Evolutionary Substitution and Replacement in N-Species Lotka-Volterra Systems*

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Abstract

Abstract: The successful invasion of a multi-species resident system by mutants has received a great deal of attention in theoretical ecology but less is known about what happens after the successful invasion. Here, in the framework of Lotka-Volterra (LV) systems, we consider the general question where there is one resident phenotype in each species and the evolutionary outcome after invasion remains one phenotype in each species but these include all the mutant phenotypes. In the first case, called evolutionary substitution, a mutant appears in only one species, the resident phenotype in this species dies out and the mutant coexists with the original phenotypes of the other species. In the second case, called evolutionary replacement, a mutant appears in each species, all resident phenotypes die out and the evolutionary outcome is coexistence among all the mutant phenotypes. For general LV systems, we show that dominance of the resident phenotype by the mutant (i.e. the mutant is always more fit) in each species where the mutant appears leads to evolutionary substitution/replacement. However, it is shown by example that, when dominance is weakened to only assuming the average fitness of the mutants is greater than the average for the resident phenotype, the residents may not die out. We also show evolutionary substitution occurs in two-species competitive LV systems when the initial invasion of the resident system (respectively, of the new coexistence system) is successful (respectively, unsuccessful). Moreover, if sequential evolutionary substitution occurs for either order that the two mutant phenotypes appear (called historically independent replacement), then it is shown evolutionary replacement occurs using a generalization of the dominance argument.

Keywords: resident and mutant phenotypes, successful invasion, evolutionarily stable strategy, competitive Lotka-Volterra systems

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1 Introduction

In this paper, we consider a resident system with N species together with a set of invaders. In order to motivate this setup, which is rooted in ecology and evolution theory, we provide relevant examples here. In ecological succession, after a disturbance (e.g. wildfire, lava flow or landslide), species from an existing pool colonize the new habitat. During the succession process, which starts with these pioneering plants and animals and stops when a long-term stable community emerges, a number of species replace other ones (Pielou 1966; Drake 1990). In ecological invasion theory, the hypothesis of "invasional meltdown" proposes that an invasive species in a new environment can facilitate the invasion of other non-native species (Simberloff and Von Holle 1999). However, there are also examples when multispecies invasion can reduce the negative impact of a single exotic plant species on the native (i.e. resident) plant community (Lenda 2019).

Invasion by multiple species can happen through human activity or by natural causes. For instance, the latter occurred during the formation of the Isthmus of Panama when the migration between North and South America led to the last and most conspicuous wave, the great American interchange, around 3 million years ago (O'Dea et al. 2016; Stehli and Webb 2013). Furthermore, sympatric speciation is the evolution of a new species from a surviving ancestral species, while both live in the same habitat. An important question is: What is the number of mutants in a large ecosystem? The number of co-existing mutants depends on the size of the ancestral species and the time duration until extinction of non-successful mutants. In particular, we cannot rule out the possibility that an already introduced non-successful mutant can survive if a new mutant arises in another species, and together can successfully invade the ancestral system.

From the biological perspective, there are two main differences between evolutionary and ecological models. Firstly, in evolution, mutation is rare in two senses; the mutant occurs with low density, and there is a long time duration between two mutation events. In ecological models, more than one invasive species can be introduced at (almost) the same time and in large numbers either by accident or on purpose through human activities. Secondly, in evolution, the mutant phenotypes are not arbitrary, contrary to ecology where the invasive species has arbitrary traits. Usually, during evolution, the mutant and the wild phenotypes do not radically differ from each other. Often, the interaction parameters in the evolutionary model either come from the same game and the phenotypes are different (see Cressman and Garay 2003a,b; Garay 2007) or interaction parameters between resident and mutant phenotypes are not so different. This contrasts to models in invasion ecology where the phenotypic similarity between exotic and native species cannot be assumed. One well-known example of dissimilar phenotypes is from Australia, when the invasive mammals substitute for the native marsupials. However, Hutchinson (1965) has already emphasized that biotic evolution cannot be separated from ecology, since ecological factors (like competition and feeding) have a curtailing effect on the evolutionary success of all mutants and/or species.

From the mathematical point of view, the examples mentioned above can be modelled by a dynamical system where several invaders appear in a resident system (with N species). For simplicity, we concentrate on the case when there is maximum of N invaders. In essence: invaders (whether they migrate from another ecosystem or are mutants) are introduced into any ecosystem, it is the ecological interactions that determine whether the new ecotypes die out or replace some resident species in the long run.

In the short term, one of the fundamental results of theoretical ecology that has received a great deal of attention in the literature (e.g. Shigesada et al, 1984; van den Driessche and Zeeman, 1998) is the characterization of the successful invasion of a stable $N-$species resident system by mutant phenotypes. Less attention has been placed on the question of what happens after the successful invasion. Possible outcomes include situations where both residents and mutants coexist in all or some species (either by approaching a stable coexistence equilibrium or through more complicated dynamics such a periodic cycles) (Zeeman, 1993). It is also possible that the ecosystem collapses through species extinction (e.g. evolutionary suicide (Gyllenberg and Parvinen, 2001)).

In this paper, we are more interested in the outcome whereby the resident phenotype dies out and is replaced by the mutant phenotype. We examine necessary conditions and sufficient conditions for two such situations. In the first, there is a single mutant phenotype in one of the species. That is, we consider the case where mutation is rare so that multiple mutant phenotypes either in the same species or in several species cannot occur at the same time. If the mutant can invade a stable equilibrium of the monomorphic $N-$species resident system that has all species present and the system evolves to a stable equilibrium of the $N-$species resident-mutant system with all species present but the one species has only the mutant phenotype, we say that "*evolutionary* *substitution*" has occurred.

At the other extreme, there are mutant phenotypes in each of the species. In this second case, if a stable equilibrium of the monomorphic $N-$species resident system that has all species present can be invaded by the mutants and the system evolves to a stable equilibrium of the $N-$species resident-mutant system with all species present but only mutant phenotypes, there has been an "*evolutionary replacement*".

Our investigation is based on the dynamics of evolving population sizes for the resident and mutant phenotypes of the $N-$species evolutionary ecology system that assumes these dynamics are of Lotka-Volterra (LV) type.[1] This extends the work of Garay and Varga (2000) and Cressman and Garay (2003a) who investigated resident stability/invadability in such LV systems rather than substitution/replacement. In particular, the monomorphic model of Cressman and Garay (2003a) examines the invadability of the resident system when there is a single mutant phenotype in each species. As we will see, the methods developed there are also essential to our results on evolutionary substitution and replacement.

In Section 2, we illustrate the problem by summarizing the theory for a single species. In Section 3, we investigate evolutionary substitution in the $N-$species LV resident-mutant dynamical system. Theorem 1 shows that, if the mutant can invade the $N-$species resident system but the resident phenotype cannot invade the equilibrium with all species present but the one species has only the mutant phenotype, then there can be no coexistence equilibrium with all phenotypes, an important requirement for evolutionary substitution to occur. Theorems 2 and 3 use this result to prove that these two invasion criteria combine to imply evolutionary substitution occurs for two-species competitive systems and for general $N-$species LV systems when the mutant phenotype dominates the resident.

In Section 4, we concentrate on evolutionary replacement in two-species (i.e. $N = 2$) since Theorem 1 does not generalize to exclude coexistence equilibria when there are mutant phenotypes in both species (see Example 2 of Section 4). Furthermore, Example 3 shows care must be taken extending

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[1] Here the resident and mutant phenotypes are fixed. Another approach to phenotype evolution (that is not pursued in this article) is based on adaptive dynamics (Dercole and Renaldi, 2008) with continuous phenotype space whereby the resident phenotypes change continuously in the direction of nearby mutant phenotypes that can successful invade. Adaptive dynamics also questions whether invasion leads to substitution/replacement (O-ba and Kigami, 2018).

the dominance concept of Section 3. However, if the successful invasions occur through a sequence of evolutionary substitutions that does not depend on whether a rare mutant first appears in species one or in species two (which we call "*historically independent replacement*"), then evolutionary replacement ensues (see Theorem 4 there). The biological importance of this concept is illustrated at the end of Section 5. This final section also discusses other results of the paper from a biological perspective.

2 Evolutionary Substitution and Replacement in Single Species LV Systems

To illustrate these evolutionary aspects, consider a single species (i.e. $N = 1$) with one resident and one mutant phenotype. In this case, evolutionary substitution and evolutionary replacement are equivalent since the question in both cases is whether the mutant phenotype becomes established in the system and the resident phenotype goes extinct.

The resident system of Lotka-Volterra type is of the form

$$\dot{\rho}_1 = \rho_1 \left(r_1 + m_{11}^{RR} \rho_1 \right) \tag{1}$$

where ρ_1 is the resident density, r_1 is the intrinsic growth rate and m_{11}^{RR} is the interaction parameter. Clearly, this system has a stable equilibrium with $\rho_1^* > 0$ (i.e. with the resident species present) if and only if the intrinsic growth is positive and the interaction term is negative (in which case, the equilibrium is $\rho_1^* = -r_1/m_{11}^{RR}$).[2]

We assume that the difference between resident and mutant behavior is contained in the interaction parameters (e.g. the parameter m_{11}^{RI} models the linear effect that the mutant density μ_1 has on the growth rate of the resident

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[2] The notation used here is consistent with the more complicated LV systems in the remainder of the paper (e.g. (3) below) . It can be considerably simplified in this special case. For instance, with $r_1 = r > 0$ and $m_{11}^{RR} = m < 0$, (1) is the logistic equation (i.e. positive intrinsic growth and negative density dependence) in more standard notation.

phenotype).[3] The corresponding resident-mutant system is then

$$\begin{aligned} \dot{\rho}_1 &= \rho_1 \left(r_1 + m_{11}^{RR}\rho_1 + m_{11}^{RI}\mu_1\right) \\ \dot{\mu}_1 &= \mu_1 \left(r_1 + m_{11}^{IR}\rho_1 + m_{11}^{II}\mu_1\right). \end{aligned} \tag{2}$$

If this models competition (i.e. all four interaction parameters are negative), it is well-known (Hofbauer and Sigmund, 1998) that the two-dimensional dynamical system evolves to the mutant equilibrium $\mu_1^* = -r_1/m_{11}^{II}$ if and only if the mutant can invade the resident equilibrium but the resident cannot invade the mutant equilibrium.

We say that general LV systems of the form (2) exhibit evolutionary substitution if (i) the one-dimensional resident system and mutant system respectively each have a stable equilibrium with positive density; (ii) the resident (respectively, mutant) equilibrium is unstable (respectively, stable) since it can be invaded by the mutant phenotype (respectively, cannot be invaded by the resident phenotype) in the two-dimensional resident-mutant system (2); and (iii) after the mutant successfully invades the resident, the system evolves to the mutant equilibrium. In fact, these two-dimensional LV systems exhibit evolutionary substitution if and only if $r_1 > 0, m_{11}^{RR} < 0, m_{11}^{II} < 0$ (i.e. the resident system and the mutant system each have a globally stable equilibrium) and $m_{11}^{IR} \geq m_{11}^{RR}, m_{11}^{II} \geq m_{11}^{RI}$ with strict inequality in at least one of these two conditions.

