

# A Game-Theoretic Model for Punctuated Equilibrium: Species Invasion and Stasis through Coevolution\*

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**Abstract:** A general theory of coevolution is developed that combines the ecological effects of species' densities with the evolutionary effects of changing phenotypes. Our approach also treats the evolutionary changes between coevolving species with discrete traits after the appearance of a new species. We apply this approach to habitat selection models where new species first emerge through competitive selection in an isolated habitat. This successful invasion is quickly followed by evolutionary changes in behavior when this species discovers the other habitat, leading to a punctuated equilibrium as the final outcome.

Keywords: stasis, evolutionary stability, invasion, habitat selection, discrete traits, punctuated equilibrium

# 1 Introduction

From the ecological perspective, one of the most important steps in the evolutionary process is the successful invasion of a new species into an already existing ecosystem. Such steps are consistent with the concept of punctuated equilibrium (Eldredge and Gould, 1972) suggested by the fossil record in paleoecology. This theory claims that evolution is not a continuous process; rather, during a short geological time, new species arrive in rapid succession and contribute revolutionary morphological changes. Following these speciation events, an evolutionary stable ecosystem rapidly evolves, where lineages are in stasis. Unfortunately, how changes occur during the speciation event cannot be understood from the fossil record which is especially incomplete within the short outbursts. That is, fossils tend to remain similar in appearance for many meters of vertical sediment corresponding to millions of years of geological time. These long periods of stasis mean the morphological mutants that arose during this time could not successfully invade this existing ecosystem and so the species look like non-changing entities.

The main purpose of this paper is to combine the essential aspects of stasis (i.e. stability) with the occasional invasion of successful mutants (either mutant species or mutant phenotypes of existing species) in a single model. In particular, we consider this problem of punctuated equilibrium at the phenotypic level when phenotypic fitnesses depend on the densities of interacting species as well as on the phenotypic distribution of the system. This contrasts with the usually assumption of evolutionary models that fitness depends on only one factor such as the individual phenotypes, the distribution of different types in a species (Gavrilets, 2003), or the species' densities (i.e. population dynamics). Our coevolutionary approach also contrasts with speciation models based on population genetics which often emphasize the importance of reproductive isolation (Coyne, 1992; Johnson and Gullberg, 1998; Lee, 2002). Since we ignore genetic effects, our approach is closer to ecological speciation models that have received renewed interest among both theoretical (Schluter, 1998, 2001; Orr and Smith, 1998; Morell, 1999; McKinnon et al., 2004) and empirical (Rundle et al., 2000 Kruse et al., 2004; Munday et al., 2004) biologists. However, our coevolutionary model also includes changes in the phenotypic makeup of the population.

Thus, one central question of this paper is what kind of new species and/or phenotypes are able to invade an already existing stable evolutionary ecosystem? Here we use the term “evolutionary ecology” since, during the

invasion, the phenotypic constitution of the currently coexisting species may also be subject to adaptive change. There are two important aspects to this problem. The first question is whether the new mutants can initially invade this ecosystem when rare. When mutants are from a different species, this first requirement guarantees that new species appear but it is not sufficient for the long-term stability of a punctuated equilibrium since it is possible that, after the initial successful invasion, the evolution in the enlarged system that includes the new species selects such changes which ultimately drive the new species to extinction. Similar theoretical instances of “evolutionary suicide” have been studied in the literature on adaptive dynamics (Gyllenberg and Parvinen, 2001; Diekmann, 2004). Thus, the second requirement for a punctuated equilibrium is that the new ecosystem must be evolutionarily stable. This corresponds to the stasis and means that further rare mutants arising within the enlarged ecosystem must die out.

It is also clear that the successful arrival of a new species not only changes the ecological system (e.g. a new equilibrium could arise where both resident and invading species coexist or the resident species could be selected out), but it may also imply an evolutionary change among the resident species that survive. Thus, a minimal model of punctuated equilibrium must deal with the potential of evolutionary change both within and between species.

As discussed above, a necessary step is that a new species establishes itself into an already existing stable ecosystem. Since ecological interactions are typically density dependent, a general theory of coevolutionary speciation must incorporate density dependent fitness effects. An elementary example of density dependent species’ interactions is the Lotka-Volterra model of competition between two species. For example, consider the following system,

$$\begin{aligned}\dot{x} &= x(20 - 2x - y) \\ \dot{y} &= y(15 - x - y).\end{aligned}\tag{1}$$

Here  $x$  and  $y$  are the population sizes (i.e. densities) of species one and two respectively. When only species one is present, there is an asymptotically stable equilibrium on the horizontal axis (see Figure 1). However, when species two invades, there is an equilibrium where both species coexist at  $x = 5$  and  $y = 10$ . The stability properties of this equilibrium are well-known for the Lotka-Volterra model (Goel et al., 1971; Hofbauer and Sigmund, 1998). In particular, these properties show for system (1) that species two successfully invades since the coexistence equilibrium is then globally asymptotically stable as in Figure 1. Here, the invasion leads to an increase in the number of

species in the ecosystem.

Figure 1 about here

However, in this classical Lotka-Volterra model, there is no diversity in a given species since one of the basic assumptions of Lotka-Volterra is that each individual in this species has the same phenotype. That is, evolutionary change within species is impossible. Thus, this classical approach cannot model the stasis phenomenon where rare mutants corresponding to a different phenotype in a resident species emerge but do not successfully invade.

Our perspective to model successful invasion and stasis in a single framework is game theoretic since we believe any coevolutionary ecological scenario must be based on individual fitness functions that depend on this individual's behavior (or phenotype) as well as on the behavior of other individuals in the system (and on population density). In contrast to the Lotka-Volterra model, this leads to changes in the phenotypic makeup of a given species and is therefore a game theoretical situation.

A question that immediately arises is what type of evolutionary variation in phenotypes is to be considered in the model. Maynard Smith (1960) made a fundamental distinction between evolutionary traits (and their morphological manifestations) that are continuous (e.g. body length, weight etc.) and that are discrete or modal (e.g. the number of fingers on a person's hand). The evolution of continuous traits has been widely investigated over the past decade (see Abrams (2001) and the references therein) through models of quantitative genetics or phenotypic models using adaptive dynamics. Our model of coevolutionary ecology will assume phenotypes are discrete (and only finitely many are possible). A genetic basis for our assumption is that the phenotype is determined by a small number of genes and so, in contrast to continuous trait models, mutant phenotypes are not pictured as being close to those of the resident ecosystem. On the other hand, we do not assume any knowledge of the genetic basis on which forms of mutant traits can appear in the coevolutionary system. That is, phenotypic fitness functions will already be given in our model rather than developed from genetic considerations. Our emphasis is then the effect these given fitnesses have on natural selection of the population phenotypes.

Game-theoretic approaches have also been used to determine whether within species invasion will be successful when individual fitnesses only depend on phenotypic frequencies. When applied to a resident species where

mutants are formed from a finite number of possible phenotypes (also called pure strategies), the method is known as “evolutionary game theory”. In its original form (e.g. Maynard Smith, 1982), this is a frequency dependent theory that considers a single asexual population in which there is phenotypic diversity. The basic game-theoretic solution concept here is that of an evolutionarily stable strategy (ESS). This is a phenotype which a rare mutant cannot invade if the overwhelming majority of the population use the ESS (i.e. if the resident system is monomorphic and at the ESS). Since evolutionary game theory has been extended to multi-species systems (Cressman et al., 2001; Cressman, 2005), it can also deal with the diversity and evolution between species, but it is frequency dependent.

The game-theoretic perspective developed in this paper for a discrete set of evolutionary traits is based on our generalization (Cressman and Garay, 2003a, 2003b) of the classical ESS conditions to  $N$ - interacting species with frequency and density dependent fitness functions. We say an ecosystem is evolutionarily stable if rare mutant phenotypes within these  $N$  species cannot successfully invade the ecosystem (cf. Maynard Smith’s original form). There are two immediate consequences of mutants being “rare”. First, in each species, only one resident and one mutant phenotype can exist at the any given time (i.e. the rate of mutation is much slower than selection and so after mutation the ecological system has enough time to select out the less fit phenotypes). Second, the mutation can be produced at arbitrarily low densities which is important since we examine invasion through a dynamical point of view. That is, we require that mutants eventually die out under the ecological selection dynamics. When there is only one resident species, this leads to the intuitive requirement that each mutant phenotype is less fit than the resident, a straightforward property that can be determined through the fitness function. However, as we will see, when there is more than one species, the mutants of some species may be initially more fit after they first appear than the residents but in the long run (more precisely, in ecological time) all mutants must die out according to the ecological dynamics. Our model also considers invasion of an evolutionarily stable ecosystem by phenotypes from new species. A successful invasion that leads to a different evolutionarily stable ecosystem involving the invading species then corresponds to a punctuated equilibrium in the fossil record.

Our use of these generalized ESS stability conditions ignores the possibility an ESS may be unstable due to stochastic effects when the population density is small (Fogel, 1997). In particular, our ecological dynamics are a

continuous-time deterministic dynamical system. Although stochastic effects are undoubtedly important for rare mutants to persist when they first appear, we assume the resident population is quite large (certainly, this must be true if these phenotypes are present in the fossil record) and so unlikely to disappear due to stochastic effects.

In Section 2, we develop a general theory of invasion and stasis. Section 3 then gives a detailed analysis of this theory applied to a two-habitat selection model where stasis and punctuated equilibria often appear automatically. Section 4 concludes by discussing the issues raised above in terms of the general theory of Section 2 and the habitat selection model of Section 3.

## 2 Successful Invasion and Stasis

As stated in the Introduction, the fossil record is consistent with the theory of punctuated equilibria where periods of stasis are followed by the occasional outburst of successful invasion by mutant species and/or mutant phenotypes of existing species. Since we want to distinguish between these two types of invasion and since a universally agreed upon definition of "species" is still unsettled (Wilson, 1999), we need an operative definition of species (Miller, 2001).

Here we again take the game theory perspective by placing an individual in a given species based on its interactions with other individuals. Specifically, two individuals are in the same species if they have the same possible behavioral phenotypes (i.e. pure strategy sets), the same interaction parameters (i.e. payoff functions) in all possible interactions, and the same basic fitness. In mathematical game theoretical terms, they are the same "player". These individuals in the same species may have different ecotypes in that they may use the possible phenotypes with different probabilities (the finite strategy case) or they may have different measures of a quantitative phenotype such as size or body weight (the case of a continuum of strategies). Of critical importance, individuals in the same species have the same payoff functions. In contrast, a new species has a new payoff function based on new phenotypes with absolutely new interactions. In game theoretical terms the new species is a new player.

