal dynamics (that model evolving population distributions) that isoclines do for the population dynamics of a two-species (competitive) system in a single patch. In particular, trajectories can only cross the species one equal payoff line (dashed line in Figs. 3 and 4) in the vertical direction in Fig. 4 (just as trajectories in the single patch population dynamics only cross the species one isocline in the vertical direction). By the same reasoning as used in isocline analysis, we see that every trajectory of the best response dynamics for payoffs given by (11) converges to a NE.

Ignoring the degenerate case depicted in Fig. 3 (panel C) for the moment means that every NE on the boundary is asymptotically stable (this remains true for all possible pairs of equal payoff lines and not only those shown in Fig. 3). Qualitatively, panels A and B show all cases where there is a single NE in the interior of the unit square. It is clear that all trajectories that start in the triangular region above and to the left of this interior NE remain in this region and converge to it (respectively, diverge from it) in panel A (respectively, panel B). In particular, panel B provides a robust example to illustrate that the IFD definition for two-species systems must require it to be more than a NE. On the other hand, in panel A, trajectories that start in any of the the other three regions also converge to the interior intersection point. Thus, the interior NE is (globally) asymptotically stable if and only if the equal payoff line for species one is steeper than that for species two (see Fig. 4).¹¹

¹¹ This statement is also true for the situation depicted in Fig. 3C. There, all points on the common equal payoff lines are rest points of the best response dynamics and so none is asymptotically stable. Furthermore, in panel C, every trajectory of these dynamics converges to a single point on the overlapping equal payoff lines but this point depends on the initial conditions of the trajectory.



Fig. 5. Two-patch predator-prey systems with an interior NE (filled or empty circle). The vertical line through the NE is the predator equal payoff line. The prey equal payoff curve corresponds to Lotka–Volterra growth rates in panel A (horizontal, V_i and W_i given by (14)), to density-dependent growth in panel B (negative slope, $V_i = r_i (1 - \frac{p_i M}{K_i} - \alpha_i q_i N)$, $K_1 = 15$ and $K_2 = 10$), and to the Holling type II functional response in panel C (positive slope, $h_1 = 0.9$, $h_2 = 1$ in (15)). The horizontal and vertical arrows indicate the directions under best (and better) response dynamics. Trajectories (shown for the best response dynamics with $v = \xi = 1$) evolve counterclockwise around the NE. Filled circles are IFDs (and weak ESSs). As shown in Section 3.3.1, IFDs are asymptotically stable for every best response dynamics whereas the non-IFD in panel C is unstable for some choices of v and ξ (e.g., trajectories diverge from the interior NE and converge to a limit cycle in Panel C). Other parameters: M = N = 10, $r_1 = r_2 = 1$, $s_1 = s_2 = 1$, $\alpha_1 = \alpha_2 = 0.1$, $\beta_1 = \beta_2 = 0.9$, $\xi = v = 1$.

Cressman et al. (2004) show this condition is equivalent to

$$r_{1}s_{1}K_{2}L_{2}(1 - \alpha_{1}\beta_{1}) + r_{1}s_{2}K_{2}L_{1}(1 - \alpha_{1}\beta_{2}) + r_{2}s_{1}K_{1}L_{2}(1 - \alpha_{2}\beta_{1}) + r_{2}s_{2}K_{1}L_{1}(1 - \alpha_{2}\beta_{2}) > 0.$$
(13)

Fig. 4 shows the actual best response trajectories for a particular choice of time scales.

It is worth noting at this point that there are (infinitely) many possible choices of dispersal dynamics that correspond to equal payoff lines given through (11) and shown in Fig. 3. The best response dynamics shown in Fig. 4 are just one possibility. The important point is that, although different dispersal rules lead to different trajectories of the distribution dynamics (12), the above argument based on the position of the equal payoff lines extends to the class of best and better response dynamics, because all these dispersal dynamics have the same equal payoff lines as the best response dynamics regardless of time scales and particular realizations of transition matrices. For instance, the triangular regions to the upper left and lower right of the interior NE in Fig. 3, panels A and B, remain invariant and so there can be no oscillation around this NE (as opposed to that shown in Fig. 5 for predator–prey systems). In particular, the eventual outcome from dispersal is a NE distribution under the class of best and better response dynamics.

In summary, all two-patch competitive systems have equal payoff lines that either do not intersect in the unit square (see Figure 2 in Křivan and Sirot (2002)) or do intersect (Fig. 3). In the first case there is exactly one NE at which at least one species occupies one patch only and this equilibrium is globally asymptotically stable under the class of best (and better) response dynamics. If equal payoff lines intersect at a single point in the unit square, then there is either exactly one NE (panel A) which is globally asymptotically stable under the same dynamics, or (panel B) there are two locally asymptotically stable boundary NE. Thus, for a two-patch competitive system, the IFD definition must characterize every boundary NE (except in the case of Fig. 3 panel C) as an IFD as well as declaring an interior NE as an IFD if and only if inequality (13) holds. Ideally, we would like a condition similar to the single-species ESS inequality (2) as our IFD definition. This is given in Section 3.3 after considering twopatch predator–prey systems.

The above analysis assumes that individual payoff functions in patch *i* are linear functions of the species proportions, p_i and q_i , in this habitat. For general non-linear payoff functions that still correspond to competitive species (i.e. they are decreasing functions of p_i and of q_i), equal payoffs for either species in a two-patch system occur along decreasing curves in the p_1, q_1 coordinate system. These two curves may intersect several times in the unit square, all of which are then NE. If we ignore cases where the curves intersect with the same tangents,¹² then a NE in the interior of the unit square is locally asymptotically stable for the class of best response dynamics if and only if the tangent line to the equal payoff line of species one is steeper than that of species two. In fact, there is at least one asymptotically stable NE (which must be on the boundary if there is none in the interior). The analysis of this section suggests a definition of the IFD which is based on the best response dynamics. Namely, a NE would be classified as an IFD if it were stable for the class of best response dynamics.¹³

3.2. Two-patch predator-prey systems

First, suppose individual payoff in each patch is given as the per capita growth rate of a Lotka–Volterra predator–prey model (Hofbauer and Sigmund, 1998). That is, the payoff functions of the prey and predator species in patch *i* are

$$V_i = r_i(1 - \alpha_i q_i N) \quad \text{and} \quad W_i = s_i(-1 + \beta_i p_i M) \tag{14}$$

respectively. Since the V_i and W_i exhibit no intraspecific effects on individual payoff, the equal payoff lines for the prey (species one) and the predator (species two) are horizontal and vertical, respectively. If one of these lines (say the vertical line for the predator) does not intersect the unit square, then any NE has all of the predators in one patch. It is an interesting observation that at this NE, all the prey must also be in only one patch (which may or may not be the same one where the predators are). That is, there is exactly one NE (it is at one of the vertices of the unit square) and it is straightforward to show that this NE is globally asymptotically stable for the best response dynamics. This predicts that distributions where either prey only, or predators only are distributed across two patches should not be observed in nature, provided both species are mobile.