As interpreted by Cressman and Garay (2003a), $r_1 > 0, m_{11}^{RR} < 0, m_{11}^{II} < 0$ are the ecological stability conditions and $m_{11}^{II} \geq m_{11}^{RI}$ with $m_{11}^{IR} > m_{11}^{RR}$ if $m_{11}^{II} = m_{11}^{RI}$ means that the mutant phenotype is an evolutionarily stable strategy (ESS). That is, in addition to ecological stability, we have evolutionary stability of the mutant phenotype since it is an ESS of the evolutionary game given by the 2 × 2 payoff matrix (or interaction matrix)

$$\begin{bmatrix} m_{11}^{RR} & m_{11}^{RI} \\ m_{11}^{IR} & m_{11}^{II} \end{bmatrix}.$$

In game-theoretic terms (Apaloo, 2006), the final condition for evolutionary substitution (i.e. $m_{11}^{IR} \geq m_{11}^{RR}$ with $m_{11}^{II} > m_{11}^{RI}$ if $m_{11}^{IR} = m_{11}^{RR}$) is equivalent

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[3] That is, the intrinsic growth rate is independent of species phenotype. The discussion here does not rely on this assumption. In fact, for the $N-$species systems of Sections 3 and 4, Theorems 1 to 4 do not depend on our assumption that, for each species k, the resident and mutant phenotypes have the same intrinsic growth rate r_k. Moreover, the proofs of these results do not rely on this assumption either.

to the mutant phenotype being a neighborhood invader strategy (NIS) of the resident phenotype (i.e. the mutant phenotype that is sufficiently rare successfully invades the resident phenotype). Strategies that satisfy both the ESS and NIS conditions for matrix games such as given by the 2×2 payoff matrix above are known as ESNIS (Apaloo, 2006).

In summary, there is evolutionary substitution/replacement in a single-species LV system if and only if

(i) there is ecological stability in the resident system and in the mutant system

(ii) the resident phenotype cannot invade the mutant phenotype (i.e. the mutant phenotype is an ESS of the interaction matrix for the resident-mutant evolutionary game), and

(iii) the mutant phenotype can invade the resident phenotype (i.e. the mutant phenotype is a NIS of the resident phenotype for this interaction matrix).

3 Evolutionary Substitution in $N-$Species

In this section, we assume that the $N-$species resident system has one resident phenotype in each species and that there is a single mutant phenotype in exactly one species (which, without loss of generality, we take as species one). If r_k and ρ_k respectively are the intrinsic growth rate and resident phenotype density of species k and μ_1 is the density of the mutant phenotype, then the resident-mutant Lotka-Volterra system is

$$\begin{aligned} \dot{\rho}_k &= \rho_k \left(r_k + \sum_{l=1}^{N} m_{kl}^{RR} \rho_l + m_{k1}^{RI} \mu_1 \right) \\ \dot{\mu}_1 &= \mu_1 \left(r_1 + \sum_{l=1}^{N} m_{1l}^{IR} \rho_l + m_{11}^{II} \mu_1 \right) \end{aligned} \tag{3}$$

where $k = 1, ..., N$. In particular, for LV systems, the individual growth rate of a given phenotype (e.g. $\dot{\rho}_k / \rho_k$) are linear functions of the densities of all phenotypes present in the system.

One interpretation of the *interaction parameters* $m_{kl}^{RR}, m_{k1}^{RI}, m_{1l}^{IR}$ and m_{11}^{II} adopts the payoff terminology of evolutionary game theory (Cressman and

Garay, 2003a). Then m_{kl}^{RR} (respectively, m_{k1}^{RI}) is the payoff to a resident phenotype (or strategy) in species k when interacting with a resident phenotype in species l (respectively, the intruder or mutant phenotype).[4] Similarly, m_{1l}^{IR} and m_{11}^{II} are payoffs to the mutant phenotype. That is, the superscripts denote the phenotypes and the subscripts are the species in the interaction where the first superscript and subscript specify the phenotype and species of the individual receiving the payoff, respectively

The first requirement for evolutionary substitution is that this resident system is stable in the absence of mutants. In particular, from the biological perspective, this means that there is species coexistence in the residence system. Mathematically, there is a locally asymptotically stable equilibrium $\rho^* = (\rho_1^*, ..., \rho_N^*)$ with all components positive (i.e. $\rho^* \in R_{>0}^N$) for the resident system

$$\dot{\rho}_k = \rho_k \left(r_k + \sum_{l=1}^{N} m_{kl}^{RR} \rho_l \right) \qquad k = 1, ..., N. \tag{4}$$

To avoid technical complications, we assume that this stability is determined through the linearization of (4) about ρ^*. That is, we assume that the resident system is *hyperbolic* (i.e. all eigenvalues of the $N \times N$ Jacobian matrix of this linearization, which has *kl* entry $\rho_k^* m_{kl}^{RR}$, have nonzero real parts).[5] Thus this hyperbolic resident system is *stable* if and only if all eigenvalues of the Jacobian matrix have negative real parts. Let M^{RR} be the $N \times N$ matrix whose entries are the payoffs m_{kl}^{RR} for interactions between residents (similarly, M^{IR} denotes the $1 \times N$ matrix of payoffs to mutants interacting with residents etc.). Then, in particular, M^{RR} is invertible since its determinant is non-zero and so $\rho^* = -\left(M^{RR}\right)^{-1} r$ where r is the column vector whose k^{th} component is the intrinsic growth rate r_k of species k.

The next requirement is that the mutant phenotype can invade. That is, $(\rho^*, 0)$ is not a locally asymptotically stable equilibrium of the resident-mutant system (3). $(\rho^*, 0)$ will be unstable in the resident-mutant system if the *invasion fitness* $\lambda_1^I \equiv r_1 + \sum_{l=1}^{N} m_{1l}^{IR} \rho_l^*$ of the mutant phenotype at

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[4] In evolutionary game theory, it is usually assumed that each individual has one random pairwise interaction per unit time. Here, the number of such interactions for an individual is proportional to the density in each species.

[5] The Jacobian matrix at the resident equilibrium ρ^* is $\begin{bmatrix} \rho_1^* & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & & \rho_N^* \end{bmatrix} M^{RR}$.

this equilibrium is greater than the fitness of the resident phenotype $r_1 + \sum_{l=1}^{N} m_{1l}^{RR}\rho_l^* = 0$ (i.e. if $\lambda_1^I > 0$). On the other hand, $(\rho^*, 0)$ is locally asymptotically stable if $\lambda_1^I < 0$. In the intermediate case where $\lambda_1^I = 0$, the mutant phenotype is initially *selectively neutral* when invading the resident equilibrium. This case was analyzed by Cressman and Garay (2003a, 2003b) who showed that, for Lotka-Volterra systems, $(\rho^*, 0)$ is invadable if and only if $M^{II} - M^{IR}\left(M^{RR}\right)^{-1} M^{RI} \geq 0$.

Finally, after successful invasion by the mutant, evolutionary substitution requires that the resident-mutant system must evolve to a locally asymptotically stable equilibrium $(0, \widehat{\rho}_2, ..., \widehat{\rho}_N, \widehat{\mu}_1)$ with all species present but species one has only mutant phenotypes. In particular, this equilibrium cannot be invaded by the resident phenotype of species one. That is, the invasion fitness of the resident phenotype of species one, $\lambda_1^R \equiv r_1 + \sum_{l=2}^{N} m_{1l}^{RR}\widehat{\rho}_l + m_{11}^{RI}\widehat{\mu}_1$ cannot be positive at $(0, \widehat{\rho}_2, ..., \widehat{\rho}_N, \widehat{\mu}_1)$.[6]

The question arises whether hyperbolic stability of ρ^* and $(\widehat{\rho}_2, ..., \widehat{\rho}_N, \widehat{\mu}_1)$ in their respective $N-$ dimensional Lotka-Volterra systems (which we assume from now on) implies evolutionary substitution if the mutant phenotype can invade $(\rho^*, 0)$ but the resident phenotype of species one cannot invade $(0, \widehat{\rho}_2, ..., \widehat{\rho}_N, \widehat{\mu}_1)$. Such an implication would generalize the evolutionary substitution in a single species discussed in Section 2. Our first result (Theorem 1) implies that a unique coexistence equilibrium is impossible in this case.

Theorem 1 *Suppose that* $E_1 \equiv (\rho^*, 0)$ *and* $E_2 \equiv (0, \widehat{\rho}_2, ..., \widehat{\rho}_N, \widehat{\mu}_1)$ *are equilibria of the* N*-species resident-mutant LV system (3) with all species present (i.e.* $\rho_i^* > 0$ *for* $i = 1, 2, ..., N$ *and* $\widehat{\rho}_j > 0$ *for* $j = 2, ..., N$ *and* $\widehat{\mu}_1 > 0$*). Also assume that* E_1 *and* E_2 *are locally asymptotically stable equilibria for system (3) restricted to their respective* $N-$*dimensional boundary face and that the mutant phenotype can invade* E_1 *but the resident phenotype of species one cannot invade* E_2*.*[7] *Then there is no isolated interior equilibrium*[8] *for the* $N + 1$ *dimensional LV system.*

Proof. Let $x^* = (x_1^*, x_2^*, ..., x_N^*, x_{N+1}^*)$ be an isolated interior equilibrium

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[6] In the threshold case when the resident phenotype is initially selectively neutral (i.e. $\lambda_1^R = 0$), the analogue of $M^{II} - M^{IR}\left(M^{RR}\right)^{-1} M^{RI}$ must now be negative (see the B-matrix method of Cressman and Garay (2003a)).

[7] Under these assumptions, we say that the invasion conditions are satisfied.

[8] That is, every neigborhood of an equilibrium with all $N + 1$ components positive contains another equilibrium.

for (3), which for convenience, we rewrite as

$$\dot{x}_i = x_i \left(r_i + \sum_{j=1}^{N+1} a_{ij} x_j \right) \text{ for } i = 1, 2, ..., N+1.$$

The isolatedness assumption implies that the $(N+1) \times (N+1)$ interaction matrix A with entries a_{ij} is invertible. An application of Cramer's Rule (see, for instance the proof of Theorem 13.5.7 in Hofbauer and Sigmund (1998)) shows that

$$x_i^* = -\frac{\mid A^i \mid}{\mid A \mid} \left(r_i + (Ax^i)_i \right) \tag{5}$$

whenever the principal submatrix A^i of A formed by deleting the i^{th} row and column is nonsingular and, apart from the i-th coordinate which is then taken as $x_i^i = 0$, the remaining coordinates of $x^i = (x_1^i, \ldots, x_{i-1}^i, 0, x_{i+1}^i, \ldots, x_{N+1}^i)$ are defined as the coordinates of the unique solution to the linear system $r_j + (Ax)_j = 0$ for all $j \neq i$.

From the assumptions in the statement of the theorem, x^1 (respectively, x^{N+1}) is the equilibrium E_2 (respectively, E_1). Since x^1 and x^{N+1} are locally asymptotically stable in their respective $N-$dimensional boundary faces, A^1 and A^{N+1} are both nonsingular $N \times N$ matrices and their determinants $\mid A^1 \mid$ and $\mid A^{N+1} \mid$ have the same sign. Moreover, since the mutant phenotype can invade the resident equilibrium, $r_{N+1} + (Ax^{N+1})_{N+1} \geq 0$ and since the resident phenotype cannot invade the mutant equilibrium, $r_1 + (Ax^1)_1 \leq 0$. Thus

$$x_1^* x_{N+1}^* = \frac{\mid A^1 \mid\mid A^{N+1} \mid}{\mid A \mid^2} \left(r_1 + (Ax^1)_1 \right) \left(r_{N+1} + (Ax^{N+1})_{N+1} \right) \leq 0$$

which contradicts that x^* is an interior equilibrium. ■

Remark 1. The proof of Theorem 1 above relies on the nonsingularity of A. For general A, (5) can be rewritten as

$$\mid A \mid x_i^* = - \mid A^i \mid \left(r_i + (Ax^i)_i \right). \tag{6}$$

In fact, this reformulation holds whenever A^i is nonsingular for any solution x^* of $Ax + r = 0$ (see the proof in Appendix A1).[9] Thus, if A is singular,

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[9] The first and fourth authors refer to this general result as the Calgary Lemma, the location where they obtained its proof that has as yet been unpublished as far as they are aware.

then $(r_i + (Ax^i)_i) = 0$ whenever A^i is nonsingular (in particular, for $i = 1$ and $i = N+1$). That is, $\lambda_1^I = 0 = \lambda_1^R$. In this case, $Ax^1 + r = 0 = Ax^{N+1} + r$ and so the line segment joining $E_2 = x^1$ and $E_1 = x^{N+1}$ are all equilibria of the system (3). In particular, E_2 is not locally asymptotically stable in the extended, $(N+1)-$dimensional phase space since there are arbitrarily close initial points on this line segment that do not evolve to it (i.e. it can be invaded by the resident phenotype of species one). Thus, the conclusion of Theorem 1 can be strengthened to show that there is no interior equilibrium for the $N+1$ dimensional LV system when the invasion conditions hold.