This operative definition is essential since we will ignore genetic effects in our models by assuming asexual populations where individuals reproduce identical offspring by some mechanism that translates payoffs directly into re-

productive success (i.e. fitness). Since no sexual reproduction is necessary in this model, it would be possible to take each lineage to be a separate species (corresponding to assuming every payoff function is unrelated to every other) and so each successful mutation would lead to a new species. Although this is an important extreme, we are more interested in modelling invasion both within existing species as well as through the appearance of new species. Since, from our point of view of asexual populations, individuals only differ through their interactions, species can only be distinguished mathematically through payoff functions based on these interactions. (This concept of species is closely related to that defined through the generating function ( $G$ -function) approach of Vincent et al. (1993, 1996) although this literature often requires that members of the same species be capable of interbreeding even though genetic effects are still ignored. With a suitable bookkeeping method, the two definitions of species are equivalent.)

However, we will also often distinguish species by the rate with which mutations occur. The more frequent type of mutation can only change phenotypes (i.e. here only the individual behavior changes and not the interaction parameters of the payoff functions). From a biological viewpoint, this kind of mutation introduces only new ecotypes within existing species. Although these are the more frequent mutations, it is still assumed that the time scale on which they occur is slower than the time scale of ecology. The most rare mutation changes the interaction parameters as well. A new player in the evolutionary game theory model appears in the ecosystem, corresponding to a new biological species arising in this case. Since we suppose that both types of mutation are very rare compared to the speed of selection in the ecological system, at most two phenotypes can coexist in each species at a given time. In this setting, there is a clear distinction between the selection process (it is an ecological process), short term evolution (a process of within species invasion by strategy mutants), and long term evolution (a process corresponding to invasion by new players in a different species).

This assumption of separate time scales for different processes is related to the discussions of Simpson (1944, 1955) and Mayr (1960) where the “mode and tempo” of evolution are considered. In our terminology, the fast tempo of the ecological process is the mode that selects the ESS of the existing phenotypes. The second mode is through the appearance of mutations and this occurs at a much slower tempo (actually at two tempos depending on whether the mutants are of the same or different species). This second mode corresponds to the emergence of novel traits.

Before analyzing the consequences of these assumptions concerning mutation rates, we should mention that reproductive isolation can also be used in conjunction with the methods discussed above to distinguish between species and is a very important mechanism for the emergence of new species (Schluter, 2001). However, there is also the opinion (Morell, 1999; Schluter, 2001) that reproductive isolation is the result of trait (i.e. phenotype) selection. This latter ecological viewpoint fits well with the objective of this paper, which is to study punctuated equilibria and stasis through phenotypic evolution. In particular, we do not take into account the issue of sympatric versus allopatric speciation that is raised by those models that emphasize the effects of reproductive isolation.

We begin by recalling the concept of evolutionary ecological stability (Cressman and Garay, 2003a) if there is at most one mutant in each species. Some notation is needed for this purpose. Let there be  $N$  interacting species. Denote by  $\rho = (\rho_1, \rho_2, \dots, \rho_N)$  the vector of densities of the resident phenotypes  $p^* = (p^{1*}, p^{2*}, \dots, p^{N*})$  (e.g. the density of phenotype  $p^{k*}$  in species  $k$  is  $\rho_k$ ). Similarly,  $\mu \equiv (\mu_1, \mu_2, \dots, \mu_N)$  gives the densities of the mutant phenotypes  $p = (p^1, p^2, \dots, p^N)$ . Initially (i.e. just after mutation), the mutant densities are all low. Together,  $(\rho, p^*, \mu, p)$  specifies the *state* of the ecosystem. This state is also denoted by  $(\rho, p^*)$  when there is only the resident system (i.e. all  $\mu_k = 0$ ).

In this ecological system, each individual may have both intra and inter-specific interactions. Thus in general, the fitness of residents,  $W_{\rho_k}$ , and of mutants,  $W_{\mu_k}$ , depends on the state of the ecosystem system. Since fitness corresponds to reproduction of identical offspring, selection is modelled by the following Kolmogorov type dynamical system:

$$\dot{\rho}_k = \rho_k W_{\rho_k}(\rho, p^*, \mu, p) \quad (2)$$

$$\dot{\mu}_k = \mu_k W_{\mu_k}(\rho, p^*, \mu, p) \quad (3)$$

where  $k = 1, 2, \dots, N$ . This system also models the situation where some species  $k$  has only one possible phenotype (i.e. the resident phenotype) by setting  $\mu_k \equiv 0$  in this case.

**Remark.** Dynamical systems of Kolmogorov type are often used in models of coevolution. For instance, the fitness generating functions that lead to the static ESS Maximum Principle promoted by Vincent and co-workers (see Cohen et al. (1999) and the references therein) are generally of this

type. In fact, Brown (1990) applies this principle to give a game-theoretic interpretation to foraging behavior equilibria found by Rosenzweig (1987) in two-habitat selection models. Our two-habitat selection model in Section 3 is also of Kolmogorov type although we assume fitness is based on direct competition among individuals rather than indirectly through foraging on limited resources. The adaptive dynamics approach to coevolution (e.g. Dieckmann and Law, 1996) also starts with fitness functions of Kolmogorov type before eliminating density effects and studying the “canonical equation” of phenotypic evolution. Unlike our theory, here the density of a monomorphic population is assumed to instantaneously track its equilibrium value given the current phenotype (i.e. evolution occurs on the “stationary density surface” as it is called by Cressman and Garay (2003a, 2003b)). In contrast, our theory includes both density and phenotypic effects as follows.

We call the state  $(\rho^*, p^*)$  an *evolutionarily stable ecological equilibrium*<sup>1</sup> if  $\rho^*$  is an equilibrium of the resident system (2) with all  $\rho_k^* > 0$  and the corresponding equilibrium  $(\rho^*, p^*, \mathbf{0}, p)$  of the system (2),(3) is locally asymptotically stable for all possible mutants  $p$ . At such an equilibrium of the resident ecological system, no within species mutants can successfully invade since all mutant densities evolve to 0 (i.e. mutants will all die out) according to the above ecological dynamics. Of course, if all species have only one possible phenotype, the ecological equilibrium is evolutionarily stable if and only if the resident system (without mutation) is asymptotically stable at  $\rho^*$ . Thus, for system (1) in the Introduction, the equilibrium on the  $x$ -axis in Figure 1 is an evolutionarily stable ecological equilibrium in this terminology when  $x$  is equated with  $\rho_1$ , the density of the only phenotype for species one. However, as pointed out there, this equilibrium can be successfully invaded by species two.

In general, suppose that, in addition to the within species selection modelled by equations (2) and (3), the  $N$ -species evolutionarily stable ecological equilibrium  $(\rho^*, p^*)$  is invaded by a new player mutation whose payoff function  $W_{\mu_{N+1}}$  is given by new interactions parameters. Let  $\mu_{N+1}$  denote its

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<sup>1</sup>In Cressman and Garay (2003a), this is called a *monomorphic* evolutionarily stable ecological equilibrium since the model there also considered polymorphic cases where there were more than one resident phenotype in some species. In Vincent et al. (1996), it is called an *ecological stable equilibrium (ESE)*.

density and  $p^{N+1}$  its phenotypic strategy. Then

$$\begin{aligned}
\dot{\rho}_k &= \rho_k W_{\rho_k}(\rho, p^*, \mu, \mu_{N+1}, p, p^{N+1}) \\
\dot{\mu}_k &= \mu_k W_{\mu_k}(\rho, p^*, \mu, \mu_{N+1}, p, p^{N+1}) \\
\dot{\mu}_{N+1} &= \mu_{N+1} W_{\mu_{N+1}}(\rho, p^*, \mu, \mu_{N+1}, p, p^{N+1})
\end{aligned} \tag{4}$$

where now  $W_{\rho_k}$  and  $W_{\mu_k}$  for  $k = 1, 2, \dots, N$  also depend on  $\mu_{N+1}$  and  $p^{N+1}$ .

We say that the new species with strategy  $p^{N+1}$  successfully invades the resident system  $(\rho^*, p^*)$  under the mutations  $\mu$  if  $(\rho^*, \mathbf{0}, 0)$  is an unstable equilibrium of (4). After a successful invasion, further evolution between species will take place since the adaptive phenotypes will change in each species according to the new ecological situation. This may or may not lead to stasis involving the new species. For instance, speciation does not occur if the mutant phenotype  $p^{N+1}$  eventually dies out and is not replaced by any other phenotype from species  $N + 1$ . From an evolutionary ecological viewpoint, a punctuated equilibrium occurs if the new  $(N + 1)$ -species ecosystem has an evolutionarily stable ecological equilibrium (i.e. an equilibrium that is stable not only from an ecological but also from an evolutionary point of view). That is, there must be  $N + 1$  phenotypes (one for each of the interacting species)  $\bar{p} = (\bar{p}^1, \bar{p}^2, \dots, \bar{p}^N, \bar{p}^{(N+1)})$  with positive densities  $\bar{\rho} = (\bar{\rho}_1, \bar{\rho}_2, \dots, \bar{\rho}_N, \bar{\rho}_{N+1})$  that forms an evolutionarily stable ecological equilibrium against all possible strategy mutants in the  $N + 1$  species. (Stasis will also occur if this  $(N + 1)$ -species ecosystem evolves to an equilibrium that includes individuals from species  $N + 1$  (i.e.  $\bar{\rho}_{N+1} > 0$ ) while some of the other species go extinct. We do not discuss this possibility further here in general terms or for the habitat-selection model of Section 3.)

Thus, assuming both competing species have only one possible phenotype, Figure 1 in the Introduction illustrates a the emergence of a new species since the successful invasion of species one (here  $y$  is equated with the density  $\mu_2$  of the mutant in species two) evolves to a new stable equilibrium where both species are present. To incorporate the stasis phenomenon into this two-species competitive system, we must allow the possibility of other phenotypes in the species.

Unfortunately, when there are several possible phenotypes for some species, the general dependence of interaction parameters on the morphological phenotypic parameters is not well understood. Moreover, an adequate description of the space of all possible morphological parameters is also problematic. Consequently, we do not discuss further directly the general theory of inva-

sion and coevolutionary speciation for the stasis and punctuated equilibria developed by the model based on (2),(3),(4).

Instead, the following section will demonstrate our approach through the ecological example of habitat selection. One reason for this choice is that the habitat selection model simplifies such issues as assortative mating (which may form the basis for the genetic process of speciation through reproductive isolation evolving in the separate habitats) (Felsenstein, 1981; Rice, 1984; Johnson and Gullberg, 1998). Our analysis ignores this genetic process by restricting the investigation to the evolutionary ecological aspects of the habitat selection process.

We examine situations where initially a single species is at a stable equilibrium in a two-habitat model. Here, there are two pure strategies; namely, which of the two habitats the individual chooses. However, we are more interested in the monomorphic perspective where all resident individuals use the same behavior strategy that specifies the proportion of their time they spend in each habitat. In Section 3.1, we briefly summarize this model and show when this resident system is stable against invasion by any other small subpopulation of this species using a mutant strategy. Then, in Section 3.2, we establish conditions when this single-species equilibrium is successfully invaded by an emerging new species. In such cases, the basic question becomes what happens to the two-species system in the long term. Section 3.3 shows we often arrive at a stable monomorphic system where both species coexist. Such a phenomenon is then interpreted as a period of stasis corresponding to a punctuated equilibrium.