As in Section 3.1, the more interesting case is shown in Fig. 5 (panel A) where these lines intersect at a NE in the unit square. Here, the horizontal and vertical arrows again indicate the direction taken by trajectories under best (as well as better) response dynamics. Unlike Fig. 3 for competitive systems, these arrows are analogous to the classical predator–prey Lotka–Volterra population dynamics in a single patch and so suggest that trajectories evolve counterclockwise around this interior NE. However, it is unclear if the NE is neutrally stable or asymptotically stable (unstable) with trajectories spiraling inwards (outwards). Contrary to the Lotka–Volterra predator–prey neutrally stable for the class of best response dynamics (Fig. 5A; Section 3.3.1).

If there is within-species negative density-dependent prey population growth in the predator-prey system corresponding to a linear individual payoff function, then the prey equal payoff line is strictly decreasing (as in Fig. 5, panel B where $V_i = r_i(1 - \frac{p_iM}{K_i} - \alpha_i q_i N)$) rather than horizontal. The NE (p^*, q^*) in this figure is still globally asymptotically stable for the class of best response dynamics (Section 3.3.1).

If the linear functional response of the predator in the Lotka–Volterra model is replaced by the Holling type II functional response of the form

$$V_{i} = r_{i} \left(1 - \frac{\alpha_{i} q_{i} N}{1 + h_{i} \alpha_{i} p_{i} M} \right) \text{ and}$$

$$W_{i} = s_{i} \left(-1 + \frac{\beta_{i} p_{i} M}{1 + h_{i} \alpha_{i} p_{i} M} \right),$$
(15)

then the prey equal payoff curve has a positive slope. Numerical simulations (such as those given in Fig. 5C) show the interior NE is not stable with respect to best response dynamics if handling times are positive. In particular, (p^*, q^*) does not meet our requirement to be called an IFD. Since no other NE exists, we conclude that the Holling type II functional response has a destabilizing effect on the spatial distribution of predators and prey similar to its destabilizing effect for predator–prey population dynamics.

From the above analysis, it is tempting to look for an IFD definition whereby an interior NE of a two-patch predator-prey system is asymptotically stable under the class of best response dynamics if and only if it is an IFD. That is, we could define an IFD as equivalent to stability under this class of dynamics. This approach works well for the single-species models of Section 2 where we saw that the original single-species IFD of Fretwell and Lucas (1970) is equivalent to global asymptotic stability under the best response dynamics (as well as under all better response dynamics). It also works well for the two-species competitive system of Section 3.1 where we proposed the same definition.

On the other hand, for predator-prey systems, none of the interior NE of Fig. 5 are asymptotically stable for the class

 $^{^{12}}$ For linear payoff functions, this means we ignore NE given by coincident equal payoff lines as in Fig. 3, panel C.

 $^{^{13}}$ Moreover, every such NE is locally asymptotically stable with respect to all better response dynamics.

of better response dynamics.¹⁴ In particular, there are interior NE that are stable for the class of best response dynamics but unstable for the class of better response dynamics. That is, any IFD defined in terms of dynamic stability will depend on the dynamics for which stability is analyzed, a situation we argued against in Section 2.3. As stated earlier, we would prefer a game-theoretic condition similar to the single-species ESS inequality (2) as our IFD definition. At this point, it is instructive to look at the evolutionary game theory literature on this issue.

3.3. The two-patch IFD from the game-theoretic perspective

There have been several attempts in the literature to extend the single-species ESS concept to general, non-symmetric, games that model multiple species interactions. An early attempt by Taylor (1979) (see also Thomas (1986)) took the sum of payoff functions for each species and searched for a single-species ESS with respect to this lumped payoff function. Applying this technique to the competitive system of Section 3.1 with parameters $(K_1 = K_2 = L_1 = L_2 =$ $r_1 = r_2 = s_1 = s_2, \, \alpha_1 = \alpha_2 = \alpha, \, \beta_1 = \beta_2 = \beta$, there is a NE at $p_1^* = q_1^* = 1/2$ for all fixed positive population sizes M and N. This point is asymptotically stable for a better response dynamics if and only if $\alpha\beta < 1$. On the other hand, it satisfies Taylor's concept if and only if the unrelated inequality $N\alpha + M\beta < 2\sqrt{MN}$ holds¹⁵ and so this concept is unacceptable for the IFD. Intuitively, this suggestion is also not acceptable on the biological grounds that it assumes that the two species "share" their payoff.

Another attempt has developed over the past twenty years through the work of Brown and Vincent (surveyed in Vincent and Brown (2005)). For a single species, an "ESS candidate" in Vincent and Brown (2005) is then defined as a NE for the game based on payoff functions for the pure strategies when the population size is fixed at its equilibrium value. To satisfy their ESS concept, this candidate must be stable under the strategy dynamics, a type of adaptive dynamics (Dieckmann and Law, 1996) on the strategy set. This approach has been extended to multiple species and to fixed non-equilibrium population sizes (for the latter, see the matrix game analysis in Chapter 9 of Vincent and Brown (2005)). When applied to a game that has linear payoffs, no ESS candidate that involves a mixed strategy qualifies as an ESS for them (p. 293 in Vincent and Brown (2005)) (see also p. 152 in Brown and Vincent (1987)). Thus $p_1^* = q_1^* = 1/2$ in the example of the previous paragraph never satisfies this concept.¹⁶ This second attempt is unacceptable as well for the definition of an IFD since it would exclude the possibility that a single population can occupy several patches.

A third attempt was developed by Cressman (1992) who defined a (two-species) ESS (p^*, q^*) as a NE such that, if the population distributions of the two species are shifted slightly to (p, q), then an individual in at least one species does better by playing its ESS strategy than by playing the slightly perturbed strategy of this species (Section 3.3.1).

Since the arrows for two-patch competitive systems (such as those illustrated in Fig. 3) determine asymptotic stability of a NE in exactly the same fashion as Section 3.3.1 characterizes the ESS, we see that (p^*, q^*) is an ESS if and only if it is locally asymptotically stable with respect to the class of best response dynamics (as well as all better response dynamics). That is, for these two-patch systems, the IFD and ESS concepts are identical.¹⁷ Condition (16) below is then the characterization of an IFD in analogy to the single-species inequality (2).

For two-patch predator-prey systems with either prey (predator) equal payoff line horizontal (vertical, such as those illustrated in Fig. 5), an interior NE is never an ESS because at distributions that lie on these lines neither prey nor predator fitness increases in the direction toward (p^*, q^*) . In fact, all predator-prey models where predator growth is density independent fall in this category. For the Lotka-Volterra system with no intraspecific payoff effects, this result also follows from Selten (1980) (see also Hofbauer and Sigmund (1998)) since the predator-prey model given above then has the form of a two-player "bimatrix" game (i.e., in Section 3.1.1 the intraspecific payoff matrices, A and D, in (17) are both zero). Selten (1980) (see also Cressman (2003)) showed every ESS (p^*, q^*) according to (16) must then be a strict NE (i.e. the inequalities in (10) are strict if $p \neq p^*$ and $q \neq q^*$) and, in particular, a pure strategy pair. A strict NE, which corresponds to a situation where all predators are in one patch and the prev are either all in the same patch or all in the other patch, is automatically asymptotically stable for evolutionary dynamics such as better response dynamics by one part of the Folk Theorem of Evolutionary Game Theory (p. 11, Cressman, 2003) applied to two-player bimatrix games. On the other hand, the NE in Fig. 5A is a Nash-Pareto pair and this led some authors (e.g., Křivan (1997), Křivan and Schmitz (2003) and Cressman et al. (2004)) to declare it to be an IFD.¹⁸

When there are intraspecific payoff effects as in Fig. 5, panels B and C, the concept of a Nash-Pareto pair is not

¹⁴ There are better response dynamics for which the interior NE is unstable even in the best possible predator–prey situation where the prey equal payoff line has negative slope as in Fig. 5, panel B. As such trajectories need only move in the direction of the arrows there, any initial point to the upper right of the NE can evolve arbitrarily close to the intersection of the vertical predator equal payoff line with the upper edge $q_1 = 1$. This can be continued in the other regions to show there exist better response dynamics that oscillate away from the NE.