For evolutionary substitution to occur, it is necessary that no interior equilibrium exists. However, the converse is not true. That is, evolutionary substitution is not guaranteed when there is no interior equilibrium as the following two-species example illustrates. In particular, ecological stability together with the invasion conditions of Theorem 1 do not imply evolutionary substitution unlike the single-species result of Section 2.

Example 1 *Consider the resident-mutant three-dimensional LV system*

$$\begin{aligned} \dot{\rho}_1 &= \rho_1(-4 - 3\rho_1 + 7\rho_2 - 4\mu_1) \\ \dot{\rho}_2 &= \rho_2(-1 - \rho_1 + 2\rho_2 - \mu_1) \\ \dot{\mu}_1 &= \mu_1(-4 + 7\rho_2 - 3\mu_1) . \end{aligned} \tag{7}$$

It is readily checked that the conditions of Theorem 1 are satisfied for $N = 2$*, equilibria* $E_1 = (\rho_1^*, \rho_2^*, 0) = (1, 1, 0)$*,* $E_2 = (0, \widehat{\rho}_2, \widehat{\mu}_1) = (0, 1, 1)$ *and* $\lambda_1^I = -4 + 7 = 3 > 0$*,* $\lambda_1^R = -4 + 7 - 4 = -1 < 0$*. The equilibria of (7) are the origin* $O = (0, 0, 0)$*,* $P_+ = E_2$ *(which are asymptotically stable*[10]*) and the saddle points* $P_- = E_1$ *and* $S = (0, \frac{1}{2}, 0)$*.*

The global dynamics of (7) as well as the dynamics of the resident subsystem

$$\begin{aligned} \dot{\rho}_1 &= \rho_1(-4 - 3\rho_1 + 7\rho_2) \\ \dot{\rho}_2 &= \rho_2(-1 - \rho_1 + 2\rho_2) \end{aligned} \tag{8}$$

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[10] Since $0 < \rho_2 < \frac{1}{2}$ implies $\dot{\rho}_2 < 0$ and thus $\dot{\rho}_2 < -\frac{1}{2}\rho_2 < 0$ as well as $\dot{\mu}_1 < -\frac{1}{2}\mu_1 < 0$, the origin attracts all points of the open, unbounded 3D rectangle $0 < \rho_1 < \infty$, $0 < \rho_2 < \frac{1}{2}$, $0 < \mu_1 < \infty$. The region of attraction of the origin is separated from the rest of the phase portrait by (the non-negative part of) the two-dimensional, unbounded stable manifold of the saddle point S.

and of the mutant subsystem

$$\begin{aligned} \dot{\mu}_1 &= \mu_1(-4 - 3\mu_1 + 7\rho_2) \\ \dot{\rho}_2 &= \rho_2(-1 - \mu_1 + 2\rho_2):, \end{aligned} \tag{9}$$

are presented in Figure 1. The three thick gray curves portray nonplanar trajectories, including the outgoing trajectory of P_-. Due to lack of space, ingoing and outgoing trajectories of the saddle point S are not shown but clearly indicated by trajectories nearby. All black trajectory curves are planar. Orientation of the trajectories is determined by the stability properties of the equilibria. The behavior of the trajectories far from the origin is nontrivial and presented in Figure 2 of Appendix A2.

When ρ_1 in (8) is changed to μ_1 in (9), it is immediate that the dynamics in the μ_1-ρ_2 plane is exactly the same as in the ρ_1-ρ_2 plane. Please observe this symmetry in both Figures.

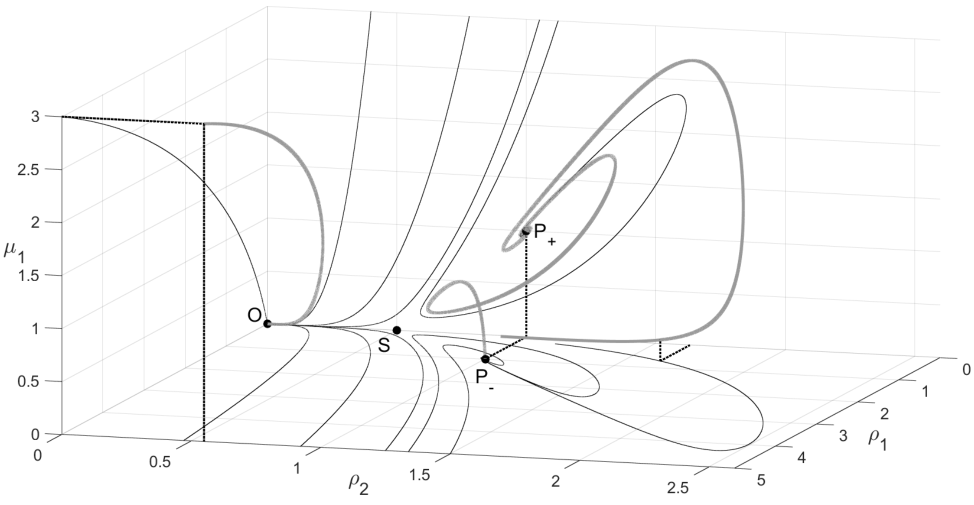

Figure 1: Phase portrait of the replicator system (7).

[ROSS: Please check that footnote 10 is placed where Barnabas intended it and that the figure is okay. The difference between the gray and black curves is not that great. Maybe the gray ones could be some other color (red?) instead? I have inserted the sentence on orientation into the text since figure 1 does not have arrows on the trajectories.]

By Example 1, the invasion criteria of Theorem 1 do not imply evolutionary substitution for two-species LV systems. On the other hand, if the LV system has more structure, the invasion criteria of Theorem 1 can be equivalent to evolutionary substitution. The following discusses two such systems of biological importance.

First, for two-species competitive LV systems, evolutionary substitution is equivalent to the invasion criteria. These resident-mutant systems have the form

$$\dot{x}_i = x_i \left(r_i + \sum_{j=1}^{3} a_{ij} x_j \right) \qquad \text{for} \quad : i = 1, 2, 3 \tag{10}$$

where $r_1 = r_3$ and r_2 are all positive and $a_{ij} < 0$ for $i, j = 1, 2, 3$. By the discussion above, the invasion criteria are necessary for evolutionary substitution. The following theorem proves the converse. In fact, for such systems, the invasion criteria imply that $E_2 = (0, \widehat{\rho}_2, \widehat{\mu}_1)$ is globally asymptotically stable.

Theorem 2 *Suppose that $E_1 \equiv (\rho_1^*, \rho_2^*, 0)$ and $E_2 \equiv (0, \widehat{\rho}_2, \widehat{\mu}_1)$ are equilibria of the two-species resident-mutant competitive LV system (10) with both species present (i.e. $\rho_i^* > 0$ for $i = 1, 2$, $\widehat{\rho}_2 > 0$ and $\widehat{\mu}_1 > 0$) and satisfying $r_1 = r_3 > 0$, $r_2 > 0$ and $a_{ij} < 0$ for $i, j = 1, 2, 3$. Also assume that E_1 and E_2 are locally asymptotically stable equilibria for system (10) restricted to their respective two-dimensional boundary face. If the mutant phenotype can invade E_1 but the resident phenotype of species one cannot invade E_2, then E_2 is globally asymptotically stable.*[11]

Proof. It is well-known (e.g. Zeeman, 1993) that the dynamic behavior of an $N+1-$dimensional competitive LV system is determined by its restriction to an invariant $N-$dimensional hypersurface called the carrying simplex (van den Driessche and Zeeman, 1998). For the three-dimensional system (10), the two-dimensional carrying simplex in the first octant is homeomorphic to a triangle whose three edges correspond to boundary invariant curves of (10)

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[11] Here, and everywhere else in the present paper, both for LV and replicator systems, global asymptotic stability (gas) of an equilibrium means that it is locally asymptotically stable (las) and attracts all interior trajectories. Similarly, "gas restricted to a face" means "las restricted to this face and attracts all interior trajectories on this face".

whose endpoints are the carrying capacities $-r_i/a_{ii}$ of the logistic equation for each species i on its own.

By Theorem 1 and Remark 1, (10) has no interior equilibria. Moreover, $E_1 \equiv (\rho_1^*, \rho_2^*, 0)$ corresponds to a saddle point on the x_1x_2 edge whose stable manifold is this edge and $E_2 \equiv (0, \widehat{\rho}_2, \widehat{\mu}_1)$ corresponds to a stable equilibrium on the x_2x_3 edge of the triangle. Thus, of the 33 possible classes of dynamic behavior classified by Zeeman (1993), the dynamics on the triangle is given by one of classes 9 to 12 depending on the behavior on the x_1x_3 edge. In all four classes, the equilibrium corresponding to E_2 is globally asymptotically stable. ■

Evolutionary substitution also occurs when the mutant phenotype "dominates" the resident phenotype it substitutes for according to the following theorem. Here, dominance is used in the game-theoretic sense in that the expected payoff (or fitness) of an individual using the mutant phenotype is greater than that of the resident phenotype (i.e. the mutant is more fit) whenever some phenotypes are present (see (11) below).

Theorem 3 *As in Theorem 1, let* $E_1 \equiv (\rho^*, 0)$ *and* $E_2 \equiv (0, \widehat{\rho}_2, ..., \widehat{\rho}_N, \widehat{\mu}_1)$ *be equilibria of the* N*-species resident-mutant LV system (3) with all species present (i.e.* $\rho_i^* > 0$ *for* $i = 1, 2, ..., N$ *and* $\widehat{\rho}_j > 0$ *for* $j = 2, ..., N$ *and* $\widehat{\mu}_1 > 0$*). Furthermore, assume that all forward trajectories of (3) are bounded*[12] *and that* E_2 *is globally asymptotically stable equilibrium for system (3) restricted to its* $N-$*dimensional boundary face. If the mutant phenotype is always more fit than the resident phenotype of species one, then there is no interior equilibrium, the resident phenotype of species one goes extinct and* E_2 *is a locally asymptotically stable equilibrium for system (3). Moreover, if no interior trajectories converge to the boundary of the* $N-$*dimensional boundary face containing* E_2*, then evolutionary substitution occurs.*

Proof. Since the mutant phenotype is always more fit than the resident phenotype of species one

$$r_1 + \sum_{l=1}^{N} m_{1l}^{IR} \rho_l + m_{11}^{II} \mu_1 > r_1 + \sum_{l=1}^{N} m_{1l}^{RR} \rho_l + m_{11}^{RI} \mu_1 \tag{11}$$

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[12] That is, each trajectory is defined for all $t \geq 0$ and all its components are less that D for some $D > 0$ that may depend on the trajectory.

for all $(\rho_1, \rho_2, ..., \rho_N, \mu_1)$ with nonnegative components and at least one component positive. In particular, this inequality holds at E_1 and E_2 (i.e. $\lambda_1^I > 0$ and $\lambda_1^R < 0$). Since $\lambda_1^R < 0$ and E_2 is globally asymptotically stable equilibrium for system (3) restricted to its $N-$dimensional boundary face, E_2 is a locally asymptotically stable equilibrium for system (3).