### **3 The Two-Habitat Monomorphic Model**

In Sections 3.1, 3.2 and 3.3, we determine the theoretical characterization of evolutionarily stable ecological equilibria in general habitat selection models with either one or two species and two habitats. Section 3.4 then develops a particular example that illustrates this theory for specific choices of population parameters. We begin by giving common assumptions for both models. Individuals in a given species are assumed to be morphologically indistinguishable, their only difference is how each individual divides its time between the two habitats. Thus, the two possible pure strategies are the choice of habitat and an individual's phenotype is the frequencies with which it uses the different habitats. We assume the fitness of a pure strategist in

a particular habitat depends only on the species' densities in this habitat. Finally, individuals move freely and without cost between the two habitats and so the phenotypic frequencies (together with species' densities in each habitat) determine individual fitness (see, for example, (7) below).

### 3.1 Single Species Evolutionarily Stable Ecological Equilibrium

Let  $m_i$  ( $i = 1, 2$ ) be the density of this species in habitat  $i$ . Then  $M = m_1 + m_2$  is the total population size and  $p_i = m_i/M$  is the proportion of the population in habitat  $i$ . The frequency vector  $p = (p_1, p_2)$  will be called the population (mean) strategy. It is a vector in the *strategy space*  $\Delta^2 \equiv \{(p_1, p_2) \mid p_1 + p_2 = 1 \text{ and } p_i \geq 0\}$ . When the population is monomorphic (i.e. when all individuals are phenotypically identical), this  $p$  also denotes the individual phenotype. We say the population is *interior* if there are individuals in both habitats (i.e. if  $p$  is in the interior of  $\Delta^2$ ).

The success  $V_i$  of an individual in habitat  $i$  is assumed to be the per capita growth rate of a logistic equation; namely,

$$V_i(m_1, m_2) = r_i \left( 1 - \frac{m_i}{K_i} \right) \quad (5)$$

where  $r_i$  is the intrinsic growth rate in habitat  $i$  and  $K_i$  is its carrying capacity. Both these parameters are positive and, when taken in combination from the two habitats, can be interpreted as the species' morphological parameters based on indirect competition for resources among individuals. (Notice a change in notation from Section 2. For the general  $N$ -species theory developed there, the index  $k$  referred to the  $k$ th species. Since there will be at most two species in Section 3, we do not index them and reserve the subscripts  $i, j$  to indicate the habitat. Furthermore,  $p \in \Delta^2$  denotes the phenotype of an individual in species one rather than  $p^1$  and, in Section 3.2 where a second species is introduced,  $q \in \Delta^2$  is an individual phenotype in species two.)

The payoffs given by (5) will usually be written as functions of the population's total size and mean strategy. Thus

$$V_i(p, M) = r_i \left( 1 - \frac{p_i M}{K_i} \right). \quad (6)$$

Since there is costless movement between habitats, an individual with phenotype  $p'$  has fitness

$$p'_1 V_1(p, M) + p'_2 V_2(p, M). \quad (7)$$

We want to check when an interior monomorphic population is “uninvadable” by any mutant monomorphic subpopulation. Let  $p^*, p \in \Delta^2$  denote the behavioral strategies of the resident and mutant populations respectively and  $\rho_1, \mu_1 \in \mathbf{R}$  the density of resident and mutant individuals. (Notice that we continue to denote these densities as  $\rho_1$  and  $\mu_1$  to emphasize they are variables for species 1. Although these subscripts could be dropped in this section, this convention becomes more important when we introduce a second species in the following section.)

Since  $p^*$  is in the interior of  $\Delta^2$ ,  $p^* = (p_1^*, p_2^*)$  where  $p_1^* > 0$  and  $p_2^* > 0$ . The fitness of the resident population is

$$\begin{aligned} W_{\rho_1}(\rho_1, p^*, \mu_1, p) &= p_1^* V_1 + p_2^* V_2 \\ &= p_1^* r_1 \left( 1 - \frac{\rho_1 p_1^* + \mu_1 p_1}{K_1} \right) + p_2^* r_2 \left( 1 - \frac{\rho_1 p_2^* + \mu_1 p_2}{K_2} \right) \end{aligned}$$

and the mutant fitness is

$$\begin{aligned} W_{\mu_1}(\rho_1, p^*, \mu_1, p) &= p_1 V_1 + p_2 V_2 \\ &= p_1 r_1 \left( 1 - \frac{\rho_1 p_1^* + \mu_1 p_1}{K_1} \right) + p_2 r_2 \left( 1 - \frac{\rho_1 p_2^* + \mu_1 p_2}{K_2} \right) \end{aligned}$$

Thus the population dynamics is

$$\begin{aligned} \dot{\rho}_1 &= \rho_1 \left( p_1^* r_1 \left( 1 - \frac{\rho_1 p_1^* + \mu_1 p_1}{K_1} \right) + p_2^* r_2 \left( 1 - \frac{\rho_1 p_2^* + \mu_1 p_2}{K_2} \right) \right) \\ \dot{\mu}_1 &= \mu_1 \left( p_1 r_1 \left( 1 - \frac{\rho_1 p_1^* + \mu_1 p_1}{K_1} \right) + p_2 r_2 \left( 1 - \frac{\rho_1 p_2^* + \mu_1 p_2}{K_2} \right) \right) \end{aligned} \quad (8)$$

If the resident population cannot be invaded by  $p = (1, 0)$  (respectively  $p = (0, 1)$ ), we see that  $r_1 \left( 1 - \frac{\rho_1 p_1^*}{K_1} \right) \leq 0$  (respectively  $r_2 \left( 1 - \frac{\rho_1 p_2^*}{K_2} \right) \leq 0$ ). Since an equilibrium  $(\rho_1^*, 0)$  of (8) with  $\rho_1^* > 0$  requires  $p_1^* r_1 \left( 1 - \frac{\rho_1^* p_1^*}{K_1} \right) + p_2^* r_2 \left( 1 - \frac{\rho_1^* p_2^*}{K_2} \right) = 0$ , we have  $\left( 1 - \frac{\rho_1^* p_1^*}{K_1} \right) = \left( 1 - \frac{\rho_1^* p_2^*}{K_2} \right) = 0$ . That is, an uninvadable resident population satisfies

$$\begin{aligned} \rho_1^* &= K_1 + K_2 \\ p_i^* &= K_i / (K_1 + K_2). \end{aligned} \quad (9)$$

This equilibrium is called the *ideal free distribution (IFD)* (Fretwell and Lucas, 1970) at equilibrium density. Intuitively, each habitat is occupied to its carrying capacity since  $m_i^* = \rho_1^* p_i^* = K_i$ . The equilibrium  $\rho_1^*$  is clearly stable for the resident system

$$\begin{aligned}\dot{\rho}_1 &= \rho_1 \left( p_1^* r_1 \left( 1 - \frac{\rho_1 p_1^*}{K_1} \right) + p_2^* r_2 \left( 1 - \frac{\rho_1 p_2^*}{K_2} \right) \right) \\ &= \rho_1 \left( \frac{r_1 (p_1^*)^2}{K_1} + \frac{r_2 (p_2^*)^2}{K_2} \right) (\rho_1^* - \rho_1)\end{aligned}$$

since  $\dot{\rho}_1 > 0$  if and only if  $\rho_1 < \rho_1^*$ . Furthermore,  $(\rho_1^*, 0)$  is asymptotically stable for (8) although this is not so obvious since its linearization automatically has a zero eigenvalue. In fact, global asymptotic stability can be shown from the two dimensional phase diagram for the dynamics (8) rewritten as

$$\begin{aligned}\dot{\rho}_1 &= \rho_1 \left[ \left( \frac{r_1 (p_1^*)^2}{K_1} + \frac{r_2 (p_2^*)^2}{K_2} \right) (\rho_1^* - \rho_1) - \left( \frac{r_1 p_1}{K_1 + K_2} + \frac{r_2 p_2}{K_1 + K_2} \right) \mu_1 \right] \\ \dot{\mu}_1 &= \mu_1 \left[ \frac{r_1 p_1 + r_2 p_2}{K_1 + K_2} (\rho_1^* - \rho_1) - \left( \frac{r_1 (p_1)^2}{K_1} + \frac{r_2 (p_2)^2}{K_2} \right) \mu_1 \right].\end{aligned}\quad (10)$$

Specifically, the linear nullclines in the first quadrant (i.e. the lines where  $\dot{\rho}_1 = 0$  and  $\dot{\mu}_1 = 0$ ) both have negative slope and  $\dot{\rho}_1 = 0$  is steeper than  $\dot{\mu}_1 = 0$ . (A similar analysis of the nullclines for Figure 1 shows global asymptotic stability of the coexistence equilibrium of system (1) in the Introduction. Local asymptotic stability of (8) can also be shown by analyzing the quadratic terms in (10) using the B-matrix approach of Cressman and Garay (2003a, 2003b). For more discussion of this technique, see also Section 3.3 below and especially the Appendix where it is used in a four dimensional system.)

Figure 2 about here.

Thus, for the single-species habitat selection model (5), the ideal free distribution  $(\rho_1^*, p^*)$  given by (9) is automatically an evolutionarily stable ecological equilibrium.

**Remark.** The results of this section can also be interpreted as illustrating stasis in a single species setting. Specifically, suppose initially all individuals are in habitat 1. The resident system will evolve to its stasis level; namely,

the carrying capacity  $K_1$  in habitat 1. Introduction of a mutant phenotype that moves between both habitats will successfully invade. Assuming the population returns to a monomorphism, the new stasis level will be the IFD with total carrying capacity  $K_1 + K_2$ .

### 3.2 Invasion by a Second (Competitive) Species

In this section, we investigate the invasion of  $(\rho_1^*, p^*)$  by a second competitive species. For the two-species competitive system, we generalize fitness (5) in each habitat by taking the general Lotka-Volterra type individual fitness functions

$$\begin{aligned} V_i^1(m_1, m_2, n_1, n_2) &= r_i \left( 1 - \frac{m_i}{K_i} - \frac{\alpha_i n_i}{K_i} \right) \quad i = 1, 2 \\ V_j^2(m_1, m_2, n_1, n_2) &= s_j \left( 1 - \frac{n_j}{L_j} - \frac{\beta_j m_j}{L_j} \right) \quad j = 1, 2. \end{aligned} \quad (11)$$

As for the single-species model of Section 3.1,  $V_i^1$  is the individual fitness of species one in habitat  $i$ ;  $m_i$  is its density;  $r_i$  and  $K_i$  are the parameters of the logistic equation (5) when the density  $n_i$  of species two is 0. When  $n_i > 0$ ,  $\alpha_i$  is the interspecific competition coefficient for species one individuals interacting with species two in habitat  $i$ . Analogously,  $V_j^2$  is the individual fitness of species two in habitat  $j$  and  $\beta_j$  is the interspecific competition coefficient for species two individuals. Notice that the fitness parameters for species two (i.e.  $s_j, L_j$  and  $\beta_j$ ) are in general totally unrelated to those of species one so that species two may model a drastic morphological change during a short evolutionary outburst following a long period of stasis. The notation for this competitive system follows that of Cressman et al. (2004) (see also Krivan and Sirot, 2002) for the special case where  $\alpha_1 = \alpha_2 = \alpha$  and  $\beta_1 = \beta_2 = \beta$ .