¹⁵ The standard single-species definition of an ESS using the Taylor (1979) approach requires that $1/2V_1(p,q) + 1/2V_2(p,q) + 1/2W_1(p,q) + 1/2W_2(p,q) > p_1V_1(p,q) + p_2V_2(p,q) + q_1W_1(p,q) + q_2W_2(p,q)$ for every (p,q) different from (1/2, 1/2). This inequality simplifies to $(1/2 - p_1)^2M + (1/2 - p_1)(1/2 - q_1)(N\alpha + M\beta) + (1/2 - q_1)^2N > 0$, which holds for all p_1 and q_1 if and only if $N\alpha + M\beta < 2\sqrt{MN}$.

 $^{^{16}}$ For an analysis of the single-species habitat selection model using this approach see Section 10.1 in Vincent and Brown (2005) where the same conclusion is reached.

 $^{^{17}}$ In Cressman et al. (2004), the IFD for two-patch competitive systems was defined as the ESS. Here, we take the IFD as one given through dynamic stability and show this is equivalent to the ESS concept.

¹⁸ The Nash–Pareto equilibrium is a NE which satisfies an additional condition that says that it is impossible for both players to increase their fitness by deviating from this equilibrium. That is, it is a NE that satisfies (16) with non-strict inequalities.

applicable since this is no longer a two-player bimatrix game. However, the inequalities in (16) may continue to hold at an interior NE if we do not insist they are strict. Such a (p^*, q^*) is an example of a weak ESS (Section 3.3.1). The weak ESSs of Fig. 5 correspond to the filled circles in panels A and B (the empty circle in panel C is not a weak ESS). That is, the weak ESSs of two-patch predator-prey systems are exactly those NE that are asymptotically stable under the class of best response dynamics. To rephrase, if we define an IFD to be a (weak) ESS, then condition (16) (up to whether the inequalities in this condition are strict) provides an appropriate analogue of the single-species ESS condition (2) that has a dynamic justification as well.

The dynamic analyses of Sections 3.1 and 3.2 (together with the game-theoretic connections summarized in Section 3.3) motivate the definition of an IFD as a strategy pair (p^*, q^*) that is an asymptotically stable NE under the class of best response dynamics that model ideal movement among patches.¹⁹

3.3.1. ESS for two species

If V_i and W_i (i = 1, 2, ..., H) are the payoffs of the first and second species, respectively, in patch *i*, then payoffs of an individual using strategy $p' = (p'_1, p'_2, ..., p'_H)$ in species one (respectively, $q' = (q'_1, q'_2, ..., q'_H)$ in species two) when the resident populations use strategies *p* and *q* are, respectively $p' \cdot V(p, q)$ and $q' \cdot W(p, q)$. The game-theoretic ESS condition taken from Cressman (1992) (see also Cressman (1996, 2003) and Cressman et al. (2004)) is a strategy pair (p^*, q^*) such that at least one of the inequalities

$$p \cdot V(p,q) < p^* \cdot V(p,q) \quad \text{or} q \cdot W(p,q) < q^* \cdot W(p,q)$$
(16)

is true for each perturbed pair of distributions (p, q) sufficiently close (but not equal) to (p^*, q^*) .

For two-patch habitat selection models, the ESS condition (16) can be visualized geometrically in terms of the equal payoff lines of the two species and their associated arrows in Figs. 3 and 5. In particular, $p \cdot V(p,q) < p^* \cdot V(p,q)$ (respectively, $q \cdot W(p,q) < q^* \cdot W(p,q)$) if and only if the horizontal arrow (respectively, vertical arrow) at (p,q) is in the same direction as $p_1^* - p_1$ (respectively, $q_1^* - q_1$). Thus, by (16), (p^*, q^*) is an ESS if and only if at least one of the arrows at every nearby (p,q) is non-zero and pointing in the direction of (p^*, q^*) . That is, the solid circles in Fig. 3 (panels A and B) are ESSs while the empty circles in Fig. 3 are not. Moreover, no intersection point (p^*, q^*) of the two equal payoff lines in Fig. 5 (for predator–prey systems) is an ESS since arrows at points on the vertical line through (p^*, q^*) have zero vertical component and so do not point towards q^* .

If there are H patches and payoffs are linear in the components of p and q (as in (11)), the payoff functions of the habitat selection game can be based on pairwise interactions

and written in the form $V_i(p,q) = (Ap + Bq)_i$, $W_i(p,q) = (Cp + Dq)_i$ where A, B, C, D are appropriate $H \times H$ matrices. For example, in the case of two patches with payoffs given by (12) these matrices are: $A = \begin{pmatrix} r_1(1 - M/K_1) & r_1 \\ r_2 & r_2(1 - M/K_2) \end{pmatrix}$, $B = \begin{pmatrix} -\alpha_1 r_1 N/K_1 & 0 \\ 0 & -\alpha_2 r_2 N/K_2 \end{pmatrix}$, $C = \begin{pmatrix} -\beta_1 s_1 M/L_1 & 0 \\ 0 & -\beta_2 s_2 M/L_2 \end{pmatrix}$, $D = \begin{pmatrix} s_1(1 - N/L_1) & s_1 \\ s_2 & s_2(1 - N/L_2) \end{pmatrix}$. Cressman (1996) (see also Cressman (2003)) shows that (p^*, q^*) in the interior of $\Delta^H \times \Delta^H$ is an ESS if and only if it is the unique NE and there is an r > 0 such that

$$(p - p^*) \cdot (A(p - p^*) + B(q - q^*)) + r(q - q^*) \cdot (C(p - p^*) + D(q - q^*)) < 0$$
(17)

for all $(p, q) \neq (p^*, q^*)$.