The resident phenotype of species one goes extinct if every interior trajectory of (3) converges to the $N-$dimensional boundary face with $\rho_1 = 0$. Actually, this convergence holds for every trajectory with ρ_1 and μ_1 initially both positive. To see this, consider a given trajectory with ρ_1 and μ_1 initially positive. The first and the last equation of system (3) yield that $\frac{d}{dt}\left(\frac{\rho_1}{\mu_1}\right)$ equals

$$\begin{aligned}
&\frac{\rho_1\mu_1\left(r_1 + \sum_{l=1}^N m_{1l}^{RR}\rho_l + m_{11}^{RI}\mu_1\right) - \rho_1\mu_1\left(r_1 + \sum_{l=1}^N m_{1l}^{IR}\rho_l + m_{11}^{II}\mu_1\right)}{\mu_1^2}\\
= \;& -\frac{\rho_1}{\mu_1}\left(\left(r_1 + \sum_{l=1}^N m_{1l}^{IR}\rho_l + m_{11}^{II}\mu_1\right) - \left(r_1 + \sum_{l=1}^N m_{1l}^{RR}\rho_l + m_{11}^{RI}\mu_1\right)\right) < 0
\end{aligned}$$

for all $(\rho_1, \rho_2, ..., \rho_N, \mu_1)$ where ρ_1 and μ_1 are both positive. The final inequality follows from (11). Thus, $\frac{\rho_1}{\mu_1}$ is a strictly decreasing function along every trajectory where ρ_1 and μ_1 are initially both positive. For the given interior trajectory, define $\lim_{t\to\infty} \frac{\rho_1(t)}{\mu_1(t)} = C \geq 0$. If $C = 0$, then $\lim_{t\to\infty} \rho_1(t) = 0$ since $\mu_1(t)$ is bounded. Suppose that ρ_1 does not converge to 0 (i.e. $\limsup_{t\to\infty} \rho_1(t) > 0$). Thus, $C > 0$ and there exists a limit point of the given trajectory with ρ_1 and μ_1 both positive. Any trajectory that is initially at this limit point is also in the limit set of the given trajectory. Since $\frac{\rho_1}{\mu_1}$ is a strictly decreasing at this initial point, $\lim_{t\to\infty} \frac{\rho_1(t)}{\mu_1(t)} < C$, a contradiction. Since the resident phenotype ρ_1 goes extinct, there can be no interior equilibrium.

As a by-product of the previous considerations, we see that interior trajectories converge to nonempty compact subsets of the $N-$dimensional boundary face $\rho_1 = 0$ of the non-negative $(N+1)-$dimensional orthant. This is the boundary face that contains equilibrium E_2. By the last assumption of the theorem, interior trajectories have a limit point with the properties $\rho_1 = 0$ and $\rho_2\rho_3 \ldots \rho_N\mu_1 > 0$. Since E_2 is globally asymptotically stable for system (3) restricted to the face $\rho_1 = 0$ and locally asymptotically stable for the full resident-intruder system (3) on $R_{\geq 0}^{N+1}$, E_2 is the only limit point of any given interior trajectory. That is, interior trajectories converge to E_2. In other words, evolutionary substitution occurs. ■

Remark 2. The condition in Theorem 3 that E_2 is globally asymptotically stable equilibria for system (3) restricted to its $N-$dimensional boundary face is necessary for the conclusion that evolutionary substitution occurs. To see this, consider Example 1 again. In it, we have that the mutant fitness $-4+7\rho_2-3\mu_1$ is always greater than the fitness $-4-3\rho_1+7\rho_2-4\mu_1$ of the resident phenotype of species one when ρ_1 and μ_1 are positive. However, evolutionary substitution does not occur in Example 1 since $(0,0,0)$ is locally asymptotically stable. Note that Theorem 3 also makes the biologically reasonable assumption that the density of each species must be bounded.

4 Evolutionary Replacement

In this section, we assume that the $N-$species system has one resident phenotype and one mutant phenotype in each species. Then the resident-mutant Lotka-Volterra system is

$$\begin{aligned} \dot{\rho}_k &= \rho_k\left(r_k+\sum_{l=1}^{N}\left(m_{kl}^{RR}\rho_l+m_{kl}^{RI}\mu_l\right)\right) \\ \dot{\mu}_k &= \mu_k\left(r_k+\sum_{l=1}^{N}\left(m_{kl}^{IR}\rho_l+m_{kl}^{II}\mu_l\right)\right) \end{aligned} \tag{12}$$

where $M^{II}, M^{RI}, M^{IR}, M^{RR}$ are now all $N\times N$ interaction matrices.

The first requirement of evolutionary replacement is that the invasion criteria for system (12) be satisfied. That is, the $N-$dimensional resident system has a locally asymptotically stable interior equilibrium $E_1\equiv(\rho^*,0)$ (where $\rho_i^*>0$ for $i=1,2,...,N$) that can be invaded by the mutant phenotypes and the $N-$dimensional mutant system has a locally asymptotically stable interior equilibrium $E_2\equiv(0,\mu^*)$ (where $\mu_i^*>0$ for $i=1,2,...,N$) that cannot be invaded by the resident phenotypes. The following example shows that these invasion conditions do not rule out the existence of a stable interior equilibrium of the resident-mutant system. Thus, the obvious generalization of Theorem 1 is not valid for evolutionary replacement.

We then examine extensions of the domination concept of Theorem 3 to replacement systems. In this section, we concentrate on examples with two species (i.e. $N = 2$) since Example 1 shows that care must already be taken when there are two species and a single mutant phenotype.

Example 2 *Consider the resident-mutant system*

$$\begin{array}{rcl} \dot{\rho}_1 & = & \rho_1(2 - \rho_1 - \mu_1) \\ \dot{\rho}_2 & = & \rho_2(3 - \rho_2 - 2\mu_1) \\ \dot{\mu}_1 & = & \mu_1(2 - 2\rho_1 + \rho_2 - \mu_1) \\ \dot{\mu}_2 & = & \mu_2(3 - 3\rho_1 + \rho_2 - \mu_2). \end{array}$$

The intrinsic growth rates of species one and two are $r_1 = 2$ *and* $r_2 = 3$ *respectively. This has an interior equilibrium at* $(\rho_1, \rho_2, \mu_1, \mu_2) = (1, 1, 1, 1)$ *that is locally asymptotically stable since the only eigenvalue of the corresponding* 4×4 *Jacobian matrix is* -1 *(with multiplicity* 4*). The resident system has a globally asymptotically stable equilibrium at* $(\rho_1^*, \rho_2^*) = (2, 3)$ *and the mutant system also has a globally asymptotically stable equilibrium at* $(\mu_1^*, \mu_2^*) = (2, 3)$*. Moreover, to analyze whether* (ρ_1^*, ρ_2^*) *can be invaded, we calculate* $\lambda_1^I = 2 - 2\rho_1^* + \rho_2^* = 1 > 0$ *and* $\lambda_2^I = 3 - 3\rho_1^* + \rho_2^* = 0$*. Similarly, to analyze whether* (μ_1^*, μ_1^*) *can be invaded, we calculate* $\lambda_1^R = 2 - \mu_1^* = 0$ *and* $\lambda_2^R = 3 - 2\mu_1^* = -1 < 0$*.*

Since the eigenvalue λ_2^I *is zero (respectively,* $\lambda_1^R = 0$*), it is not immediately clear whether* $(\rho_1^*, \rho_2^*, 0, 0) = (2, 3, 0, 0)$ *(respectively,* $(0, 0, \mu_1^*, \mu_2^*) = (0, 0, 2, 3)$*) can be invaded. To avoid the use of B-matrix methods for these neutral invasion coefficients (Cressman and Garay, 2003a), we consider instead the slightly perturbed system*

$$\begin{array}{rcl} \dot{\rho}_1 & = & \rho_1(2 - \rho_1 - (1 + \varepsilon)\mu_1) \\ \dot{\rho}_2 & = & \rho_2(3 - \rho_2 - 2\mu_1) \\ \dot{\mu}_1 & = & \mu_1(2 - 2\rho_1 + \rho_2 - \mu_1) \\ \dot{\mu}_2 & = & \mu_2(3 - 3\rho_1 + (1 + \varepsilon)\rho_2 - \mu_2) \end{array} \tag{13}$$

with some $\varepsilon > 0$*. The new interior equilibrium* $\left(\frac{1-5\varepsilon}{1-2\varepsilon}, \frac{1-6\varepsilon}{1-2\varepsilon}, \frac{1}{1-2\varepsilon}, \frac{1+4\varepsilon-6\varepsilon^2}{1-2\varepsilon}\right)$ *will still be locally asymptotically stable when* ε *is sufficiently small. Moreover, the equilibrium of the resident system remains unchanged at* $(\rho_1^*, \rho_2^*, 0, 0) = (2, 3, 0, 0)$ *as does the equilibrium for the mutant system* $(0, 0, \mu_1^*, \mu_2^*) = (0, 0, 2, 3)$*.*

However, it is now clear that both invader phenotypes can invade $(\rho_1^*, \rho_2^*, 0, 0)$*, since* $\lambda_1^I = 2-2\rho_1^*+\rho_2^* = 1 > 0$ *and* $\lambda_2^I = 3-3\rho_1^*+(1+\varepsilon)\rho_2^* = 3\varepsilon > 0$*. Also, at* $(0, 0, \mu_1^*, \mu_2^*)$*, neither resident phenotype can invade since* $\lambda_1^R = 2-(1+\varepsilon)\mu_1^* = -2\varepsilon < 0$ *and* $\lambda_2^R = 3 - 2\mu_1^* = -1 < 0$*.*

By Example 2, it is clear that more conditions are needed besides our invasion criteria in order to guarantee evolutionary replacement. One possibility is to assume that the mutant phenotype "dominates" the resident phenotype in each species as in Theorem 3 (i.e. the mutant phenotype is always more fit than the resident phenotype in each species). Keeping the boundedness assumption on forward trajectories, we see that all interior trajectories of the $2N-$dimensional resident-mutant system converge to nonempty compact subsets of the $N-$dimensional mutant system. In particular, there are no interior equilibria. Moreover, the proof of Theorem 3 easily extends to show that there will be evolutionary replacement when the $N-$dimensional mutant system has a globally asymptotically stable equilibrium $(\mu_1^*, \mu_2^*, ..., \mu_N^*)$ with all species present if interior trajectories do not converge to the boundary of the $N-$dimensional mutant system.[13]

The dominance concept discussed in the previous paragraph is very strong. A weaker form of dominance borrowed from game theory (Hofbauer and Sigmund, 1998) is that some weighted average of the mutant phenotypes is always more fit than some weighted average of the resident phenotypes. This also guarantees there is no interior equilibrium of the resident-mutant system.[14]

Unfortunately, the following example based on Akin and Hofbauer (1982) shows this dominance does not guarantee interior trajectories converge to the

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[13] Specifically, by the dominance assumption, ρ_i/μ_i for $i = 1, 2, ..., N$ are all strictly decreasing when ρ_i and μ_i are initially positive. Since all forward trajectories are bounded, the proof of Theorem 3 shows that $\lim_{t\to\infty} \rho_i(t) = 0$ for all i (i.e. all resident phenotypes go extinct). Moreover, since no interior trajectories converge to the boundary of the $N-$dimensional mutant system, each such trajectory has a limit point in the interior of the $N-$dimensional mutant face. Global asymptotic stability of $(\mu_1^*, \mu_2^*, ..., \mu_N^*)$ on this face combined with its local asymptotic stability in the full resident-mutant system guarantees that it is the only limit point of each interior trajectory.

[14] To see this, consider $\left(\prod_{i=1}^{N} \rho_i^{w_i}\right) / \left(\prod_{i=1}^{N} \mu_i^{v_i}\right)$ where $w_i > 0$ are the weights for the residents and $v_i > 0$ are the weights for the mutants. These weights satisfy $\sum w_i = 1 = \sum v_i$. In view of (12), this expression is strictly decreasing at all interior points and so there is no interior equilibrium.

$N-$dimensional mutant system.