As in Section 3.1, the invasion of a monomorphism requires fitness functions be written in terms of the species' frequencies and total population sizes. Let  $M$  and  $N$  be the total population sizes of species one and two respectively; vector  $p = (p_1, p_2)$  be the mean strategy of species one (i.e.  $p_i$  is the proportion of species one in habitat  $i$ ); vector  $q = (q_1, q_2)$  be the mean strategy of species two. (Note that we continue to use  $p = (p_1, p_2)$  and  $q = (q_1, q_2)$  for the mean strategy of species one and two respectively in place of the notation  $p^1$  and  $p^2$  in Section 2.) Then the fitness of pure strategists

can be rewritten as

$$\begin{aligned} V_i^1(p, M, q, N) &= r_i \left( 1 - \frac{p_i M}{K_i} - \frac{\alpha_i q_i N}{K_i} \right) \quad i = 1, 2 \\ V_j^2(p, M, q, N) &= s_j \left( 1 - \frac{q_j N}{L_j} - \frac{\beta_j p_j M}{L_j} \right) \quad j = 1, 2. \end{aligned} \quad (12)$$

An individual in species one (respectively, two) with phenotype  $p'$  (respectively  $q'$ ) has fitness  $p'_1 V_1^1(p, M, q, N) + p'_2 V_2^1(p, M, q, N)$  (respectively,  $q'_1 V_1^2(p, M, q, N) + q'_2 V_2^2(p, M, q, N)$ ).

Suppose the single-species evolutionarily stable ecological equilibrium  $(\rho_1^*, p^*)$  of Section 3.1 is invaded by the mutant monomorphic subpopulations of species one and two with phenotypes  $p$  and  $q$  respectively. From (9), we have  $\rho_1^* = K_1 + K_2$  and  $p_i^* = K_i / (K_1 + K_2)$ . Let  $\rho_1, \mu_1$  and  $\mu_2$  be the densities of individuals with phenotypes  $p^*, p$  and  $q$ . Then, for instance,  $W_{\rho_1}(\rho_1, p^*, \mu_1, \mu_2, p, q) = p_1^* V_1^1(\frac{\rho_1 p^* + \mu_1 p}{\rho_1 + \mu_1}, \rho_1 + \mu_1, q, \mu_2) + p_2^* V_2^1(\frac{\rho_1 p^* + \mu_1 p}{\rho_1 + \mu_1}, \rho_1 + \mu_1, q, \mu_2)$ . Thus, the invasion dynamics (cf. (4)) becomes (using fitnesses  $V_i^1$  and  $V_j^2$  written in the form (12) evaluated at  $(\frac{\rho_1 p^* + \mu_1 p}{\rho_1 + \mu_1}, \rho_1 + \mu_1, q, \mu_2)$ )

$$\begin{aligned} \dot{\rho}_1 &= \rho_1 (p_1^* V_1^1 + p_2^* V_2^1) \\ \dot{\mu}_1 &= \mu_1 (p_1 V_1^1 + p_2 V_2^1) \\ \dot{\mu}_2 &= \mu_2 (q_1 V_1^2 + q_2 V_2^2). \end{aligned} \quad (13)$$

Since  $(\rho_1^*, 0)$  is a (globally) asymptotically stable equilibrium for the single-species system (i.e. when  $\mu_2$  is absent or taken as  $\mu_2 \equiv 0$ ), this invasion is successful if the individual fitness of mutant  $q$  at this equilibrium

$$W_{\mu_2}(\rho_1, p^*, \mu_1, \mu_2, p, q) = q_1 V_1^2(\rho_1^* p^*, \rho_1^*, 0, 0) + q_2 V_2^2(\rho_1^* p^*, \rho_1^*, 0, 0)$$

is positive (and unsuccessful if negative). Here, we make the nondegeneracy assumption that the invasion fitness,  $W_{\mu_2}(\rho_1, p^*, \mu_1, \mu_2, p, q)$ , of mutant  $q$  of species two is not zero. (Note that we cannot assume this for the species one mutant phenotype  $p$  since its fitness is automatically zero at  $(\rho_1^*, 0)$ .) Since  $\rho_1^* p_i^*$  is the carrying capacity  $K_i$  of species one in habitat  $i$ ,  $q_1 V_1^2(\rho_1^* p^*, \rho_1^*, 0, 0) + q_2 V_2^2(\rho_1^* p^*, \rho_1^*, 0, 0) = q_1 s_1 \left( 1 - \frac{\beta_1 K_1}{L_1} \right) + q_2 s_2 \left( 1 - \frac{\beta_2 K_2}{L_2} \right)$ .

In summary, there will be some mutant strategy  $q$  in species two (i.e. some  $q \in \Delta^2$  with  $0 \leq q_1 \leq 1$ ) that can invade the single-species evolutionarily stable ecological equilibrium  $(\rho_1^*, p^*)$  if

$$\text{either } \beta_1 K_1 < L_1 \text{ or } \beta_2 K_2 < L_2. \quad (14)$$

That is, successful invasion is equivalent to the requirement that, for at least one habitat  $i$ , the carrying capacity of species two (i.e.  $L_i$ ) is larger than that of species one adjusted by the interspecific competition coefficient of species two (i.e. larger than  $\beta_i K_i$ ). From the ecological viewpoint, this means that in at least one of the habitats, one species cannot exhaust the resources from the perspective of the other species.

### 3.3 Two Species Evolutionarily Stable Ecological Equilibrium and Stasis through Coevolutionary

The previous section completely characterizes through condition (14) when there is the potential for the single species IFD of Section 3.1 to evolve to a period of stasis involving a second species. We are particularly interested in situations where, after successful invasion since (14) holds, the resultant two-species system has an equilibrium where both species are present in both habitats. Such a two-species interior equilibrium can be found by considering the polymorphic case where each individual is a pure strategist (i.e. every individual spends all its time in one of the habitats). Then  $V_i^1$  and  $V_i^2$  must both be zero in (11) for  $i = 1, 2$ . The algebraic solution is

$$\bar{m}_i^* = \frac{K_i - \alpha_i L_i}{1 - \alpha_i \beta_i}, \quad \bar{n}_i^* = \frac{L_i - \beta_i K_i}{1 - \alpha_i \beta_i}, \quad \text{for } i = 1, 2.$$

From (14), the positivity of both  $n_1^*$  and  $n_2^*$  implies  $L_i > \beta_i K_i$  for  $i = 1, 2$ . That is, any mutant strategy  $q \in \Delta^2$  of species two can successfully invade the IFD of species one (i.e. the single-species evolutionarily stable ecological equilibrium) given in Section 3.1. Furthermore, this positivity also implies

$$1 - \alpha_i \beta_i > 0 \tag{15}$$

for  $i = 1, 2$ . Inequality (15) is interesting in its own right since this is the classical condition (cf. Hofbauer and Sigmund, 1998) that two-species coexistence is stable in each separate single-habitat model (see also the discussion after (18) below). It also implies that  $K_i > \alpha_i L_i$  (i.e. species one mutants can successfully invade the single-species evolutionarily stable ecological equilibrium of species two). We will assume these inequalities

$$\begin{aligned} 1 - \alpha_i \beta_i &> 0 \\ K_i - \alpha_i L_i &> 0 \\ L_i - \beta_i K_i &> 0 \end{aligned} \tag{16}$$

for the remainder of this section unless otherwise stated.

The corresponding monomorphic equilibrium has resident strategies  $p^*$  and  $q^*$  in the interior of  $\Delta^2$  given by

$$\begin{aligned}\bar{p}_i^* &= \frac{K_i - \alpha_i L_i}{K_i - \alpha_1 L_1 + K_2 - \alpha_2 L_2} \\ \bar{q}_i^* &= \frac{L_i - \beta_i K_i}{L_i - \beta_1 K_1 + L_2 - \beta_2 K_2}.\end{aligned}$$

and equilibrium densities  $(\bar{\rho}_1^*, \bar{\rho}_2^*) = (\bar{m}_1^* + \bar{m}_2^*, \bar{n}_1^* + \bar{n}_2^*)$ . A two-species co-evolutionary period of stasis will emerge if this equilibrium is a two-species evolutionarily stable ecological equilibrium (i.e. it must be locally asymptotically stable for the resident system and it cannot be successfully invaded by mutant phenotypes  $p$  and  $q$  in species one and two respectively).

Let us first get stability conditions for the resident dynamics. The resident dynamics is

$$\begin{aligned}\dot{\rho}_1 &= \rho_1 (\bar{p}_1^* V_1^1(\rho_1 \bar{p}_1^*, \rho_1 \bar{p}_2^*, \rho_2 \bar{q}_1^*, \rho_2 \bar{q}_2^*) + \bar{p}_2^* V_2^1(\rho_1 \bar{p}_1^*, \rho_1 \bar{p}_2^*, \rho_2 \bar{q}_1^*, \rho_2 \bar{q}_2^*)) \\ \dot{\rho}_2 &= \rho_2 (\bar{q}_1^* V_1^2(\rho_1 \bar{p}_1^*, \rho_1 \bar{p}_2^*, \rho_2 \bar{q}_1^*, \rho_2 \bar{q}_2^*) + \bar{q}_2^* V_2^2(\rho_1 \bar{p}_1^*, \rho_1 \bar{p}_2^*, \rho_2 \bar{q}_1^*, \rho_2 \bar{q}_2^*))\end{aligned}\quad (17)$$

with equilibrium  $(\bar{\rho}_1^*, \bar{\rho}_2^*) = (\bar{m}_1^* + \bar{m}_2^*, \bar{n}_1^* + \bar{n}_2^*)$ . The linearized dynamics is

$$\begin{bmatrix} \dot{\rho}_1 \\ \dot{\rho}_2 \end{bmatrix} \cong \begin{bmatrix} \bar{\rho}_1^* & 0 \\ 0 & \bar{\rho}_2^* \end{bmatrix} J^{RR} \begin{bmatrix} \rho_1 - \bar{\rho}_1^* \\ \rho_2 - \bar{\rho}_2^* \end{bmatrix} \text{ where } J^{RR} \text{ has entries}$$