To show the interior ESS (p^*, q^*) is globally asymptotically stable for the class of best response dynamics, we generalize the single-species Lyapunov function used in Hofbauer and Sigmund (1998). Specifically, for a fixed ν and ξ , define

$$F(p,q) = \max_{i} (Ap + Bq)_{i} - p \cdot (Ap + Bq)$$
$$+ \frac{r\xi}{\nu} (\max_{i} (Cp + Dq)_{i} - q \cdot (Cp + Dq)).$$

Then $F(p,q) \ge 0$ for all (p,q) with equality if and only if $(p,q) = (p^*,q^*)$. When (p,q) has a unique best response b_1 and b_2 for species one and two respectively, then $\frac{dp}{dt} = v(b_1 - p)$ and $\frac{dq}{dt} = \xi(b_2 - q)$ (see (12)). Thus

$$\begin{aligned} \frac{dF}{dt} &= -\nu(b_1 - p) \cdot (Ap + Bq) + (b_1 - p) \cdot [\nu A(b_1 - p) \\ &+ \xi B(b_2 - q)] - \frac{r\xi^2}{\nu} (b_2 - q) \cdot (Cp + Dq) \\ &+ \frac{r\xi}{\nu} (b_2 - q) \cdot [\nu C(b_1 - p) + \xi D(b_2 - q)] \\ &\leq \nu \left[(b_1 - p) \cdot \left(A(b_1 - p) + \frac{\xi}{\nu} B(b_2 - q) \right) \\ &+ \frac{r\xi}{\nu} (b_2 - q) \cdot \left(C(b_1 - p) + D\frac{\xi}{\nu} (b_2 - q) \right) \right] \\ &\leq 0 \end{aligned}$$

by (17) where $b_1 - p$ is a non-negative scalar multiple of some $\hat{p} - p^*$ and $\frac{\xi}{\nu}(b_2 - q)$ is a non-negative scalar multiple of some $\hat{q} - q^*$. In fact, $\frac{dF}{dt} = 0$ if and only if (p, q) is a NE (and so equal to (p^*, q^*)).

The above argument also holds when (p, q) does not have a unique best response by simply taking b_1 and b_2 as the directions of the vector field in (12) whenever the trajectory of the best response dynamics has a tangent line (which occurs for almost all positive times t). Then $\frac{dF}{dt} \leq 0$ at all such points and so F is decreasing. This shows that (p^*, q^*) is globally asymptotically stable.

For predator-prey systems, the concept of a weak ESS is also important. The strategy pair (p^*, q^*) is a weak ESS if condition (16) is true whenever $p \neq p^*$, $q \neq q^*$ and (p,q)is close to (p^*, q^*) . For an interior weak ESS, there exists an

 $^{^{19}}$ It must be kept in mind, however, that this definition of IFD for predator–prey systems is not equivalent to dynamic stable for all intuitive dispersal dynamics (e.g. the class of better response dynamics).

r > 0 such that (cf. inequality (17))

$$(p - p^*) \cdot (A(p - p^*) + B(q - q^*)) + r(q - q^*) \cdot (C(p - p^*) + D(q - q^*)) \le 0$$

and this implies that $\frac{dF}{dt} \leq 0$ is still true. In Fig. 5, the interior NE is a weak ESS in panels A and B but not in panel C.²⁰ These inequality conditions are sufficient to prove that a weak ESS (p^*, q^*) of the two-patch predator-prey system is asymptotically stable for all best response dynamics.

3.4. Parker's matching principle for two species

Parker's matching principle was extended under various specific assumptions to multiple species (e.g., Parker and Sutherland (1986), Possingham (1992), Hugie and Grand (1998), Grand and Dill (1999), Grand (2002b), Grand (2002a), Křivan (2003) and Berec et al. (2006)). These articles typically treat two consumer species with fixed sizes M and N in a two-patch environment where individuals compete through exploiting a shared resource. Suppose the constant resource input rate is r_i in patch i and λ (Λ) is the per capita consumption rate of species one (two). If resources in both patches are consumed immediately and individual payoffs are equated to the consumption rate, then consumer per capita payoffs V_i and W_i for species one and two respectively in patch i (=1, 2) are

$$V_i(p_i M, q_i N) = \lambda \frac{r_i}{\lambda p_i M + \Lambda q_i N} \text{ and}$$

$$W_i(p_i M, q_i N) = \Lambda \frac{r_i}{\lambda p_i M + \Lambda q_i N}.$$
(18)

Notice that these payoffs are decreasing non-linear functions of both species' patch density.

If both patches are occupied at a NE, then $V_1 = V_2$ and $W_1 = W_2$. However, these two equations for unknowns p_1 and q_1 (we recall that $p_2 = 1 - p_1$ and $q_2 = 1 - q_1$) are dependent and they reduce to a single equation given by the line

$$q_1 = \frac{r_1(\lambda M + \Lambda N)}{\Lambda N(r_1 + r_2)} - \frac{\lambda M}{\Lambda N} p_1.$$
(19)

In particular, this means that the NE of the two-species competitive system cannot be uniquely computed if the two species coexist in both patches. Any distribution (p_1, q_1) that satisfies (19) is possible.²¹ Qualitatively, we have the same situation as shown in Fig. 3C. Thus, there is no ESS or IFD with the species coexisting in both patches.

Grand and Dill (1999) included in the above model a risk of predation which they assumed to be patch and species dependent. If the ratio of the predation risk in the two patches is different for the two species, the two equal payoff lines do not coincide anymore, but are parallel in the resource 1–resource 2 density phase space (Possingham, 1992; Grand, 2002a). Thus, there is a unique NE and it must occur on the boundary of the unit square. In particular, if one species occupies both patches at this ESS/IFD, the other species is confined to a single patch only.

If resources are not assumed to be consumed immediately (i.e. there is a positive standing resource crop), the corresponding two-species Parker's matching principle is derived in Section 3.4.1. Calculations there show the same qualitative outcomes as summarized above. In particular, the payoffs (18) correspond to species food intake rate at the resource equilibrium densities provided functional responses are linear.

The argument in Section 3.4.1 can be extended to multiple patches. We find that an IFD can only occur as follows. The first possibility is that no patch is occupied by both species and the patches occupied by a given species form the singlespecies IFD for this species in its occupied patches. The only other possibility is that exactly one patch is occupied by both species with one species only in this patch and the other species distributed according to the single-species IFD among all the patches. These two possibilities suggest a competitive exclusion principle (also called "ghost of competition past", Connell, 1980; Morris, 1999) for habitat selection models based on two consumer species competing over resources undergoing population dynamics.

3.4.1. Parker's extended matching principle for two species

Here we extend Parker's single-species matching principle to two species that exploitatively compete for shared resources in each patch (Berec et al., 2006). Similar to the singlespecies model, we assume that resources are not consumed immediately and the resource dynamics are described by the following general model

$$\frac{dR_1}{dt} = r_1(R_1) - f_1(R_1)p_1M - g_1(R_1)q_1N$$

$$\frac{dR_2}{dt} = r_2(R_2) - f_2(R_2)p_2M - g_2(R_2)q_2N$$
(20)

where *M* and *N* are fixed densities of the two consumer species, R_i is the resource *i* density, r_i is the resource input rate in patch *i*, and f_i and g_i are functional responses. For constant resource inflow rate (i.e. $r(R_i) = r_i$) and linear functional responses $f_i(R_i) = \lambda R_i$ and $g_i(R_i) = \Lambda R_i$ the resource equilibrium densities are $R_i^{\star} = \frac{r_i}{\lambda p_i M + \Lambda q_i N}$, (*i* = 1, 2). Thus, the payoff functions given by (18) satisfy $V_i(p_i M, q_i N) = f_i(R_i^{\star}) = \lambda R_i^{\star}$ and $W_i(p_i M, q_i N) = g_i(R_i^{\star}) = \Lambda R_i^{\star}$ at the resource equilibrium.