Example 3 *Consider the two-species resident-mutant competitive system*

$$\begin{aligned}
\dot{\rho}_1 &= \rho_1(1 - 2\rho_1 - 5\rho_2 - \mu_1 - 5\mu_2) \\
\dot{\rho}_2 &= \rho_2(1 - 5\rho_1 - 2\rho_2 - 5\mu_1 - \mu_2) \\
\dot{\mu}_1 &= \mu_1(1 - 3\rho_1 - \rho_2 - 2\mu_1 - 3\mu_2) \\
\dot{\mu}_2 &= \mu_2(1 - \rho_1 - 3\rho_2 - 3\mu_1 - 2\mu_2).
\end{aligned} \tag{14}$$

There is no interior equilibrium since the average fitness of the mutants dominates the average of the residents (i.e. $1-2\rho_1-2\rho_2-\frac{5}{2}\mu_1-\frac{5}{2}\mu_2 > 1-\frac{7}{2}\rho_1-\frac{7}{2}\rho_2-3\mu_1-3\mu_2$*). Since the intrinsic growth rates for both species are the same, the frequencies* x_i *of the four phenotypes* $\big($*e.g.* $x_1 = \rho_1/(\rho_1+\rho_2+\mu_1+\mu_2)\big)$ *evolve according to the replicator equation with payoff matrix*

$$A = \begin{bmatrix} -2 & -5 & -1 & -5 \\ -5 & -2 & -5 & -1 \\ -3 & -1 & -2 & -3 \\ -1 & -3 & -3 & -2 \end{bmatrix}$$

given by the interaction coefficients (Hofbauer and Sigmund, Exercise 7.5.2, 1998). If each entry of A *is increased by* 2 *(which does not change the replicator equation) and the variables in (14) are reordered by interchanging* ρ_1 *with* μ_2*, the payoff matrix becomes*

$$A' = \begin{bmatrix} 0 & -1 & -1 & 1 \\ 1 & 0 & -3 & -3 \\ -1 & 1 & 0 & -1 \\ -3 & -3 & 1 & 0 \end{bmatrix}$$

which is the example analyzed by Akin and Hofbauer (1982). They prove that all interior trajectories approach a heteroclinic cycle that follows the edges of the three-dimensional strategy simplex (i.e. the tetrahedron) in the order of vertices $\rho_1 \to \mu_2 \to \rho_2 \to \mu_1 \to \rho_1$*. In particular, the resident phenotypes do not go extinct even though* $\frac{\rho_1\rho_2}{\mu_1\mu_2}$ *evolves to* 0*.*

In Example 3, notice that the equilibrium of the resident system $(1/7, 1/7)$ for (14) can be invaded by both mutant phenotypes since $\lambda_1^I = \lambda_2^I = 1-3/7-1/7 > 0$ whereas the equilibrium of the mutant system $(1/5, 1/5)$ cannot be invaded by either resident phenotype since $\lambda_1^R = \lambda_2^R = 1 - 2/5 - 5/5 < 0$. On the other hand, these equilibria are unstable in their respective two-dimensional system since the determinant of the linearization is negative in both cases. This leaves open the possibility that combining dominance with conditions that these boundary equilibria are locally asymptotically stable in their respective two-dimensional system implies evolutionary replacement. As we will see in the following section, this is indeed the case for two-species competitive systems in biologically significant scenarios where dominance must occur.

Remark 3. Before leaving this section, notice that the time-reversed dynamics for the replicator equation of Example 3 given by the payoff matrix $-A$ provides an excellent illustration of evolutionary replacement. Indeed, since the average payoff of the first two strategies dominates the average payoff of the last two strategies, we also reverse the order of the four strategies and analyze the payoff matrix

$$A'' = \begin{bmatrix} -8 & -7 & -7 & -9 \\ -7 & -8 & -9 & -7 \\ -9 & -5 & -8 & -5 \\ -5 & -9 & -5 & -8 \end{bmatrix}$$

formed by subtracting 10 from each entry of $-A$ with reordered strategies. The analysis of Akin and Hofbauer (1982) shows that the equilibrium of the replicator equation corresponding to $(0, 0, 1/13, 1/13)$ (i.e. the frequency vector $(0, 0, 1/2, 1/2)$) is globally asymptotically stable.

For the resident-mutant competitive system corresponding to A'',

$$\begin{aligned} \dot{\rho}_1 &= \rho_1(1 - 8\rho_1 - 7\rho_2 - 7\mu_1 - 9\mu_2) \\ \dot{\rho}_2 &= \rho_2(1 - 7\rho_1 - 8\rho_2 - 9\mu_1 - 7\mu_2) \\ \dot{\mu}_1 &= \mu_1(1 - 9\rho_1 - 5\rho_2 - 8\mu_1 - 5\mu_2) \\ \dot{\mu}_2 &= \mu_2(1 - 5\rho_1 - 9\rho_2 - 5\mu_1 - 8\mu_2) \end{aligned} \tag{15}$$

the residents have equilibrium $\frac{1}{15}(1, 1)$ which is globally asymptotically stable on this face and invadable by the mutants since $\lambda_{1,2}^I = 1-(9+5)/15 > 0$. The mutants have equilibrium $\frac{1}{13}(1, 1)$ (which is globally asymptotically stable on this face) and this is not invadable since $\lambda_{1,2}^R = 1 - (7 + 9)/13 < 0$.

The mutant phenotypes invade the resident system but the residents cannot invade the mutants. Furthermore, all interior trajectories of (15) that start close to the resident equilibrium evolve to the equilibrium of the mutant system. That is, the mutant phenotypes have replaced the residents.

4.1 Historically independent replacement

As mentioned in the Introduction (see also Section 5), if the successful invasions occur through a sequence of evolutionary substitutions that does not depend on whether a rare mutant first appears in species one or in species two, then evolutionary replacement ensues. This is shown for two-species competitive LV systems in Theorem 4 below.

For two-species competitive LV systems, the invasion conditions completely characterize evolutionary substitution by Section 3. Since we are not concerned about the order that mutants appear for historically independent replacement, we assume that the stable two-dimensional systems consisting of one phenotype from each species satisfy

$$\begin{aligned}
&\text{(i) } \rho_1\rho_2 \text{ can be invaded by both } \mu_1 \text{ and } \mu_2\\
&\text{(ii) } \mu_1\rho_2 \text{ can be invaded by } \mu_2 \text{ but not by } \rho_1\\
&\text{(iii) } \rho_1\mu_2 \text{ can be invaded by } \mu_1 \text{ but not by } \rho_2\\
&\text{(iv) } \mu_1\mu_2 \text{ cannot be invaded by } \rho_1 \text{ or by } \rho_2.
\end{aligned} \tag{16}$$

By Theorem 2, each subsystem consisting of three phenotypes has a globally asymptotically stable equilibrium where exactly one of the resident phenotypes goes extinct.

The sequence of evolutionary substitutions given by rare mutations can then serve as a model of punctuated equilibrium based on the fossil record in paleontology, a concept suggested by Eldredge and Gould (1972). This theory claims that 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. We have previously demonstrated that, in a two-species coevolutionary model, successful invasion is quickly followed by evolutionary changes in behavior, leading to a sequence of punctuated equilibrium (Cressman and Garay 2006). Historically independent replacement implies that the final outcome for the ecosystem can be predicted without knowing the sequence of mutations and their intermediate stasis events.

Theorem 4 *Suppose a two-species competitive system exhibits historically independent replacement. In other words, the four two-dimensional faces* $\rho_1\rho_2$*,* $\rho_2\mu_1$*,* $\rho_1\mu_2$ *and* $\mu_1\mu_2$ *have globally asymptotically stable interior equilibria that satisfy (16). Then there is no interior equilibrium where mutants and residents coexist. Moreover, the equilibrium* $(0, 0, \mu_1^*, \mu_2^*)$ *with both mutants present is globally asymptotically stable for the resident-mutant system (12) with* $N = 2$*. That is, evolutionary replacement occurs.*

Proof. The general two-species competitive resident-mutant system has the form

$$\begin{aligned} \dot{\rho}_1 &= \rho_1(r_1 - a_{11}\rho_1 - a_{12}\rho_2 - a_{13}\mu_1 - a_{14}\mu_2) \\ \dot{\rho}_2 &= \rho_2(r_2 - a_{21}\rho_1 - a_{22}\rho_2 - a_{23}\mu_1 - a_{24}\mu_2) \\ \dot{\mu}_1 &= \mu_1(r_1 - a_{31}\rho_1 - a_{32}\rho_2 - a_{33}\mu_1 - a_{34}\mu_2) \\ \dot{\mu}_2 &= \mu_2(r_2 - a_{41}\rho_1 - a_{42}\rho_2 - a_{43}\mu_1 - a_{44}\mu_2) \end{aligned} \tag{17}$$

where $r_1 > 0, r_2 > 0$ and $a_{ij} > 0$ for all i, j correspond to the entries of the interaction matrix $-A$. Consider the associated system

$$\begin{aligned} \dot{\rho}_1 &= \rho_1\big(1 - \frac{a_{11}}{r_1}\rho_1 - \frac{a_{12}}{r_1}\rho_2 - \frac{a_{13}}{r_1}\mu_1 - \frac{a_{14}}{r_1}\mu_2\big) \\ \dot{\rho}_2 &= \rho_2\big(1 - \frac{a_{21}}{r_2}\rho_1 - \frac{a_{22}}{r_2}\rho_2 - \frac{a_{23}}{r_2}\mu_1 - \frac{a_{24}}{r_2}\mu_2\big) \\ \dot{\mu}_1 &= \mu_1\big(1 - \frac{a_{31}}{r_1}\rho_1 - \frac{a_{32}}{r_1}\rho_2 - \frac{a_{33}}{r_1}\mu_1 - \frac{a_{34}}{r_1}\mu_2\big) \\ \dot{\mu}_2 &= \mu_2\big(1 - \frac{a_{41}}{r_2}\rho_1 - \frac{a_{42}}{r_2}\rho_2 - \frac{a_{43}}{r_2}\mu_1 - \frac{a_{44}}{r_2}\mu_2\big). \end{aligned} \tag{18}$$

This is also a competitive system where the interaction matrix $-\widehat{A}$ is given by

$$\widehat{a}_{ij} = \begin{cases} \frac{a_{ij}}{r_i} & \text{if } i = 1, 2 \\ \frac{a_{ij}}{r_{i-2}} & \text{if } i = 3, 4 \end{cases}.$$

System (18) has the same interior equilibria as well as the same equilibria on each boundary face as the original system (17).

In general, the stability of the same equilibrium for systems (17) and (18) can be different. However, for each equilibrium on a two-dimensional boundary face, their stability properties for both systems are the same. For example, $(0, 0, \mu_1^*, \mu_2^*)$ is an equilibrium in the interior of the mutant system

(17) if and only if it is for system (18). Also, $(0,0,\mu_1^*,\mu_2^*)$ is locally asymptotically stable on its two-dimensional face for system (17) if and only if the determinant $a_{33}a_{44} - a_{34}a_{43}$ of $\begin{bmatrix} -a_{33} & -a_{34} \\ -a_{43} & -a_{44} \end{bmatrix}$ is positive if and only if the determinant of $\begin{bmatrix} -\frac{a_{33}}{r_1} & -\frac{a_{34}}{r_1} \\ -\frac{a_{43}}{r_2} & -\frac{a_{44}}{r_2} \end{bmatrix}$ is positive if and only if $(0,0,\mu_1^*,\mu_2^*)$ is locally asymptotically stable on its two-dimensional face for system (18). Finally, $(0,0,\mu_1^*,\mu_2^*)$ can by invaded by the resident phenotype of species 1 for system (17) if and only if $r_1 - a_{13}\mu_1^* - a_{14}\mu_2^* > 0$ if and only if $1 - \frac{a_{13}}{r_1}\mu_1^* - \frac{a_{14}}{r_1}\mu_2^* > 0$ if and only if $(0,0,\mu_1^*,\mu_2^*)$ can by invaded by the resident phenotype of species 1 for system (18).

By Hofbauer and Sigmund (1998, Exercise 7.5.2), the dynamics of system (18) is the "same" as the replicator equation on the three-dimensional strategy simplex $\Delta^4 \equiv \{(x_1,x_2,x_3,x_4) \mid x_i \geq 0, \sum x_i = 1\}$ with payoff matrix $-\widehat{A}$. Moreover, this replicator equation is also given by a payoff matrix of the form B where

$$B \equiv \begin{bmatrix} 0 & b_{12} & \mathbf{b}_{13} & b_{14} \\ b_{21} & 0 & b_{23} & \mathbf{b}_{24} \\ \mathbf{b}_{31} & b_{32} & 0 & b_{34} \\ b_{41} & \mathbf{b}_{42} & b_{43} & 0 \end{bmatrix} \tag{19}$$

by subtracting the diagonal entry of $-\widehat{A}$ from all entries in its column. We want to show the assumptions that the four two-dimensional faces $\rho_1\rho_2$, $\rho_2\mu_1$, $\rho_1\mu_2$ and $\mu_1\mu_2$ have globally asymptotically stable interior equilibria that satisfy (16) imply that this matrix game has no equilibrium in the interior of Δ^4.