$$J_{ij}^{RR} \equiv \frac{\partial (\dot{\rho}_i / \rho_i)}{\partial \rho_j}.$$

The calculation of these partials evaluated at the equilibrium yields

$$-J^{RR} = \begin{bmatrix} \hat{r}_1 \bar{p}_1^{*2} + \hat{r}_2 \bar{p}_2^{*2} & \alpha_1 \hat{r}_1 \bar{p}_1^* \bar{q}_1^* + \alpha_2 \hat{r}_2 \bar{p}_2^* \bar{q}_2^* \\ \beta_1 \hat{s}_1 \bar{p}_1^* \bar{q}_1^* + \beta_2 \hat{s}_2 \bar{p}_2^* \bar{q}_2^* & \hat{s}_1 \bar{q}_1^{*2} + \hat{s}_2 \bar{q}_2^{*2} \end{bmatrix}$$

with  $\hat{r}_i \equiv \frac{r_i}{K_i}$  and  $\hat{s}_i \equiv \frac{s_i}{L_i}$ . Assuming nondegeneracy, since the diagonal entries of  $J^{RR}$  are negative, the resident system is asymptotically stable if and only if

$$\begin{aligned}\det J^{RR} &= (\hat{r}_1 \bar{p}_1^{*2} + \hat{r}_2 \bar{p}_2^{*2}) (\hat{s}_1 \bar{q}_1^{*2} + \hat{s}_2 \bar{q}_2^{*2}) \\ &\quad - (\alpha_1 \hat{r}_1 \bar{p}_1^* \bar{q}_1^* + \alpha_2 \hat{r}_2 \bar{p}_2^* \bar{q}_2^*) (\beta_1 \hat{s}_1 \bar{p}_1^* \bar{q}_1^* + \beta_2 \hat{s}_2 \bar{p}_2^* \bar{q}_2^*) \\ &= \hat{r}_1 \hat{s}_1 \bar{p}_1^{*2} \bar{q}_1^{*2} (1 - \alpha_1 \beta_1) + \hat{r}_2 \hat{s}_2 \bar{p}_2^{*2} \bar{q}_2^{*2} (1 - \alpha_2 \beta_2) \\ &\quad + \hat{r}_1 \hat{s}_2 (\bar{p}_1^{*2} \bar{q}_2^{*2} - \alpha_1 \beta_2 \bar{p}_1^* \bar{q}_1^* \bar{p}_2^* \bar{q}_2^*) + \hat{r}_2 \hat{s}_1 (\bar{p}_2^{*2} \bar{q}_1^{*2} - \alpha_2 \beta_1 \bar{p}_1^* \bar{q}_1^* \bar{p}_2^* \bar{q}_2^*) \\ &> 0.\end{aligned}\quad (18)$$

From (18), the stability of the resident system is not the same as stability of the two separate habitat models (which, from (15) has the exact requirement  $1 - \alpha_i\beta_i > 0$  for  $i = 1, 2$ ). In particular, there are two-habitat systems where a single-species evolutionarily stable ecological equilibrium can be successfully invaded by a second species and the resultant two-species two-habitat system has an equilibrium with both species present in habitats 1 and 2 but this equilibrium does not yield a period of stasis since it is not a two-species evolutionarily stable ecological equilibrium.

For the remainder of this section, suppose the resident two-species system is stable at an interior equilibrium (i.e. all the inequalities in (16) and (18) hold). For instance, this will happen if the products  $\alpha_i\beta_j$  of interspecific competition coefficients are small for all  $i$  and  $j$ . For this to be a two-species evolutionarily stable ecological equilibrium, we require it to be locally asymptotically stable under invasion by any mutant strategies  $p$  and  $q$  in species one and two respectively. From (2) and (3) using the notation of Section 3, we have the four-dimensional system

$$\begin{aligned}
\dot{\rho}_1 &= \rho_1 \left( \begin{array}{l} \bar{p}_1^* V_1^1(\rho_1 \bar{p}_1^* + \mu_1 p_1, \rho_1 \bar{p}_2^* + \mu_1 p_2, \rho_2 \bar{q}_1^* + \mu_2 q_1, \rho_2 \bar{q}_2^* + \mu_2 q_2) \\ + \bar{p}_2^* V_2^1(\rho_1 \bar{p}_1^* + \mu_1 p_1, \rho_1 \bar{p}_2^* + \mu_1 p_2, \rho_2 \bar{q}_1^* + \mu_2 q_1, \rho_2 \bar{q}_2^* + \mu_2 q_2) \end{array} \right) \\
\dot{\rho}_2 &= \rho_2 \left( \begin{array}{l} \bar{q}_1^* V_1^2(\rho_1 \bar{p}_1^* + \mu_1 p_1, \rho_1 \bar{p}_2^* + \mu_1 p_2, \rho_2 \bar{q}_1^* + \mu_2 q_1, \rho_2 \bar{q}_2^* + \mu_2 q_2) \\ + \bar{q}_2^* V_2^2(\rho_1 \bar{p}_1^* + \mu_1 p_1, \rho_1 \bar{p}_2^* + \mu_1 p_2, \rho_2 \bar{q}_1^* + \mu_2 q_1, \rho_2 \bar{q}_2^* + \mu_2 q_2) \end{array} \right) \\
\dot{\mu}_1 &= \mu_1 \left( \begin{array}{l} p_1 V_1^1(\rho_1 \bar{p}_1^* + \mu_1 p_1, \rho_1 \bar{p}_2^* + \mu_1 p_2, \rho_2 \bar{q}_1^* + \mu_2 q_1, \rho_2 \bar{q}_2^* + \mu_2 q_2) \\ + p_2 V_2^1(\rho_1 \bar{p}_1^* + \mu_1 p_1, \rho_1 \bar{p}_2^* + \mu_1 p_2, \rho_2 \bar{q}_1^* + \mu_2 q_1, \rho_2 \bar{q}_2^* + \mu_2 q_2) \end{array} \right) \\
\dot{\mu}_2 &= \mu_2 \left( \begin{array}{l} q_1 V_1^2(\rho_1 \bar{p}_1^* + \mu_1 p_1, \rho_1 \bar{p}_2^* + \mu_1 p_2, \rho_2 \bar{q}_1^* + \mu_2 q_1, \rho_2 \bar{q}_2^* + \mu_2 q_2) \\ + q_2 V_2^2(\rho_1 \bar{p}_1^* + \mu_1 p_1, \rho_1 \bar{p}_2^* + \mu_1 p_2, \rho_2 \bar{q}_1^* + \mu_2 q_1, \rho_2 \bar{q}_2^* + \mu_2 q_2) \end{array} \right).
\end{aligned} \tag{19}$$

From the Appendix, we find that two-species stability of the monomorphic resident system (that has mutual coexistence in both habitats) implies the resident system is uninvadable by any monomorphic subsystem  $(p, q)$ .<sup>2</sup> That is, inequalities (16) and (18) characterize the existence of an interior two-species evolutionarily stable ecological equilibrium. For the habitat selection model, Cressman et al. (2004) call this equilibrium a two-species ideal free

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<sup>2</sup>Notice that this is the same result as for a single species (in Section 3.1) except for single species the monomorphic resident system with both habitats occupied is globally asymptotically stable through a phase plane analysis of the two-dimensional dynamical system. For two-species, the four-dimensional phase portrait is intractable and only local asymptotic stability is shown in the Appendix by using B-matrices.

distribution at equilibrium densities, in analogy to the single-species IFD of Fretwell and Lucas (1970).

In summary, the single-species IFD of Section 3.1 becomes a punctuated equilibrium in the long run for the two-habitat selection model whenever an interior two-species IFD exists.

### 3.4 An Example

This section examines evolutionarily stable ecological equilibria for a particular set of population parameters in (12) in order to illustrate the general theory developed in Sections 3.1, 3.2 and 3.3 for two-habitat selection. Specifically, for species one, let  $r_i = 20$ ,  $K_i = 5$  and  $\alpha_i = \frac{1}{2}$  for  $i = 1, 2$ . In particular, the two habitats are identical as far as species one is concerned. They are also identical for species two where we take  $s_i = 15$ ,  $L_i = \frac{15}{2}$  and  $\beta_i = 1$  for  $i = 1, 2$ . This set of parameters was chosen in such a way that the existence of a two-species evolutionarily stable ecological equilibrium is closely related to the Lotka-Volterra competition system (1) in the Introduction (see system (20) below).

Following Section 3.1, the (single-species) ideal free distribution (9) is  $(\rho_1^*, p^*)$  where  $\rho_1^* = 10$  and  $p^* = (\frac{1}{2}, \frac{1}{2})$ . This evolutionarily stable ecological equilibrium is a monomorphism that successfully invades the unstable equilibrium where all individuals are in only one of the habitats and density is 5. See Figure 2. The latter unstable equilibrium corresponds to a period of stasis before this species discovers the other habitat and the population evolves quickly to its carrying capacity in both habitats.

From Section 3.2, the second species will successfully invade  $(\rho_1^*, p^*)$  since condition (14) is satisfied (i.e.  $\beta_i K_i = 5 < \frac{15}{2} = L_i$ ). In fact, since both inequalities in (14) hold, any monomorphic species two population with strategy  $q = (q_1, q_2)$  (i.e. each individual of species two spends a proportion  $q_i$  of its time in habitat  $i$ ) can invade. However, it seems more plausible that the initial invaders from species two will only appear in one of the habitats, say habitat 1 and so  $q = (1, 0)$ . With our set of parameters, the new monomorphic equilibrium from (12) with species one in both habitats and species two only in habitat 1 is then  $(\rho_1, p, \rho_2, q)$  with  $\rho_1 = \frac{15}{2}$ ,  $p = (\frac{1}{3}, \frac{2}{3})$ ,  $\rho_2 = 5$  and  $q = (1, 0)$ . As a resident system, this equilibrium is stable and so represents another period of stasis until individuals in species two discover the benefit of spending part of their time in habitat 2. That is,  $(\rho_1^*, p^*)$  has been replaced temporarily by  $(\rho_1, p, \rho_2, q)$ . In other words, the single-species evolutionarily

stable ecological equilibrium strategy  $p^* = (\frac{1}{2}, \frac{1}{2})$  is completely eliminated by the monomorphism at  $p = (\frac{1}{3}, \frac{2}{3})$  through the introduction of species two individuals in habitat 1.

Figure 3 about here.