In the general case described by model (20), the functional responses may be non-linear (e.g., of Holling type II) and the inflow rate can be density dependent. We assume that consumers maximize their food intake rate in analogy with the single-species case (i.e. species one (two) feeds on resource 1 if $f_1(R_1) > f_2(R_2)$ ($g_1(R_1) > g_2(R_2)$) and on resource 2 if the reverse inequality holds), and that resource dynamics (20) converge to an equilibrium (for linear functional responses and logistic resource growth this was proved in Křivan and Vrkoč (2007)).

²⁰ In Fig. 3C, every NE is a weak ESS.

²¹ Notice that this line intersects the interior of the unit square since $q_1 > 0$ when $p_1 = 0$ and $q_1 < 1$ when $p_1 = 1$.

First, we search for possible IFD where both species occupy both patches at the resource equilibrium. At the resource equilibrium $r_i(R_i) = f_i p_i M + g_i q_i N$ (i = 1, 2), from which we get $q_1 = \frac{r_1(R_1)}{g_1(R_1)N} - \frac{f_1(R_1)M}{g_1(R_1)N} p_1$ and $q_1 = 1 - \frac{r_2(R_2) - f_2(R_2)M}{g_2(R_2)N} - \frac{f_2(R_2)M}{g_2(R_2)N} p_1$. At the interior NE, individual payoff in both patches must be the same for species one ($f_1 = f_2$) and for species two ($g_1 = g_2$). Thus, both equal fitness lines have the same slope. Moreover, the sum of the two equations for resource equilibria gives $r_1(R_1) + r_2(R_2) = f_1(R_1)M + g_1(R_1)N$ which implies that the two equal fitness lines coincide. This means that there are infinitely many Nash equilibria (exactly as shown in Fig. 3C), but not a single IFD.

Now we search for IFDs where one species occupies one patch only. For instance, if species one occupies both patches while species two does not (i.e. $0 < p_1 < 1$ and $q_1 = 1$), the resource equilibrium must satisfy $r_1(R_1) =$ $f_1(R_1)p_1M + g_1(R_1)N$ and $r_2(R_2) = f_2(R_2)p_2M$. Together with the NE condition $f_1(R_1) = f_2(R_2)$, there are three equations for the three unknowns (R_1, R_2, p_1) which provide a unique distribution of the first species and equilibrium resource densities. For this distribution to be a NE, $g_1(R_1^*) > g_2(R_2^*)$ (i.e. the payoff of species two in its occupied patch is greater than that in its unoccupied patch). In this case, we automatically have a boundary ESS/IFD (as in Section 3.5.2) and here Parker's single-species matching rule $p_1/p_2 = (r_1(R_1^*) - g_1(R_1^*)N)/r_2(R_2^*)$ applies.

Finally, each species may occupy one patch only (this patch can be the same for both species or distinct). For example, assume the first species occupies patch 1 and the second species patch 2 (i.e. $p_1 = 1$ and $q_1 = 0$ in model (20)). From (20), the two equations for the resource equilibrium, $r_1(R_1) = f_1(R_1)M$ and $r_2(R_2) = g_2(R_2)N$, define the resource equilibrium densities, R_1^* and R_2^* . As we assume that patch 1 is better for species one and patch 2 for species two, the following inequalities must be satisfied at these resource equilibrium densities: $f_1(R_1^*) > f_2(R_2^*)$ and $g_2(R_2^*) > g_1(R_1^*)$. Indeed, under these inequalities, the species distribution $(p_1, q_1) =$ (1, 0) is a strict NE and so an ESS/IFD of the two-patch consumer selection model.

3.5. Multiple patch IFD

From Section 3.3, the IFD for two-patch systems is closely related to the ESS concept (i.e. condition (16)). Specifically, every ESS is an IFD and every IFD is a weak ESS. Unfortunately, the geometric intuition of Figs. 3 and 5 that proved so effective for the dynamic analysis of these two-patch models is no longer available when there are multiple (i.e. $H \ge$ 3) patches. In particular, although the ESS condition (16) applies to any number of patches, its geometric interpretation when $H \ge 3$ is not in the literature. By Section 3.3.1, an interior ESS is globally asymptotically stable for all best response dynamics applied to multi-patches²² and so is an IFD but general game-theoretic conditions that completely characterize dynamic stability under the best response dynamics are unknown. There are, however, special types of multi-patch habitat selection games of biological importance where the connection between ESS and dynamic stability can be made.

3.5.1. Dominant species

The first such type of biological significance is the case of two competing species where one species (species one, say) is dominant and the other (species two) is subordinate. By this, we mean that the payoff to individuals in species one in each patch is independent of the density of species two there. There is considerable evidence that such asymmetric interspecific competition is quite common in nature (Schoener, 1983). For example, this was shown for hummingbirds (Pimm et al., 1985), for rodents (Abramsky et al., 1990), for isopods (Franke et al., 2007), and for fish (Berec et al., 2006).

In a dominant-subordinate system, any ESS (p^*, q^*) must have p^* as the unique single-species ESS/IFD of the dominant species one. Now, with $p = p^*$ in (16), we see that q^* is the unique single-species ESS of species two conditional on species one being fixed at p^* . The converse is also true and so every dominant-subordinate system has a unique ESS (p^*, q^*) . If all patches are occupied by species one at p^* , it is well known (p. 97, Theorem 8.4.4 in Hofbauer and Sigmund (1998)) that the single-species best response dynamics converge to p^* in finite time and stays there. After this time, species two will evolve under the single-species best response dynamics (conditional on species one being fixed at p^*) to q^* . Thus, for all dominantsubordinate systems, there will be a unique ESS (p^*, q^*) and it will be the only IFD in the sense of dynamic stability with respect to the class of best response dynamics.

Clearly, the above argument generalizes to hierarchical biological systems with more than two species. Here, species one is dominant in that its payoff function in each patch depends only on its density there. Patch payoffs of species two depend only on densities of species one and two there, etc. For example, the three species of hummingbirds (bluethroated, blackchinned, and Rivoli's) studied by Pimm et al. (1985) constitute a hierarchical system. Such systems will have a unique multi-species ESS (Cressman et al., 2001; Cressman, 2006) and it will be globally asymptotically stable under the class of multi-species best response dynamics (and so a multi-species IFD).

3.5.2. Boundary and interior IFD

For fixed positive population sizes M and N, every habitat selection game with H habitats has at least one NE (p^*, q^*) .²³ Suppose the second species is absent from some patch (say, patch H, $q_H^* = 0$) at this species' distribution. Then (p^*, q^*) is a boundary NE and $W_H(p^*, q^*) \leq W^*$ (recall that W^* is the payoff to species two in each occupied patch at the NE).

²² It is also well known that an ESS is asymptotically stable for the replicator equation (Cressman, 1996, 2003), a result that is not so relevant for the habitat selection game since this dynamics is not a realistic dispersal process.

 $^{^{23}}$ This follows from the fact that these habitat selection games are (two-species) population games (Sandholm, 2007). A sufficient condition to guarantee the existence of a NE is the continuity of the payoffs (such as in (11)) as functions of the species' distributions.