First, globally asymptotic stability of interior equilibria on the four two-dimensional faces implies that $b_{12}, b_{14}, b_{21}, b_{23}, b_{32}, b_{34}, b_{41}, b_{43}$ are all positive. The other entries in B, indicated by boldface in (19), may be positive or negative. The invasion assumptions correspond to the following eight inequalities in (20). For instance, the interior resident equilibrium for the replicator equation is $(\rho_1^*, \rho_2^*) = \left(\frac{b_{12}}{b_{12}+b_{21}}, \frac{b_{21}}{b_{12}+b_{21}}\right)$. This is invadable by mutant strategy of species 1 if $\mathbf{b}_{31}\rho_1^* + b_{32}\rho_2^* - \rho_1^* b_{12}\rho_2^* - \rho_2^* b_{21}\rho_1^* > 0$, which is the first inequality listed $\big($i.e. $\mathbf{b}_{31}b_{12} + b_{32}b_{21} \; > \; b_{12}b_{21}\big)$.

$$\begin{array}{rlcllll}
\text{(a)} & \mathbf{b}_{31}b_{12} + b_{32}b_{21} & > & b_{12}b_{21} & & & \\
\text{(b)} & b_{41}b_{12} + \mathbf{b}_{42}b_{21} & > & b_{12}b_{21} & & & \\
\text{(c)} & b_{12}b_{23} + \mathbf{b}_{13}b_{32} & < & b_{23}b_{32} & \Rightarrow & \text{(c0)} & b_{23} > \mathbf{b}_{13} \\
\text{(d)} & \mathbf{b}_{42}b_{23} + b_{43}b_{32} & > & b_{23}b_{32} & & & \\
\text{(e)} & b_{21}b_{14} + \mathbf{b}_{24}b_{41} & < & b_{14}b_{41} & \Rightarrow & \text{(e0)} & b_{14} > \mathbf{b}_{24} \\
\text{(f)} & \mathbf{b}_{31}b_{14} + b_{34}b_{41} & > & b_{14}b_{41} & & & \\
\text{(g)} & \mathbf{b}_{13}b_{34} + b_{14}b_{43} & < & b_{34}b_{43} & \Rightarrow & \text{(g0)} & b_{43} > \mathbf{b}_{13} \\
\text{(h)} & b_{23}b_{34} + \mathbf{b}_{24}b_{43} & < & b_{34}b_{43} & \Rightarrow & \text{(h0)} & b_{34} > \mathbf{b}_{24}
\end{array} \qquad (20)$$

By Akin (1980), there is no equilibrium in the interior of Δ^4 if and only if there is some dominance relation among the four strategies. In fact, we show in Appendix A3 that a convex combination of the two mutant strategies dominates a convex combination of the two resident strategies. That is, for matrix B, we show dominance of the form $y(\text{row}_1) + (1-y)(\text{row}_2) < x(\text{row}_3) + (1-x)(\text{row}_4)$ for some $x, y \in [0,1]$. Thus, the replicator equation has no interior equilibrium and so neither does (17).

Given an interior trajectory of (17), the dominance in matrix B means that $\frac{\rho_1^{x/r_1}\rho_2^{(1-x)/r_2}}{\mu_1^{y/r_1}\mu_2^{(1-y)/r_2}}$ is strictly decreasing. Moreover, since the trajectory converges to the carrying simplex of the competitive system (and so is bounded as well as bounded away from the origin), the method of proof of Theorem 3 generalizes to show that $\lim_{t\to\infty} \rho_1\rho_2 = 0$. Thus, there can be no limit point in the interior of a three-dimensional face since this face must include the $\mu_1\mu_2$ plane in which case the only limit point is $(0, 0, \mu_1^*, \mu_2^*)$. That is, if the trajectory does not converge to $(0, 0, \mu_1^*, \mu_2^*)$, then all its limit points must be in the four curves of the carrying simplex contained in the $\rho_1\mu_1$, $\rho_1\mu_2$, $\rho_2\mu_1$, $\rho_2\mu_2$ planes. The trajectory cannot converge to an equilibrium point on any of these four curves since all such points have an unstable manifold of at least one-dimension. That is, either the trajectory converges to $(0, 0, \mu_1^*, \mu_2^*)$ or else to a heteroclinic cycle around these four curves (in analogy to Example 3). This latter scenario is impossible due to the locally asymptotically stable equilibrium for the curve in the $\rho_1\mu_2$ plane (or the $\rho_2\mu_1$ plane). In summary, every interior trajectory converges to $(0, 0, \mu_1^*, \mu_2^*)$, which is then globally asymptotically stable. ■

5 Conclusion

Our motivation is rooted in evolutionary game theory. Specifically, the approach we adopt has parallels with invasion and stability concepts used in frequency-dependent selection theory modelled by evolutionary game theory. There, the concept of an evolutionarily stable strategy (ESS) was introduced by Maynard Smith and Price (1973) as a population state that cannot be invaded by any mutant strategy that is sufficiently rare. Later, Apaloo (1997) defined a neighborhood invader strategy (NIS) as a strategy that can successfully invade all nearby strategies. The combination of these two concepts for matrix games yields an ESNIS (Apaloo, 2006) that exhibits the frequency-dependent version of evolutionary substitution. On the other hand, evolution works on the ecological system too, where the interactions are also density-dependent. As we saw in Section 2, ecological stability together with the mutant phenotype being an ESNIS is equivalent to evolutionary substitution for single-species LV systems (that also includes population density effects). This answers one of the questions posed by Garay (2007) (i.e. what kind of mutant is able to substitute for or replace the resident clone) who was also interested in circumstances when stable coexistence of resident and mutant phenotypes arises. In the present paper, we extend these concepts of substitution and replacement to $N-$species LV systems, relying as well on the notion of evolutionary stability introduced earlier for these systems (Garay and Varga, 2000; Cressman and Garay, 2003a). From this perspective, the paper can be viewed as extending the theory of ecological and evolutionary stability to $N-$species LV systems.

Simultaneous invasion by two species occurs naturally as the following example shows. When an invasive species appears, it is usually introduced at a low density. An important question is whether the invasive species can or cannot substitute for the native species. For instance, Grey squirrels (Sciurus carolinensis) originated in North America and are a vector for a smallpox virus that evolved there. Grey squirrels (and this virus) have been introduced in many places throughout the world (e.g. England and continental Europe) where they do not need large numbers to start a new population. In Great Britain, grey squirrels have been able to spread 17-25 times faster through competitive exclusion (Bertolino et al. 2008) of the red squirrel (Sciurus vulgaris) due to increased mortality of reds from the squirrelpox virus which was not resident in Europe (Sandro, 2008; Strauss, 2012). Grey squirrels do not die from this virus but the virus can spread from them and infect red squirrels, causing death. Clearly, in this case, two species (i.e. grey squirrels and its virus) simultaneously invade into the European ecosystems, and the interactions in the whole ecosystem determine the success of grey squirrels.

In the evolutionary process, past historical events play a crucial role in explaining structural and functional features (Herrera 1992) in the ecosystem. For instance, nectarivory and pollination by birds is common in southern Australia, while in Europe social bees play these roles (Ford 1985). However, ecosytem convergence has been considered by ecologists as evidence not only in the present (Ojeda et al 2001) but also between the Pleistocene period and the present (Cowling at al. 1994, 1999). This means that under similar conditions (e.g. climate, soils), similar ecosystems evolve. Since mutation is a random process, the histories of evolution of these ecosystems are different but the outcome is similar as would be expected if it is independent of the order mutations occur. For such biological systems, we feel that the concept of historically independent replacement introduced in Section 4.1 is important.

References

[1] Akin E (1980) Domination or equilibrium. Math Biosciences 50:239-250

[2] Akin E, Hofbauer J (1982) Recurrence of the unfit. Math Biosciences 61:51-63

[3] Apaloo J (1997) Revisiting strategic models of evolution: the concept of neighborhood invader strategies. Theor Pop Biol 52:71-77

[4] Apaloo J (2006) Revisiting matrix games: the concept of neighborhood invader strategies. Theor Pop Biol 69:235-242

[5] Bertolino S, Lurz PWW, Sanderson R, Rushton SP (2008) Predicting the spread of the American grey squirrel (Sciurus carolinensis) in Europe: A call for a co-ordinated European approach. Biological Conservation 141:2564-2575

[6] Bomze I (1983) Lotka–Volterra equation and replicator dynamics: a two-dimensional classification. Biological Cybernetics 48:201-211

[7] Bomze I (1995) Lotka–Volterra equation and replicator dynamics: new issues in classification. Biological Cybernetics 72:447-453

[8] Cressman R, Garay J (2003a) Evolutionary stability in Lotka-Volterra systems. J Theor Biol 222:233-245

[9] Cressman R, Garay J (2003b) Stability in $N-$species coevolutionary systems. Theor Pop Biol 64:519-533

[10] Cressman R, Garay, J (2006) A game-theoretical model for punctuated equilibrium: species invasion and stasis through coevolution. BioSystems 84: 1-14

[11] Cowling RM, Cartwright CR, Parkington JE, Allsopp JC (1999) Fossil wood charcoal assemblages from Elands Bay Cave, South Africa: implications for Late Quaternary vegetation and climates in the winter-rainfall fynbos biome. J Biogeogr 26:367-378

[12] Cowling RM, Witkowski ETF, Milewski AV, Newbey KR (1994) Taxonomic, edaphic and biological aspects of narrow endemism on matched sites in mediterranean South Africa and Australia. J Biogeogr 21:651-664

[13] Dercole F, Rinaldi S (2008) Analysis of evolutionary processes. Princeton Series in Theoretical and Computational Biology. Princeton University Press.

[14] Drake JA (1990) The mechanics of community assembly and succession. J Theor Biol 147:213-233.

[15] Eldredge N, Gould SJ (1972) Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf TJM (ed) Models in paleobiology. WH Freeman and Cooper, San Francisco, pp 82-115

[16] Ford HA (1985). Nectarivory and pollination by birds in southern Australia and Europe. Oikos 44:127-131

[17] Garay J (2007) Adaptive dynamics based on ecological stability. In: Jorgensen S, Quincampoix M, Vincent TL (eds) Advances in dynamics game theory: numerical methods, algorithms and applications to ecology and economics. Annals of International Society of Dynamics Games, Birkhauser, Boston, Basel, Berlin, pp 271-287

[18] Garay J, Varga Z. (2000) Strict ESS for $n-$species systems. Biosystems 56:131-137.