The above application of the theory from Section 3.2 does not mean the new (two-species) equilibrium  $(\rho_1, p, \rho_2, q)$  is an evolutionarily stable ecological equilibrium. However, from (12), there is in fact an interior equilibrium where both species are present in both habitats; namely,  $(\bar{\rho}_1^*, \bar{p}^*, \bar{\rho}_2^*, \bar{q}^*)$  where  $\bar{\rho}_1^* = 5, \bar{p}^* = (\frac{1}{2}, \frac{1}{2}), \bar{\rho}_2^* = 10, \bar{q}^* = (\frac{1}{2}, \frac{1}{2})$ . From (17), the dynamical system for the resident monomorphic populations with phenotypes  $\bar{p}^*$  and  $\bar{q}^*$  is

$$\begin{aligned}\dot{\rho}_1 &= \rho_1 (20 - 2\rho_1 - \rho_2) \\ \dot{\rho}_2 &= \rho_2 (15 - \rho_1 - \rho_2).\end{aligned}\tag{20}$$

This system is identical to (1) and so, from the Introduction, the resident system is globally asymptotically stable (see Figure 1 there). From Section 3.3, it is also asymptotically stable with respect to simultaneous invasion by monomorphic subpopulations in both species. Thus,  $(\bar{\rho}_1^*, \bar{p}^*, \bar{\rho}_2^*, \bar{q}^*)$  is an evolutionarily stable ecological equilibrium corresponding to a punctuated equilibrium involving two species. Stasis will be maintained at least until this equilibrium is successfully invaded by a rare mutant from a third species.

## 4 Conclusion

This paper develops a general theory of invasion and stasis through coevolution by combining the ecological effects of species' densities with the evolutionary effects of changing phenotypes. One step in this process is the successful invasion by a new monomorphic species with a fixed phenotype. Since phenotypes are fixed and only densities vary in this initial step, the successful invasion is then an instance of ecological speciation as described by Schluter (2001). However, this ecological speciation approach does not take account of the evolutionary effects the new species will eventually have on the phenotypic makeup of the system. That is, ecological speciation is only concerned with short term stasis. Our coevolutionary theory goes further by modelling the evolutionary effects through the game-theoretical method of individual fitness functions depending on both the density and phenotypic

makeup of the species. Here, long term stasis corresponds to resident systems where no monomorphic subpopulations exhibiting fixed mutant phenotypes can successfully invade. Long term stasis is then given by an evolutionarily stable ecological equilibrium which persists until successfully invaded by another new species. If successful new species rarely appear, this process can produce a sequence of punctuated equilibria where there are long periods of stasis separated by short outbursts of evolving ecosystems.

Our theory of punctuated equilibria does not include population genetics explicitly as it is based on the standard assumption of evolutionary game theory that individual fitness translates into reproduction of offspring with identical phenotypes. On the other hand, one of the cornerstones of many speciation models is the reproductive isolation of subpopulations that have adapted genetically either through assortative mating (sympatric speciation) or through physical separation (allopatric speciation). Clearly, population genetics plays an important role in speciation as an intuitive requirement that two species are different is that they cannot interbreed.

However, it is not so clear whether this reproductive separation is the initial cause of speciation or simply the end result of ecological or evolutionary factors. Take, for example, the two-habitat selection model of Section 3. Assuming mating occurs only between individuals in the same habitat, the indirect competition between individuals to settle in the better habitat results in assortative mating without involving population genetics. It seems here that ecological factors favoring the emergence of new species are paramount and reproductive isolation is only a byproduct.

This habitat selection model also illustrates nicely the process of invasion by species two into one of the habitats followed by the phenotypic evolution of the resultant two species system to an evolutionarily stable ecological equilibrium (i.e. the ensuing coevolutionary effects) where both habitats are occupied by each species. The methods developed here can be extended to coevolutionary speciation events where successful new species drive (some) existing species to extinction. The fossil record seems to indicate successful invasion is often combined with mass extinctions. Outside these drastic perturbations, it is an open question in biology whether ecological or genetical factors are more important in keeping the number of species relatively constant (Charles et al., 2001). Our analysis supports the relevance of ecology in such matters.

## 5 Appendix

For the single-species two-habitat model of Section 3.1, the invasion of the evolutionarily stable ecological equilibrium  $(\rho_1^*, p^*)$  by a monomorphic sub-population, where all individuals are using strategy  $p$ , leads to the dynamical system (10) whose linearization about  $(\rho_1, \mu_1) = (\rho_1^*, 0)$  automatically has a zero eigenvalue since  $\frac{\partial \dot{\mu}_1}{\partial \mu_1} = 0$ . In this situation, Cressman and Garay (2003a, 2003b) say the invasion is by a selectively neutral mutant strategy. Similarly, the two-species evolutionarily stable ecological equilibrium  $(\bar{\rho}_1^*, \bar{p}^*, \bar{\rho}_2^*, \bar{q}^*)$  for the two-habitat model of Section 3.3 is simultaneously invaded by selectively neutral mutant strategies by both species (i.e. all of the corresponding eigenvalues are zero). The dynamical systems, (10) and (19) respectively, for both the single-species and two-species invasion of the resident systems are of the form

$$\begin{aligned}\dot{\rho}_i &= \rho_i f_i(\rho, \mu) \\ \dot{\mu}_i &= \mu_i g_i(\rho, \mu)\end{aligned}\tag{21}$$

where  $i = 1$  for a single species and  $i = 1, 2$  for a two species system.

Although asymptotic stability of  $(\rho_1^*, p^*)$  can be shown by a phase plane analysis for a single species (see Figure 2), this is no longer possible for the two-species four-dimensional dynamical system (19). Another method that is applicable to both systems is the expansion of (21) about the equilibrium up to quadratic terms. Following Cressman and Garay (2003a, 2003b), the four Jacobian matrices

$$\begin{aligned}J_{ij}^{RR} &\equiv \frac{\partial(\dot{\rho}_i/\rho_i)}{\partial \rho_j} & J_{ij}^{RI} &\equiv \frac{\partial(\dot{\rho}_i/\rho_i)}{\partial \mu_j} \\ J_{ij}^{IR} &\equiv \frac{\partial(\dot{\mu}_i/\mu_i)}{\partial \rho_j} & J_{ij}^{II} &\equiv \frac{\partial(\dot{\mu}_i/\mu_i)}{\partial \mu_j}\end{aligned}$$

are used where these partial derivatives are evaluated at the equilibrium. They showed that the equilibrium is asymptotically stable if and only if the resident system is asymptotically stable (i.e. the eigenvalues of  $J^{RR}$  have negative real parts) and  $J \equiv J^{II} - J^{IR} (J^{RR})^{-1} J^{RI}$  is a B-matrix.

**Remark.** The B-matrix conditions for an  $N \times N$  matrix  $J$  are given in Hofbauer and Sigmund (1998). For  $N = 1$ , the only entry of  $J$  must be negative. For  $N = 2$ , we need both diagonal entries of  $J$  being negative and its determinant positive. If the  $N \times N$  matrix  $J$  satisfies the degenerate condition that it has a zero ray (i.e. a nonzero vector  $X$  with nonnegative components such that  $X_i \sum_{j=1}^N J_{ij} X_j = 0$  for all  $i$ ), then the equilibrium

may be asymptotically stable without  $J$  being a B-matrix (Cressman and Garay, 2003b). For the general speciation and invasion model of Section 2, the mutants need not be selectively neutral. Any mutant strategy that is not selectively neutral must be at a selective disadvantage (i.e. its corresponding eigenvalue must be negative) or else it can successfully invade the resident system.

For the single-species two-habitat model of Section 3.1, each Jacobian matrix has a single entry given by

$$\begin{aligned} J^{RR} &\equiv -\left(\frac{r_1(p_1^*)^2}{K_1} + \frac{r_2(p_2^*)^2}{K_2}\right) & J^{RI} &\equiv -\left(\frac{r_1 p_1^* p_1}{K_1} + \frac{r_2 p_2^* p_2}{K_2}\right) \\ J^{IR} &\equiv -\left(\frac{r_1 p_1^* p_1}{K_1} + \frac{r_2 p_2^* p_2}{K_2}\right) & J^{II} &\equiv -\left(\frac{r_1(p_1)^2}{K_1} + \frac{r_2(p_2)^2}{K_2}\right). \end{aligned}$$

The eigenvalue of  $J^{RR}$ ,  $-\left(\frac{r_1(p_1^*)^2}{K_1} + \frac{r_2(p_2^*)^2}{K_2}\right)$ , is clearly negative. Thus,  $(\rho_1^*, 0)$  is asymptotically stable if and only if the only entry of  $J$  is negative. Here

$$\begin{aligned} J &= -\left(\frac{r_1(p_1)^2}{K_1} + \frac{r_2(p_2)^2}{K_2}\right) - \frac{\left(-\left(\frac{r_1 p_1^* p_1}{K_1} + \frac{r_2 p_2^* p_2}{K_2}\right)\right)^2}{-\left(\frac{r_1(p_1^*)^2}{K_1} + \frac{r_2(p_2^*)^2}{K_2}\right)} \\ &= -\frac{r_1 r_2}{K_1 K_2} (p_1^* p_2 - p_2^* p_1)^2. \end{aligned}$$

This is negative if and only if  $p \neq p^*$ . That is,  $(\rho_1^*, p^*)$  is uninvadable by any other strategy  $p$  in this single species.

To analyze the asymptotic stability of the equilibrium  $(\bar{\rho}_1^*, \bar{\rho}_2^*, 0, 0)$  of the two-species system (19), we assume  $(\bar{\rho}_1^*, \bar{\rho}_2^*)$  is an asymptotically stable equilibrium of the resident system (17) and find the  $2 \times 2$  Jacobian matrices. These are given by (note that the matrix  $J^{RR}$  is already given in Section 3.3)

$$\begin{aligned} -J^{RR} &= \begin{bmatrix} \hat{r}_1 \bar{p}_1^{*2} + \hat{r}_2 \bar{p}_2^{*2} & \alpha_1 \hat{r}_1 \bar{p}_1^* \bar{q}_1^* + \alpha_2 \hat{r}_2 \bar{p}_2^* \bar{q}_2^* \\ \beta_1 \hat{s}_1 \bar{p}_1^* \bar{q}_1^* + \beta_2 \hat{s}_2 \bar{p}_2^* \bar{q}_2^* & \hat{s}_1 \bar{q}_1^{*2} + \hat{s}_2 \bar{q}_2^{*2} \end{bmatrix} \\ -J^{RI} &= \begin{bmatrix} \hat{r}_1 \bar{p}_1^* p_1 + \hat{r}_2 \bar{p}_2^* p_2 & \alpha_1 \hat{r}_1 \bar{p}_1^* q_1 + \alpha_2 \hat{r}_2 \bar{p}_2^* q_2 \\ \beta_1 \hat{s}_1 p_1 \bar{q}_1^* + \beta_2 \hat{s}_2 p_2 \bar{q}_2^* & \hat{s}_1 \bar{q}_1^* q_1 + \hat{s}_2 \bar{q}_2^* q_2 \end{bmatrix} \\ -J^{IR} &= \begin{bmatrix} \hat{r}_1 p_1 \bar{p}_1^* + \hat{r}_2 p_2 \bar{p}_2^* & \alpha_1 \hat{r}_1 p_1 \bar{q}_1^* + \alpha_2 \hat{r}_2 p_2 \bar{q}_2^* \\ \beta_1 \hat{s}_1 \bar{p}_1^* q_1 + \beta_2 \hat{s}_2 \bar{p}_2^* q_2 & \hat{s}_1 q_1 \bar{q}_1^* + \hat{s}_2 q_2 \bar{q}_2^* \end{bmatrix} \end{aligned}$$

$$-J^{II} = \begin{bmatrix} \widehat{r}_1 p_1^2 + \widehat{r}_2 p_2^2 & \alpha_1 \widehat{r}_1 p_1 q_1 + \alpha_2 \widehat{r}_2 p_2 q_2 \\ \beta_1 \widehat{s}_1 p_1 q_1 + \beta_2 \widehat{s}_2 p_2 q_2 & \widehat{s}_1 q_1^2 + \widehat{s}_2 q_2^2 \end{bmatrix}.$$