Unless we have a degenerate situation such as in Fig. 3 (panel C), this inequality will be strict. In this case, the payoff of an individual in species two that occasionally stays in habitat Hwill be lower than the payoff of an individual that avoids this patch (i.e. $q \cdot W(p,q) < q^* \cdot W(p,q)$ for all (p,q) sufficiently close to (p^*, q^*) with $q_H > 0$). Thus, to confirm that (p^*, q^*) is an ESS, it is sufficient to check condition (16) for those (p,q) with $q_H = 0$. In other words, the analysis of the ESS condition at a boundary NE simplifies since the mathematical problem is reduced by at least one dimension. Moreover, the asymptotic stability of a boundary NE is also determined by stability restricted to this lower dimensional face since any best (or better) response dynamics will satisfy $\frac{dq_H}{dt} < 0$ if q_H is positive and sufficiently close to 0 (because all other patches are better than patch H for species two). Thus, both the ESS and IFD concepts simplify mathematically at a boundary NE.

In the extreme case where species two occupies only one patch at the boundary NE (p^*, q^*) , the iterated reduction in dimension implies that (p^*, q^*) is an IFD if and only if p^* is the single-species NE of species one with respect to the payoff function $V_i(p)$ that assumes q is fixed at q^* . In particular, this argument applies to Parker's multi-patch matching principle mentioned at the end of Section 3.4. It also applies to the twopatch competitive systems of Section 3.1 where it immediately implies that every boundary NE there is an ESS and IFD (except when the two equal payoff lines happen to intersect exactly on the boundary of the unit square such as in Fig. 3, panel C).

By the above discussion, the existence of boundary NE simplifies the problem of determining ESS and/or IFD. In other words, the most difficult situation shows that a NE (p^*, q^*) is an ESS and/or IFD occurs when (p^*, q^*) is in the interior (i.e. no component of p^* or q^* is zero). As mentioned at the beginning of Section 3.4, no general analysis exists in the literature in these circumstances. However, some intuitive results are possible when payoff functions are related.

For example, suppose the payoffs for a multi-patch competitive system given by (11) satisfy, for some positive constant *c*, that $r_i/K_i = cs_i/L_i$ for all i = 1, ..., H. That is, the ratios of the intrinsic growth rates and carrying capacities of the two species remain constant across patches. Since the ratio r_i/K_i (s_i/L_i) defines the slope of the payoff function for the first (second) species with respect to its own density, competitive systems with the same intraspecific competition effect in each patch are included in this example. Then, an interior NE is an ESS if $\max_{i,j} \alpha_i \beta_j < 1.^{24}$ Moreover, by

Section 3.3.1, every ESS is an IFD (i.e. dynamically stable with respect to the class of best response dynamics). In particular, if payoffs are the same for patches with identical densities (i.e. $V_i = V_j$ and $W_i = W_j$ when $p_i M = p_j M$ and $q_i N = q_j N$, then the uniform distribution (p^*, q^*) (i.e. $p_i^* = 1/H = q_i^*$ for all i = 1, 2, ..., H) is an interior NE. Moreover, (p^*, q^*) is an IFD if and only if $\alpha\beta < 1$ (where $\alpha_i = \alpha$ for all i and $\beta_i = \beta$ for all i). That is, if a homogeneous environment is divided into identical patches, the uniform distribution (p^*, q^*) is globally asymptotically stable under the class of best response dynamics if and only if the interspecific competition coefficients, α and β , satisfy the same inequality condition that is equivalent to the global asymptotic stability of the coexistence equilibrium for the population dynamics of a competitive Lotka–Volterra system in a single patch.

3.6. Habitat selection combined with population dynamics from the game-theoretic perspective

In this section, we consider the relevance of the NE, ESS and IFD concepts when overall species densities are not fixed but evolve according to a population dynamics (c.f. Section 2.4 for the single-species treatment). First, we study whether the demographic process drives the two-species distribution in two patches to the IFD even without any dispersal between patches (Section 3.6.1) before combining the demographic process with dispersal (Section 3.6.2).

3.6.1. The two-species NE as a result of competitive consumer population dynamics alone

Let m_i and n_i be the density of species one and two, respectively, in patch *i*. If animal per capita population growth rate equals the patch payoffs V_i for species one and W_i for species two, the population dynamics are described by the following model

$$\frac{dm_i}{dt} = m_i V_i(m_i, n_i), \quad i = 1, 2
\frac{dn_j}{dt} = n_j W_j(m_j, n_j), \quad j = 1, 2.$$
(21)

The above model does not consider resource dynamics explicitly. Instead, it assumes that the resource levels equilibrate quickly with consumer densities and that the species are competitive in that the payoff functions (V_i and W_i) are all decreasing in both variables m_i and n_i . As in Section 2.4, we write payoffs, V_i and W_i , in patch *i* as functions of $(m_i, n_i) = (p_i M, q_i N)$ instead of (p, q) since *M* and *N* are also evolving here.

It is well known (Theorem 2.2, p. 35 in Smith (1995)) that, for two-species competitive systems such as (21), all trajectories that start with both species present in a particular patch converge to equilibrium densities (m_i^*, n_i^*) . Then, from (21), $V_i(p_i^*M^*, q_i^*N^*) = 0$ and $W_j(p_j^*M^*, q_j^*N^*) = 0$ for every occupied patch. Furthermore, $V_i(p_i^*M^*, q_i^*N^*) \le 0$ in any unoccupied patch *i* by species one (otherwise $\frac{dm_i}{dt} > 0$ near the equilibrium which implies p_i does not evolve to 0). Combined with the analogous result for species two, we

²⁴ From (13), this inequality is sufficient for an interior NE of a two-patch competitive system to be an IFD without further conditions on the intrinsic growth rates and carrying capacities. For multiple patches with $r_i/K_i = cs_i/L_i$, the sufficiency of this inequality follows from the fact that (16) holds if and only if $p^*(q^*)$ is a single-species ESS when the other species' spatial distribution is fixed at $q^*(p^*)$ and $((p-p^*) \cdot A(p-p^*))((q-q^*) \cdot D(q-q^*)) > ((p-p^*) \cdot B(q-q^*))((q-q^*) \cdot C(p-p^*))$ for all $(p,q) \neq (p^*,q^*)$ where A, B, C, D are given in (17) (see Definition 3.2.2 (v) in (Cressman (1992), p. 33)). With $x = p - p^*$ and $y = q - q^*$, we have the quadratic expressions $((p-p^*) \cdot B(q-q^*))((q-q^*) \cdot C(p-p^*)) = c \sum_{i,j} \frac{r_i}{K_i} \frac{r_j}{K_j} x_i^2 y_j^2$ and $((p-p^*) \cdot B(q-q^*))((q-q^*) \cdot C(p-p^*)) = c \sum_{i,j} \alpha_i \beta_j \frac{r_i}{K_i} \frac{r_j}{K_j} x_i x_j y_j$. Thus, the latter inequality results from $|||u||^2 |||v||^2 \ge (u \cdot v)^2$ with $u_i \equiv \sqrt{r_i/K_i} ||x_i||$ and $v_i \equiv \sqrt{r_i/K_i} ||y_i||$.

conclude that (p^*, q^*) is a NE of the completely different model which assumes that there is only animal dispersal and that the overall population densities are fixed at M^* and N^* .