[19] Gyllenberg M, Parvinen K (2001) Necessary and sufficient conditions for evolutionary suicide. Bull Math Biol 63:981-993

[20] Herrera CM (1992). Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in mediterranean woody plants. Am Nat 140:421-446

[21] Hofbauer J, Sigmund K (1998) Evolutionary games and population dynamics. Cambridge University Press, Cambridge

[22] Hutchinson GE (1965) The Ecological Theater and the Evolutionary Play. Yale University Press, New Haven

[23] Maynard Smith J, Price G (1973) The logic of animal conflicts. Am Nat 246:15-18

[24] Oba T, Kigami J (2018) Why does invasion imply substitution? Beyond the paradigm of invasion fitness. J Math Biol 77:1493-1532

[25] O'Dea A, Lessios HA, Coates AG et al. (2016). Formation of the Isthmus of Panama. Science Advances 2 (8): e1600883

[26] Ojeda F, Mark ST, Arroyo J, Teodoro M, Cowling RM (2001) Biodiversity in South African fynbos and Mediterranean heathland. J Vegetation Science 12:867-874

[27] Pielou EC (1966) Species-diversity and pattern-diversity in the study of ecological succession. J Theor Biol 10:370-383

[28] Strauss, A., White, A., Boots, M. (2012) Invading with biological weapons: the importance of disease-mediated invasions. Functional Ecology, 26, 1249-1261

[29] Sandro B. (2008) Introduction of the American grey squirrel (Sciurus carolinensis) in Europe: a case study in biological invasion. Current Science 95:903-906

[30] Shigesada N, Kawasaki K, Teramoto, E (1984) The effects of interference competition on stability, structure and invasion of multi-species systems. J Math Biol 21:97-113

[31] Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1:21–32

[32] Stehli FG, Webb SD (1985) The great American biotic interchange. Plenum Press, New York

[33] van den Driessche P, Zeeman ML (1998) Three-dimensional competitive Lotka-Volterra systems with no periodic orbits. SIAM J App Math 52:227-234

[34] Zeeman ML (1993) Hopf bifurcations in competitive three dimensional Lotka-Volterra systems. Dynam Stability Systems 8:189-217

Appendix A1. Remark 1

Proof of formula (6) in Remark 1. Here, we prove that

$$|A|:x_1^* = -\left|A^1\right|\left(r_1 + (Ax^1)_1\right)$$

when $N = 2$ and $A^1 = \begin{bmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{bmatrix}$ is nonsingular. The general proof of (6) is a straightforward extension of the methods provided here.

Since A^1 is nonsingular, $(Ax^1)_1 = a_{12}x_2^1 + a_{13}x_3^1$ where $x^1 = \begin{bmatrix} 0 \\ x_2^1 \\ x_3^1 \end{bmatrix}$ has components given by the solution of $\begin{bmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{bmatrix}\begin{bmatrix} x_2^1 \\ x_3^1 \end{bmatrix} + \begin{bmatrix} r_2 \\ r_3 \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$. By Cramer's Rule,

$$x_2^1 = -\frac{1}{|A^1|}\begin{vmatrix} r_2 & a_{23} \\ r_3 & a_{33} \end{vmatrix} \quad \text{and} \quad x_3^1 = -\frac{1}{|A^1|}\begin{vmatrix} a_{22} & r_2 \\ a_{32} & r_3 \end{vmatrix}$$

and so

$$\left|A^1\right|\left(r_1 + (Ax^1)_1\right) = r_1\begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix} - a_{12}\begin{vmatrix} r_2 & a_{23} \\ r_3 & a_{33} \end{vmatrix} - a_{13}\begin{vmatrix} a_{22} & r_2 \\ a_{32} & r_3 \end{vmatrix}.$$

Set $W_1 = \begin{bmatrix} r_1 & a_{12} & a_{13} \\ r_2 & a_{22} & a_{23} \\ r_3 & a_{32} & a_{33} \end{bmatrix}$. Expanding $|W_1|$ along the first row, we obtain

$$|W_1| = r_1 \begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix} - a_{12} \begin{vmatrix} r_2 & a_{23} \\ r_3 & a_{33} \end{vmatrix} + a_{13} \begin{vmatrix} r_2 & a_{22} \\ r_3 & a_{32} \end{vmatrix}.$$

In particular, $|W_1| = |A^1| \, (r_1 + (Ax^1)_1)$.

Since x^* is a solution of $Ax + r = 0$ for $N = 2$, a simple rearrangement gives $W_1 \begin{bmatrix} 1 \\ x_2^* \\ x_3^* \end{bmatrix} = -x_1^* \begin{bmatrix} a_{11} \\ a_{21} \\ a_{31} \end{bmatrix}$. The first coordinate of vector $\begin{bmatrix} 1 \\ x_2^* \\ x_3^* \end{bmatrix}$ can be expressed as

$$1 = -{:}\frac{x_1^*|A|}{|W_1|} \qquad \text{whenever } {:}|W_1| \neq 0{:}.$$

In other words, condition $|W_1| \neq 0$ implies formula (6) for $i = 1$ and $N = 2$. If $|W_1| = 0$, there are two cases depending on the (non)singularity of A. If A is nonsingular, then Cramer's Rule applies to $Ax^* = -r$ and yields $x_1^* = 0$. By using $|W_1| = |A^1| \, (r_1 + (Ax^1)_1)$ again, the nonsingularity of A^1 implies the $x_1^* = 0 = (r_1 + (Ax^1)_1)$ special case of (6). In the second case where A is singular, then $|A| = 0$ and, as before, $(r_1 + (Ax^1)_1) = 0$ and we are done. ■

Appendix A2. Example 1

Discussion of Example 1 (continued). To describe the global phase portrait of the three-dimensional (3D) LV system (7) investigated in Example 1, we pass to the associated 4D replicator system[15] (Bomze, 1983; Hofbauer and Sigmund, 1998)

$$\dot{x}_i = x_i\big((\mathbf{Ax})_i - \mathbf{x} \cdot \mathbf{Ax}\big) \qquad \text{where} \qquad \mathbf{A} = \begin{pmatrix} 0 & 5 & -1 & -4 \\ 2 & 0 & 2 & -1 \\ 3 & 5 & 0 & -4 \\ 3 & -2 & 3 & 0 \end{pmatrix} \tag{21}$$

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[15] We use Bomze's normalization of choosing $a_{11} = a_{22} = a_{33} = a_{44} = 0$

is the payoff matrix, $\mathbf{x}\cdot\mathbf{A}\mathbf{x}$ is the dot product $\Sigma_i x_i(\mathbf{A}\mathbf{x})_i$ of the column vectors $\mathbf{x}$ and $\mathbf{A}\mathbf{x}$, and

$$x_1 = \frac{\rho_1}{\kappa}\ ,\ x_2 = \frac{\rho_2}{\kappa}\ ,\ x_3 = \frac{\mu_1}{\kappa}\ ,\ x_4 = \frac{1}{\kappa} \tag{22}$$

with $\kappa = \rho_1 + \rho_2 + \mu_1 + 1$. When doing this, the non-negative octant $(\rho_1, \rho_2, \mu_1) \in R^3_{\geq 0}$ is replaced by the three-dimensional unit simplex

$$\Delta^4 = \{(x_1, x_2, x_3, x_4)^T \in R^4_{\geq 0} \mid x_1, x_2, x_3, x_4 \geq 0 \ \text{ and } \ x_1 + x_2 + x_3 + x_4 = 1\}$$

with barycentric coordinates. Clearly the vertices of Δ^4 (i.e., $V_1 = \mathbf{e}_1$, $V_2 = \mathbf{e}_2$, $V_3 = \mathbf{e}_3$, $V_4 = \mathbf{e}_4$) are equilibria of the 4D replicator system in (21). Three nontrivial equilibria are lying on 1D edges, namely

$$S = \frac{1}{3}\big(\mathbf{e}_2 + 2\mathbf{e}_4\big)\ ,\ Q_- = \frac{1}{7}\big(5\mathbf{e}_1 + 2\mathbf{e}_2\big)\ ,\ Q_+ = \frac{1}{7}\big(2\mathbf{e}_2 + 5\mathbf{e}_3\big)$$

and two more equilibria are lying on 2D faces, namely

$$P_- = \frac{1}{3}\big(\mathbf{e}_1 + \mathbf{e}_2 + \mathbf{e}_4\big)\ ,\ P_+ = \frac{1}{3}\big(\mathbf{e}_2 + \mathbf{e}_3 + \mathbf{e}_4\big):.$$

It is an easy but somewhat lengthy task to apply the standard Grobman-Hartman lemma in the vicinity of each equilibrium. The Jacobian is computed by the general formula

$$J_{ij} = \delta_{i,j}\big((\mathbf{A}\mathbf{x})_i - \mathbf{x}\cdot\mathbf{A}\mathbf{x}\big) : + : x_i\big(a_{ij} - (\mathbf{A}\mathbf{x})_j - \mathbf{a}_j\cdot\mathbf{x}\big) :, \quad i, j = 1, 2, 3, 4 :$$

where $\mathbf{a}_j$ is the jth column of $\mathbf{A}$. Eigenvectors which are not perpendicular to the normal vector of the 3D plane of equation $x_1 + x_2 + x_3 + x_4 = 1$ have to be disregarded. Our final result is demonstrated in Figure 2.

In order to illustrate the behavior of the resident-mutant system (7) far from the origin of $R^3_{\geq 0}$, triangle $V_1V_2V_3$ is replaced by the front-right-top octant of a sphere. A quick analysis of (22) implies that the properties observed in the last paragraph of Example 1 are lifted to the level of the associated replicator subsystems. In particular, the $x_3 = 0$ and the $x_1 = 0$ restrictions of the full replicator system (21)—shown as the ‘circular sectors’ $V_1V_4V_2$ and $V_3V_4V_2$ in Figure 2—are dynamically the same and of Type 12 in Bomze’s classification of 2D replicator systems (see Bomze, 1983; Bomze,

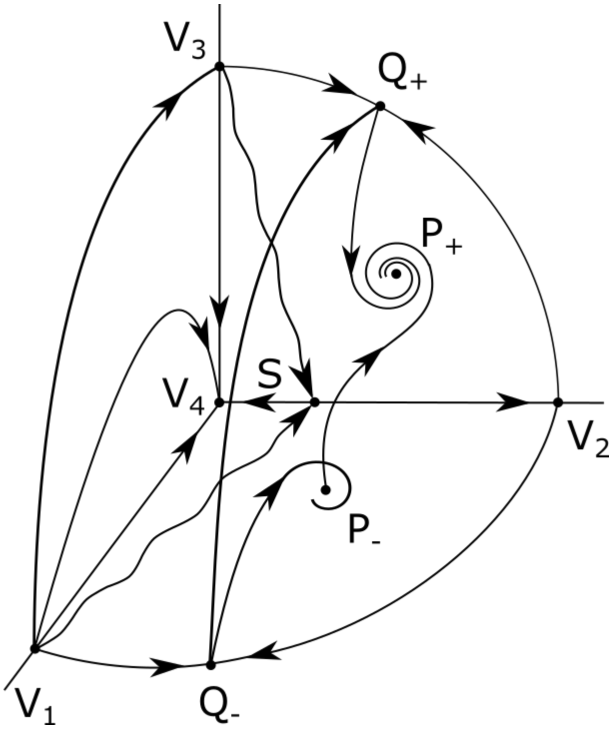

Figure 2: Schematic phase portrait of the replicator system (21).

1995); cf. with Figure 7.1 in Hofbauer and Sigmund (1998) and Figure 37 (a) in Maynard Smith (1982). The rest follows from inequalities

$$\frac{d}{dt}\left(\frac{x_3}{x_1}\right) = \frac{x_3}{x_1}\,(3x_1 + x_3) > 0 \qquad \text{and} \qquad \frac{d}{dt}\left(\frac{\mu_1}{\rho_1}\right) = \frac{\mu_1}{\rho_1}\,(3\rho_1 + \mu_1) > 0,$$

valid for trajectories of systems (21) and (7) with $x_1, x_3 \in (0,1)$ and $\rho_1, \mu_1 > 0$, respectively.[16]

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[16] The local phase portraits in the vicinity of the nine equilibria are clearly visible in Figure 2. Note that V_1 is a repellor, V_4 and P_+ are attractors. All the other equilibria are saddles. Equilibria V_2 and V_3 have a unique ingoing trajectory each. Equilibria P_- and Q_+ have a unique outgoing trajectory each. Equilibria S and Q_- have two outgoing and two ingoing trajectories, respectively. On the 2D faces containing P_- and P_+, both P_- and P_+ are stable foci created by the complex eigenvalue pair $\frac{-1\pm i\sqrt{3}}{6}$. The unstable eigendirection at P_- is $(-11,-2,13,0)^T$ with eigenvalue $\lambda_4 = 1$. The strongly-stable eigendirection

Appendix A3. Theorem 4

Proof of Theorem 4 (continued). It is left to point out that a convex combination of the two mutant strategies dominates a convex combination of the two resident strategies.