We start with the diagonal terms of  $-J$ . With

$$(J^{RR})^{-1} = \frac{1}{\det J^{RR}} \begin{bmatrix} -\widehat{s}_1 \overline{q}_1^{*2} - \widehat{s}_2 \overline{q}_2^{*2} & \alpha_1 \widehat{r}_1 \overline{p}_1^* \overline{q}_1^* + \alpha_2 \widehat{r}_2 \overline{p}_2^* \overline{q}_2^* \\ \beta_1 \widehat{s}_1 \overline{p}_1^* \overline{q}_1^* + \beta_2 \widehat{s}_2 \overline{p}_2^* \overline{q}_2^* & -\widehat{r}_1 \overline{p}_1^{*2} - \widehat{r}_2 \overline{p}_2^{*2} \end{bmatrix},$$

we find  $(-J)_{11}$  is equal to  $\widehat{r}_1 p_1^2 + \widehat{r}_2 p_2^2$  plus the matrix product

$$\begin{bmatrix} \widehat{r}_1 p_1 \overline{p}_1^* + \widehat{r}_2 p_2 \overline{p}_2^* & \alpha_1 \widehat{r}_1 p_1 \overline{q}_1^* + \alpha_2 \widehat{r}_2 p_2 \overline{q}_2^* \end{bmatrix} (J^{RR})^{-1} \begin{bmatrix} \widehat{r}_1 \overline{p}_1^* p_1 + \widehat{r}_2 \overline{p}_2^* p_2 \\ \beta_1 \widehat{s}_1 p_1 \overline{q}_1^* + \beta_2 \widehat{s}_2 p_2 \overline{q}_2^* \end{bmatrix}.$$

Thus  $(\det J^{RR}) (-J)_{11}$  is equal to

$$(\widehat{r}_1 p_1^2 + \widehat{r}_2 p_2^2) \begin{bmatrix} \widehat{r}_1 \widehat{s}_1 \overline{p}_1^{*2} \overline{q}_1^{*2} (1 - \alpha_1 \beta_1) + \widehat{r}_2 \widehat{s}_2 \overline{p}_2^{*2} \overline{q}_2^{*2} (1 - \alpha_2 \beta_2) \\ + \widehat{r}_1 \widehat{s}_2 (\overline{p}_1^{*2} \overline{q}_2^{*2} - \alpha_1 \beta_2 \overline{p}_1^* \overline{q}_1^* \overline{p}_2^* \overline{q}_2^*) + \widehat{r}_2 \widehat{s}_1 (\overline{p}_2^{*2} \overline{q}_1^{*2} - \alpha_2 \beta_1 \overline{p}_1^* \overline{q}_1^* \overline{p}_2^* \overline{q}_2^*) \end{bmatrix}$$

plus the matrix product

$$\begin{bmatrix} \widehat{r}_1 p_1 \overline{p}_1^* + \widehat{r}_2 p_2 \overline{p}_2^* & \alpha_1 \widehat{r}_1 \overline{p}_1^* \overline{q}_1^* + \alpha_2 \widehat{r}_2 p_2 \overline{q}_2^* \end{bmatrix} \begin{bmatrix} \begin{bmatrix} -(\widehat{s}_1 \overline{q}_1^{*2} + \widehat{s}_2 \overline{q}_2^{*2}) (\widehat{r}_1 \overline{p}_1^* p_1 + \widehat{r}_2 \overline{p}_2^* p_2) \\ + (\alpha_1 \widehat{r}_1 \overline{p}_1^* \overline{q}_1^* + \alpha_2 \widehat{r}_2 \overline{p}_2^* \overline{q}_2^*) (\beta_1 \widehat{s}_1 p_1 \overline{q}_1^* + \beta_2 \widehat{s}_2 p_2 \overline{q}_2^*) \end{bmatrix} \\ \begin{bmatrix} (\beta_1 \widehat{s}_1 \overline{p}_1^* \overline{q}_1^* + \beta_2 \widehat{s}_2 \overline{p}_2^* \overline{q}_2^*) (\widehat{r}_1 \overline{p}_1^* p_1 + \widehat{r}_2 \overline{p}_2^* p_2) \\ -(\widehat{r}_1 \overline{p}_1^{*2} + \widehat{r}_2 \overline{p}_2^{*2}) (\beta_1 \widehat{s}_1 p_1 \overline{q}_1^* + \beta_2 \widehat{s}_2 p_2 \overline{q}_2^*) \end{bmatrix} \end{bmatrix}.$$

This simplifies to  $(\det J^{RR}) (-J)_{11} = \widehat{r}_1 \widehat{r}_2 [\widehat{s}_1 \overline{q}_1^{*2} (1 - \alpha_1 \beta_1) + \widehat{s}_2 \overline{q}_2^{*2} (1 - \alpha_2 \beta_2)] (p_1 - \overline{p}_1^*)^2$ .

Similarly  $(\det J^{RR}) (-J)_{22} = \widehat{s}_1 \widehat{s}_2 [\widehat{r}_1 \overline{p}_1^{*2} (1 - \alpha_1 \beta_1) + \widehat{r}_2 \overline{p}_2^{*2} (1 - \alpha_2 \beta_2)] (q_1 - \overline{q}_1^*)^2$ .

Since  $1 - \alpha_i \beta_i < 0$  by (16), the diagonal terms are negative as required for  $J$  to be a B-matrix.

To calculate the determinant of  $J$ , we also need the off diagonal terms.

Adapting the above steps, we find

$$(\det J^{RR}) (-J)_{12} = \widehat{r}_1 \widehat{r}_2 [\alpha_2 \widehat{s}_1 \overline{p}_1^* \overline{q}_1^* (1 - \alpha_1 \beta_1) + \alpha_1 \widehat{s}_2 \overline{p}_2^* \overline{q}_2^* (1 - \alpha_2 \beta_2)] (p_1 - \overline{p}_1^*) (q_1 - \overline{q}_1^*)$$

and  $(\det J^{RR}) (-J)_{21} = \widehat{s}_1 \widehat{s}_2 [\beta_2 \widehat{r}_1 \overline{p}_1^* \overline{q}_1^* (1 - \alpha_1 \beta_1) + \beta_1 \widehat{r}_2 \overline{p}_2^* \overline{q}_2^* (1 - \alpha_2 \beta_2)] (p_1 - \overline{p}_1^*) (q_1 - \overline{q}_1^*)$ .

Thus  $\det J$  is the product of  $\left[ \frac{\widehat{r}_1 \widehat{r}_2 \widehat{s}_1 \widehat{s}_2 (p_1 - \overline{p}_1^*)^2 (q_1 - \overline{q}_1^*)^2}{(\det J^{RR})^2} \right]$  and

$$\begin{bmatrix} (\widehat{s}_1 \overline{q}_1^{*2} (1 - \alpha_1 \beta_1) + \widehat{s}_2 \overline{q}_2^{*2} (1 - \alpha_2 \beta_2)) (\widehat{r}_1 \overline{p}_1^{*2} (1 - \alpha_1 \beta_1) + \widehat{r}_2 \overline{p}_2^{*2} (1 - \alpha_2 \beta_2)) \\ -(\alpha_2 \widehat{s}_1 \overline{p}_1^* \overline{q}_1^* (1 - \alpha_1 \beta_1) + \alpha_1 \widehat{s}_2 \overline{p}_2^* \overline{q}_2^* (1 - \alpha_2 \beta_2)) (\beta_2 \widehat{r}_1 \overline{p}_1^* \overline{q}_1^* (1 - \alpha_1 \beta_1) + \beta_1 \widehat{r}_2 \overline{p}_2^* \overline{q}_2^* (1 - \alpha_2 \beta_2)) \end{bmatrix}.$$

Since

$$\begin{aligned} & (\widehat{s}_1 \overline{q}_1^{*2} (1 - \alpha_1 \beta_1) + \widehat{s}_2 \overline{q}_2^{*2} (1 - \alpha_2 \beta_2)) (\widehat{r}_1 \overline{p}_1^{*2} (1 - \alpha_1 \beta_1) + \widehat{r}_2 \overline{p}_2^{*2} (1 - \alpha_2 \beta_2)) \\ & - (\alpha_2 \widehat{s}_1 \overline{p}_1^* \overline{q}_1^* (1 - \alpha_1 \beta_1) + \alpha_1 \widehat{s}_2 \overline{p}_2^* \overline{q}_2^* (1 - \alpha_2 \beta_2)) (\beta_2 \widehat{r}_1 \overline{p}_1^* \overline{q}_1^* (1 - \alpha_1 \beta_1) + \beta_1 \widehat{r}_2 \overline{p}_2^* \overline{q}_2^* (1 - \alpha_2 \beta_2)) \end{aligned}$$

is equal to  $(1 - \alpha_1\beta_1)(1 - \alpha_2\beta_2) \det J^{RR}$ , we have  $\det J = \frac{(1-\alpha_1\beta_1)(1-\alpha_2\beta_2)\hat{r}_1\hat{r}_2\hat{s}_1\hat{s}_2(p_1-\bar{p}_1^*)^2(q_1-\bar{q}_1^*)^2}{\det J^{RR}}$ . In particular,  $\det J > 0$  if and only if  $\det J^{RR} > 0$ . That is,  $(\bar{\rho}_1^*, \bar{\rho}_2^*, 0, 0)$  is asymptotically stable for (19) if and only if  $(\bar{\rho}_1^*, \bar{\rho}_2^*)$  is asymptotically stable for (17). ■