Thus, we see that the same animal distribution (namely, the NE) may emerge either due to demographic processes without any actual dispersal between patches, or, alternatively, by dispersal alone. In Section 3.6.2, we investigate the relation between the stability of the species distribution with respect to either the population dynamic process modeled by (21), or to the dispersal process modeled by (12) (or a combination of the two).

3.6.2. The two-species IFD when animal dispersal and population dynamics are combined

When there is a coexistence equilibrium of the competitive process (21) in each of the separate patches, Section 3.6.1 shows that it is also a NE of the dispersal process (12) when consumer densities are fixed at their equilibrium values. That is, this NE is an equilibrium of two different independent processes: dispersal dynamics and population dynamics. Correspondingly, there are also two different types of dynamic "stability" of the resulting distribution. The first "stability" relates to stability with respect to dispersal dynamics. That is, is the distribution an IFD at fixed equilibrium population densities? The second type of stability of the distribution is with respect to population dynamics (21).

A question arises then whether or not animal dispersal can destabilize stable population equilibrium of the model (21) without dispersal. We have already seen in Section 2.4 this cannot happen for a single species when the dispersal process is a better response dynamics. However, for two competing species, Cressman et al. (2004) showed that dispersal can destabilize the demographic process because the condition for dynamic stability of the population equilibrium for the model without dispersal does not in general imply that the animal distribution is an IFD. Specifically, for two-patch competitive systems, the interior IFD condition (13) that guarantees stability of the distribution with respect to small perturbations requires not only products $\alpha_i \beta_i$ of interspecific competition coefficients to be small in either patch, but also products of interspecific competition coefficients in different patches (e.g., $\alpha_1\beta_2$) to be small. Heuristically, this latter condition is needed because an animal encounters heterospecific animals in both patches due to dispersal. However, the familiar condition for population stability of two competing species (in a single patch) requires that only the products of interspecific competition coefficients in this patch are small. Thus, Cressman et al. (2004) were able to construct examples of two competing species with a globally stable equilibrium and coexistence in both patches when animals do not disperse between patches (i.e. for model (21)). However, in these examples, this spatial distribution was not the IFD for the model which assumed dispersal only (i.e. model (12)).

These results are illustrated clearly by the following simulations of the dynamics based on Abrams et al. (2007). The dispersal dynamics when both competing species are at their population equilibrium are qualitatively similar to those shown in Fig. 4B. In particular, at these fixed population sizes, the interior NE is not an IFD but there are two alternative boundary IFDs. If population dynamics (21) are combined with distribution dynamics (12), we get the following model (cf. (9))

$$\frac{dm_i}{dt} = m_i V_i(m_i, n_i) + \nu \left(\sum_{j=1}^H I_{ij}(m, n)m_j - m_i \right),
\frac{dn_i}{dt} = n_i W_i(m_i, n_i) + \xi \left(\sum_{j=1}^H J_{ij}(m, n)m_j - m_i \right)$$
(22)

for i = 1, 2. In analogy to Section 2.4, ν and ξ are positive parameters that characterize the relative time scale between population and dispersal processes.

Numerical simulations of model (22) with best response distributional dynamics reveal that the stable equilibrium for the population dynamics (Fig. 6, top panel, no dispersal, $\nu =$ $\xi = 0$) is destabilized when individuals start to disperse (Fig. 6, middle, $\nu = \xi = 0.01$), leading to periodic cycling in both animal distribution and abundance. As the dispersal process becomes even faster with respect to the population dynamics time scale (Fig. 6, bottom panel, $\nu = \xi = 0.1$), animal distribution fluctuates wildly (see also Abrams et al. (2007)).

In summary, the instability of the interior NE for the dispersal dynamics suggests that the combined population/dispersal dynamics will also be unstable at the population equilibrium, especially as the rate of dispersal relative to the population dynamics increases. Moreover, since the boundary IFDs do not correspond to stable population equilibria, we do not expect the combined system to approach an equilibrium solution (and this is illustrated in Fig. 6, middle and bottom panels). That is, unless the population equilibrium corresponds to an IFD, the game-theoretic perspective predicts non-convergent system behavior. This conclusion contrasts markedly with the singlespecies results of Section 2.4 where we showed that dispersal dynamics cannot destabilize population dynamics.

By analogous reasoning, an interior IFD which corresponds to an unstable population equilibrium will also be unstable in the combined dispersal and population dynamical system when dispersal rates are low. In fact, Cressman et al. (2004) show by example that such an interior IFD remains unstable even when dispersal rates are very high.

On the other hand, for predator-prey systems with linear functional response (as in Fig. 5, panel B), an interior NE corresponding to a population equilibrium is an IFD as well as neutrally stable for the population dynamics. Simulations confirm the intuition that this NE is asymptotically stable for all choices of dispersal rates, a result that was shown analytically by Cressman et al. (2004) when dispersal rates are high. Finally, it is easy to construct examples of unstable interior NE under the combined dynamics for two-patch predator-prey systems where predators have a Holling type II functional response (Abrams, 2007). This is intuitively clear since, as noted in Section 3.2, this functional response has a destabilizing effect both for the spatial distribution of predator and prey and for the population dynamics.



Fig. 6. Dependence of combined dispersal and population dynamics (see model (22)) on dispersal and population time scales. The left panel shows animal distribution (p_1 -solid line, q_1 -dashed line) and the right panel shows total animal abundance (*M*-solid line, *N*-dashed line). The upper panel illustrates population dynamics with no animal dispersal ($\nu = \xi = 0$). Here, the system approaches the population equilibrium M = N = 10 even though the corresponding interior NE is not an IFD at these densities. The middle panel assumes low animal dispersal ($\nu = \xi = 0.01$) and the bottom panel assumes faster dispersal dynamics ($\nu = \xi = 0.1$). In both these panels, the system appears to be evolving to a limit cycle with the population switching quickly in the bottom panel between the two unstable boundary NE where the two species are segregated into separate patches. Other parameters are $r_1 = 1$, $r_2 = 0.1$, $s_1 = 0.1$, $s_2 = 1$, $K_1 = 19$, $K_2 = 2$, $L_1 = 2$, $L_2 = 19$, $\alpha_1 = 9$, $\alpha_2 = 0.1$, $\beta_1 = 0.1$, $\beta_2 = 9$.

4. Discussion

In this article, we reviewed and synthesized theoretical works on the IFD from the game-theoretical point of view. For a single species, the Fretwell and Lucas (1970) IFD concept is given in game-theoretic terms as a NE of the habitat selection game (i.e. a distribution among the patches such that the "suitabilities" in all occupied patches are equal and at least as large as the suitability in any unoccupied patch). Although it was often assumed in the literature that the IFD is also an ESS, to our knowledge, a formal proof was given just recently (Cressman et al., 2004; Cressman and Křivan, 2006). This guarantees that the IFD concept is robust with respect to invasions of individuals with different strategies but the same payoffs. In other words, the observed animal distribution is stable when the ability to find better patches is adaptive and there are small spatial perturbations to IFD patch preferences. Since the ESS concept is independent of the dispersal process

per se, we have also surveyed some explicit dispersal processes and compared their stability with the game-theoretical stability of the IFD.

A classical approach to model animal dispersal assumes passive dispersal between patches (e.g., Hastings (1983), Holt (1985), Johnson and Gaines (1990), Houston et al. (1995) and Holt and Barfield (2001)). Under the IFD there will be more individuals in the better patch when compared with the poorer patch. Since passive dispersal between patches tends to equalize animal densities across patches, animal density is lower in the best patch (and higher in the worst patch) when compared with the IFD. This phenomenon of "undermatching" necessarily leads to a decrease in fitness of those dispersing animals that leave the better patch which is the reason why evolution of dispersal should select against dispersal in spatially varying but temporally constant environments (Hastings, 1983; Holt, 1985; Holt and Barfield, 2001). On the contrary to such passive dispersal, we reviewed in this article some recent work on dispersal dynamics that assumes an active dispersal to patches with a higher fitness. The choice of such dispersal dynamics is not unique and, in principle, one can think of infinitely many possible dispersal dynamics. We discussed in detail dispersal dynamics that are consistent with the ideal and free assumptions made by Fretwell and Lucas. In particular, these dynamics assume that animals are omniscient and they move always to the patch with the highest fitness. Such dynamics are well known in game theory under the name, best response dynamics (Hofbauer and Sigmund, 1998). For each animal distribution, animals move to the patch which provides them with the best response (=highest fitness) for the current state (=distribution). In fact, these best response dispersal dynamics are an example of a more general class of "better response" dispersal dynamics which assume that animals never disperse to patches with a lower payoff and some animals always disperse to a patch with the highest payoff. These assumptions on local myopic behavior relax the original Fretwell and Lucas assumption of globally omniscient animals. All better response dynamics lead to the IFD. This can then explain why the IFD is observed in cases where consumers do not have global information about their environment. Thus, for a single species the IFD is stable from two different perspectives: (1) it is stable in the static sense of being Evolutionarily Stable, and (2) it is the stable equilibrium of a wide class of distribution dynamics that we call better response dynamics. The static nature of the first perspective makes the IFD a very robust concept from the biological point of view because it does not consider any distribution dynamics.

The relationship between static and dynamic stability is not so clearcut in the case of multiple species. First, in contrast to the single-species case, there can now be a two-species distribution that corresponds to a NE which is not stable with respect to either the game-theoretical point of view (i.e., it is not an ESS) or the best response dynamics (i.e. distribution dynamics described by the best response dynamics do not converge to this NE). That is, the intuitive description (p. 22, Fretwell and Lucas, 1970) of an IFD by saying "the distribution is stable only when suitabilities are equal in all habitats" is correct for single-species habitat selection games but not for two species. By examining two-patch models of both competitive and predator-prey systems, we showed that the IFD for two species is given through the ESS introduced by Cressman (1992) (see also Cressman (2003)). The IFD is then asymptotically stable for all best response dynamics irrespective of different species' dependent rates of movement to the best patch (i.e., irrespective of species specific differences in time scales of dispersal). A second complication for two-patch predator-prey systems is that the IFD is not asymptotically stable for all better response dynamics. These complications emphasize that the ideal free assumptions are more crucial for two-species models as compared to the singlespecies case and that stability of the IFD depends on properties of the dispersal dynamics.

Using the two-species IFD, we also examined how the single-species Parker's matching principle extends to two species. Under this extension, it is quite unlikely that two exploitatively competing species will distribute over both patches. That is, either they completely segregate, or one species occupies both patches while the second species occupies one patch only. In the ecological literature, this exclusion principle was termed "the ghost of competition past" (Connell, 1980; Morris, 1999). The case where both species occupy both habitats can happen only under some special conditions (e.g., the two patches differ in the resource input rate only and functional responses of both competing species are linear). If these conditions hold, the resulting distribution is not uniquely given and it is not an IFD because it is not stable with respect to mutant invasions.

One interesting prediction which emerges from recent work on the IFD is the fact that the IFD can be reached even if animals do not disperse between patches but they undergo population dynamics. This is because, if every patch reaches its population equilibrium, the animal fitness there must be zero, and thus it equalizes across all occupied habitats. Although this is a very simple observation, it can be another reason why observed distributions are often close to the IFD. That is, the IFD can be reached by two different processes: on a short time scale by animal dispersal, on a longer time scale by population dynamics.

Accordingly, there are two different types of dynamic stability related to the two-species IFD concept: demographic and dispersal. For a single species, these two types of stability are the same. That is, if the animal distribution is the outcome of demographic processes only, it is also the IFD of the pure dispersal process and vice versa. However, this is no longer true for two-species models (Cressman et al., 2004), because the mathematical conditions for the two types of stability of the animal distribution are not the same. In fact, dispersal can destabilize a stable population distribution which was reached solely by a demographic process, and, similarly, population dynamics can destabilize an IFD of a system which does not consider population dynamics. Such results (see also Abrams et al. (2007)) show that ecologists need to pay attention to dispersal mechanisms and time scales on which near-to-IFD distributions are observed. The reason is that the IFD can be reached either on a short time scale (which is the case of most experimental work on the IFD), or on a longer population dynamical scale by different processes.

The game-theoretic perspective developed in this paper is most successful when either applied to single-species habitat selection games with two or more patches or applied to two-species games in a two-patch environment. As we have seen (e.g. the hierarchical competitive systems and those with boundary NE in Section 3.5), the IFD approach also shows potential to explain observed spatial distributions in multi-patch systems with two or more species, although the theory here is far from complete. IFD theory also needs to be tested for multispecies systems where within-patch interspecific interactions are not of competitive or predator–prey type (e.g., mutualistic systems).

There are several other directions for future research where the game-theoretic perspective will prove useful. For instance, an underlying assumption of the IFD approach is that the payoff to an individual is the same for all animals of the same species in the same patch. Furthermore, our dispersal dynamics assume that all such animals have the same dispersal probabilities between patches. These assumptions mean that each species is monomorphic. The question arises as to the effect of having a polymorphic species with multiple phenotypes in the same patch whose payoffs and dispersal probabilities depend on the phenotypic distribution (as well as the spatial distribution) of the species. An extreme example has some phenotypes within the population that specialize in a particular patch and do not disperse. An animal's strategy is then a simultaneous choice of habitat and phenotype from the game-theoretic perspective, which is the natural setting to explore connections between NE, ESS and possibly IFD in such circumstances.

Another assumption of the IFD is that movement between patches is free. In particular, there is no cost either in terms of energy spent by, or added danger to, the dispersing individual. Initially, phenotypes that avoid such costs by specializing in one patch would seem to have an advantage. However, as differences in patch payoffs increase, it will eventually pay individuals to be mobile (e.g. in a bacterial culture that feeds on two types of sugar, some bacteria switch their metabolism to produce enzymes that process the alternative type if the preferred type is at low density). In theory, such costs and benefits can be incorporated into the payoff structure of the underlying habitat selection game. The effects of such changes on the IFD and on the stability of the system need to be further examined.

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