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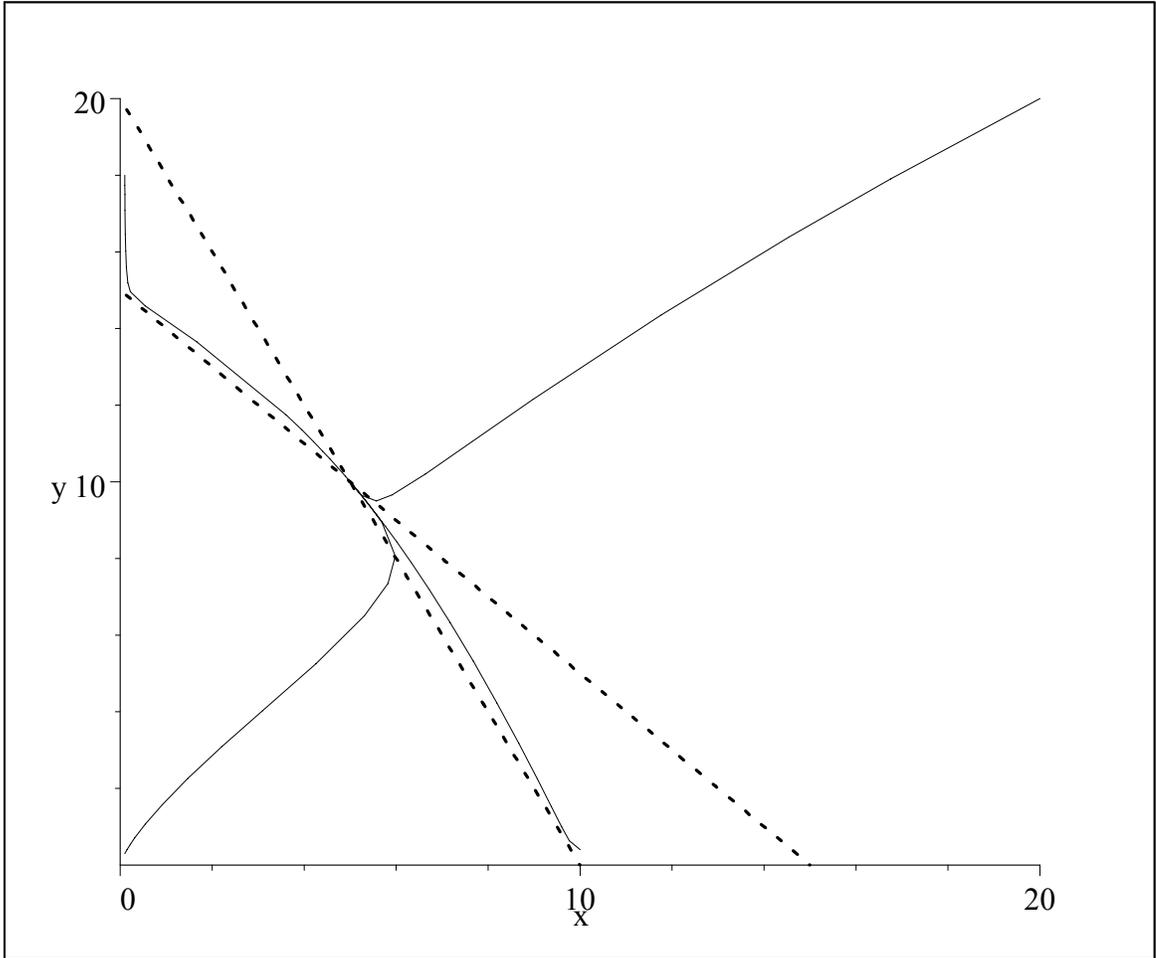


Figure 1. The phase diagram for the Lotka-Volterra system (1). Four trajectories are plotted (the solid curves evolving to the interior equilibrium  $(5, 10)$ ) as well as the isoclines through this equilibrium (the two dotted lines).

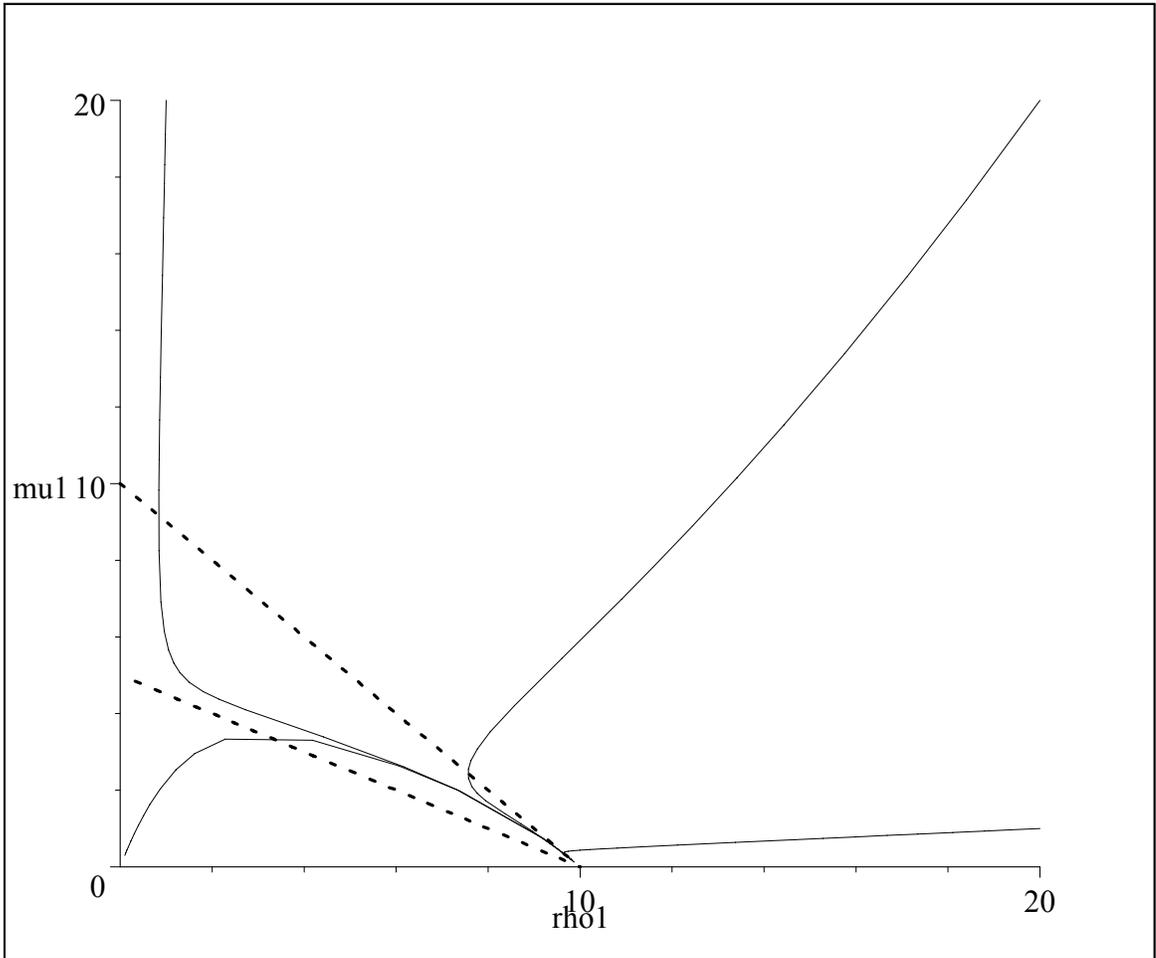


Figure 2. The phase diagram for the invasion dynamics (10) of the single-species IFD (the system parameters used are those of the example in Section 3.4). Four trajectories are plotted (the solid curves evolving to the boundary equilibrium  $(10, 0)$  corresponding to the IFD  $(\rho_1^*, p^*) = (10, (\frac{1}{2}, \frac{1}{2}))$ ) as well as the isoclines through this equilibrium (the two dotted lines). The top isocline is where  $\dot{\rho}_1 = 0$  and the bottom where  $\dot{\mu}_1 = 0$ .

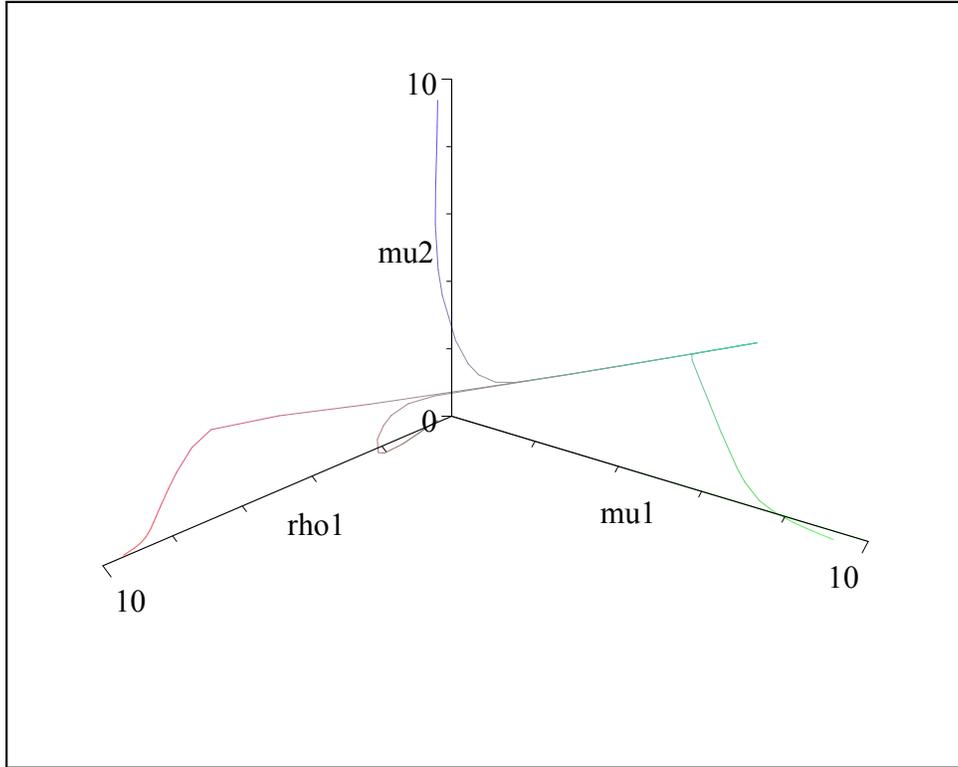


Figure 3. The phase diagram for system (13) using the system parameters of Section 3.4 when the monomorphic single-species IFD at  $(\rho_1^*, p^*) = (10, (\frac{1}{2}, \frac{1}{2}))$  is invaded by the mutant monomorphic subpopulations  $p = (\frac{1}{3}, \frac{2}{3})$  (corresponding to density  $\mu_1$ ) and  $q = (1, 0)$  (corresponding to density  $\mu_2$ ). One trajectory is shown that starts near this IFD (i.e. near  $(\rho_1, \mu_1, \mu_2) = (10, 0, 0)$ ), evolving to the two-species equilibrium at  $(0, \frac{15}{2}, 5)$  where  $p^*$  has been completely eliminated. In fact, this two-species equilibrium is globally asymptotically stable for the system with individual strategies  $p^*, p, q$  as indicated by the other three trajectories evolving to it from various initial points in the phase diagram. This equilibrium results from an invasion by species two in habitat one and will eventually be replaced by a two-species evolutionarily stable equilibrium where both species coexist in each habitat.