Given a 4×4 matrix B in (19) whose entries are subject to conditions

$$b_{ii} = 0 \text{ whenever } i = 1,2,3,4 \text{ and } b_{ij} > 0 \text{ whenever } i+j = 2k+1,\ k = 1,2,3$$

and to the conditions listed in (20), we look for dominance of the form

$$y(\text{row}_1) + (1-y)(\text{row}_2) < x(\text{row}_3) + (1-x)(\text{row}_4) \tag{23}$$

with some $x = x^* \in [0,1]$ and $y = y^* \in [0,1]$ suitably chosen.

Each column of matrix B—more precisely, each coordinate vector of the row vectors in (23)—leads to a linear, strict inequality in the $xy-$plane. All in all, we are facing four open half-planes defined by the linear inequalities

$$\begin{aligned} y > \ell_1(x) = 1 - \frac{x\mathbf{b}_{31} + (1-x)b_{41}}{b_{21}} \quad &, \quad y < \ell_2(x) = \frac{xb_{32} + (1-x)\mathbf{b}_{42}}{b_{12}}, \\ y > \ell_3(x) = \frac{b_{23} - (1-x)b_{43}}{b_{23} - \mathbf{b}_{13}} \quad &, \quad y < \ell_4(x) = \frac{xb_{34} - \mathbf{b}_{24}}{b_{14} - \mathbf{b}_{24}}, \end{aligned} \tag{24}$$

respectively. The line of equation $y = \ell_i(x)$ will be denoted by L_i, $i = 1,2,3,4$. Please note that all denominators are positive (for $i = 3$ and $i = 4$, recall that $b_{23} > \mathbf{b}_{13}$ by (20c0) and $b_{14} > \mathbf{b}_{24}$ by (20e0)). As a by-product, both L_3 and L_4 have positive slopes.

Our aim is to construct a solution pair $x = x^* \in [0,1]$ and $y = y^* \in [0,1]$ to the linear system of inequalities (24). Depending on the properties of the lines L_1, L_2, L_3, L_4, a lengthy separation of cases will be required. But first

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at P_+ is $(3,2,-13,8)^T$ with $\lambda_1 = -\frac{1}{3}$. The center-unstable and the strongly-unstable eigendirections at Q_- are $(-85,8,0,77)^T$ with $\lambda_3 = \frac{1}{7}$ and $(-31,-4,35,0)^T$ with $\lambda_4 = \frac{15}{7}$, respectively. The center-stable and the unstable eigendirections at Q_+ are $(-7,4,3,0)^T$ with $\lambda_3 = -\frac{5}{7}$ and $(0,8,-85,77)^T$ with $\lambda_4 = \frac{1}{7}$, respectively. The 2D stable quadrant at S is the convex span of eigendirections $(0,1,-9,8)^T$ and $(-9,1,0,8)^T$ belonging to the double eigenvalue $\lambda_{1,2} = -\frac{1}{3}$. Finally, let us note that all α-limit sets and all ω-limit sets of (21) are one of the nine equilibria.

we collect some inequalities which are valid for all cases to be investigated.

Note that L_2 is always strictly above L_1 for $0 \leq x \leq 1$ since $\big(0, 1 - \frac{b_{41}}{b_{21}}\big)$ and $\big(1, 1 - \frac{\mathbf{b}_{31}}{b_{21}}\big)$ are points on L_1, $\big(0, \frac{\mathbf{b}_{42}}{b_{12}}\big)$ and $\big(1, \frac{\mathbf{b}_{32}}{b_{12}}\big)$ are points on L_2 and $1 - \frac{b_{41}}{b_{21}} < \frac{\mathbf{b}_{42}}{b_{12}}$ by (20b) and $1 - \frac{\mathbf{b}_{31}}{b_{21}} < \frac{b_{32}}{b_{12}}$ by (20a). Similarly, note that L_3 is strictly to the right of L_4 for $0 \leq y \leq 1$ since $\big(1 - \frac{b_{23}}{b_{43}}, 0\big)$ and $\big(1 - \frac{\mathbf{b}_{13}}{b_{43}}, 1\big)$ are points on L_3, $\big(\frac{\mathbf{b}_{24}}{b_{34}}, 0\big)$ and $\big(\frac{b_{14}}{b_{34}}, 1\big)$ are points on L_4, and $1 - \frac{b_{23}}{b_{43}} > \frac{\mathbf{b}_{24}}{b_{34}}$ by (20h) and $1 - \frac{\mathbf{b}_{13}}{b_{43}} > \frac{b_{14}}{b_{34}}$ by (20g). A major consequence is that geometrically, our task is to find a point (x^*, y^*) in the unit square $[0,1]^2$ that is (strictly) above L_1, below L_2, to the left of L_3, and to the right of L_4.

Set $y_{0i} = \ell_i(0)$ and $y_{1i} = \ell_i(1)$, $i = 1, 2, 3, 4$. Let x_{0i} be the $x-$coordinate of L_i at $y = 0$. Let x_{1i} be the $x-$coordinate of L_i at $y = 1$. $\big($If the slope of L_i is zero—which may happen only for $i = 1$ and $i = 2$—then x_{0i} and x_{1i} are not defined. In what follows we shall give a special attention to this degenerate possibility.$\big)$ Using the new notation, our results so far can be rewritten as

$$y_{12} > y_{11} \ \ , \ \ y_{02} > y_{01} \ \ , \ \ x_{04} < x_{03} \ \ , \ \ x_{14} < x_{13} \, . \tag{25}$$

Observe that L_2 and L_4 both have positive height at $x = 1$ $\big($i.e. $y_{12} = \frac{b_{32}}{b_{12}} > 0$ and $y_{14} = \frac{b_{23} - \mathbf{b}_{24}}{b_{14} - \mathbf{b}_{24}} > 0$ by (20h0) and (20e0)$\big)$and that the heights of L_1 and L_3 are both less than 1 at $x = 0$ $\big($i.e. $y_{01} = 1 - \frac{b_{41}}{b_{21}} < 1$ and $y_{03} = \frac{b_{23} - b_{43}}{b_{23} - \mathbf{b}_{13}} < 1$ by (20c0) and (20g0)$\big)$:

$$y_{12} > 0 \ , \ y_{14} > 0 \ , \ y_{01} < 1 \ , \ y_{03} < 1. \tag{26}$$

In view of inequalities (20c), (20e), (20h), (20g), we obtain that

$$y_{12} > y_{13} > 0 \ , \ y_{01} < y_{04} < 1 \ , \ x_{04} < x_{03} < 1 \ , \ x_{13} > x_{14} > 0. \tag{27}$$

Combining the very first inequalities in (25) and in (27), we conclude that

$$y_{12} > \max\{y_{11}, y_{13}\} > 0. \tag{28}$$

Note that $y_{14} > 0$ is equivalent to $x_{04} < 1$ and $y_{14} \leq 1$ is equivalent to $x_{14} \geq 1$. There are several equivalencies of the types above, e.g. the equivalence between $x_{13} > 0$ and $y_{03} < 1$ etc.

From now on, we have to distinguish CASES 1,2,3,4 depending on the sign of the slopes of L_1 and L_2.

CASE 1. Assume that L_1 and L_2 have nonnegative slopes.

CASE 2. Assume that L_1 has negative slope and L_2 has nonnegative slope.

CASE 3. Assume that L_1 has nonnegative slope and L_2 has negative slope.

CASE 4. Assume that L_1 and L_2 have negative slopes.

In view of (24), Slope$(L_1) = \frac{b_{41}-\mathbf{b}_{31}}{b_{21}}$ and the Slope$(L_2) = \frac{b_{32}-\mathbf{b}_{42}}{b_{12}}$.

Within each CASE, recalling $y_{12} > 0$ and $y_{14} > 0$ from (26), we have three subcases according to

$$\text{(i) } 0 < y_{14} \leq 1\ ,\ \text{(ii) } 0 < y_{12} \leq 1 \ \&\ y_{14} > 1\ ,\ \text{(iii) } y_{12} > 1 \ \&\ y_{14} > 1.$$

In *Cases* 1(i), 2(i), 3(i), 4(i), 1(ii), 2(ii), 3(ii), and 4(ii), our choice for $x = x^* \in [0,1]$ and $y = y^* \in [0,1]$ will be

$$(x^*, y^*) = (1, \min\{y_{12}, y_{14}\} - \varepsilon) \quad \text{where } \ \varepsilon > 0 \ \text{ is sufficiently small.}$$

In view of inequality (28) and assumption $0 < y_{14} \leq 1$ (for (i)) or assumptions $0 < y_{12} \leq 1$ and $y_{14} > 1$ (for (ii)), (x^*, y^*) is above L_1, below L_2 and to the right of L_4. Thus, the mutant strategy of species 1 will dominate a convex combination of the two resident strategies if (x^*, y^*) is to the left of L_3. That is, it remains to check that

$$y_{14} > \max\{y_{11}, y_{13}\}. \tag{29}$$

Case 1(i). Recall that $y_{14} \leq 1$ is equivalent to $x_{14} \geq 1$. With the help of a little plane geometry, $y_{14} > y_{13}$ is implied[17] by $x_{04} < x_{03} < 1$ and $1 \leq x_{14} < x_{13}$. In order to prove inequality $y_{14} > y_{11}$, the cases Slope$(L_1) > 0$ and Slope$(L_1) = 0$ will be considered separately. Note that the lines L_2, L_3, and L_4 are already fixed. If Slope$(L_1) > 0$, then x_{11} is defined and satisfies $x_{14} < x_{11}$. In fact, $x_{14} = \frac{b_{14}}{b_{34}} < \frac{b_{41}}{b_{41}-\mathbf{b}_{31}} = x_{11}$ follows directly from assumption $b_{41} > \mathbf{b}_{31}$ and (20f). Combining $1 \leq x_{14} < x_{11}$ and $y_{01} < y_{04} < 1$ (the second chain of inequalities in (27)), inequality $y_{14} > y_{11}$ follows by an elementary geometric argument for two lines in the plane. The degenerate case Slope$(L_1) = 0$ is easier. Then x_{11} does not exist but $y_{11} = y_{01} < y_{04} < y_{14}$ and we are done.

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[17] Note that a purely algebraic proof of inequality $y_{14} = \frac{b_{34}-\mathbf{b}_{24}}{b_{14}-\mathbf{b}_{24}} > \frac{b_{23}}{b_{23}-\mathbf{b}_{13}} = y_{13}$ is considerably harder. Elementary examples show that $y_{14} \geq y_{13}$ does not follow from $x_{04} < x_{03} < 1$ and $0 < x_{14} < x_{13}$. Thus the equivalence between $y_{14} \leq 1$ and $x_{14} \geq 1$ (due to the fact that the slope of L_4 is positive) leads to a crucial improvement of (27).

Case 1(ii). By using (28), both $y_{11} < 1$ and $y_{13} < 1$ follow from assumption $0 < y_{12} \leq 1$. Since $y_{14} > 1$, we conclude that inequality (29) holds true in the slightly stronger form $y_{14} > 1 > \max\{y_{11}, y_{13}\}$.

The proof of inequality $y_{14} > y_{11}$ in *Case* 1(i) above works also in *Case* 3(i). For the remaining *Cases* 2(i) and 4(i), the slope of L_1 is negative (and the slope of L_4 is positive). Thus $y_{14} > y_{11}$ is a direct consequence of inequality $y_{01} < y_{04}$ in (27). Fortunately, the proofs of inequality $y_{14} > y_{13}$ are the same in *Cases* 1(i), 2(i), 3(i), and 4(i). Moreover, the proof in *Case* 1(ii) can be repeated in *Cases* 2(ii), 3(ii), and 4(ii), too. Absolutely no modifications are needed.

Thus only *Cases* 1(iii), 2(iii), 3(iii), and 4(iii) are left. We claim that an (x^*, y^*) in the unit square of the form $(x^*, 1)$ will work in all these cases. Recall that, by assumption, $y_{12} > 1$ and $y_{14} > 1$. Similarly, $y_{13} > 0$ by (27). In what follows, inequalities from (25)–(27) will be recalled without any further notice.

Case 1(iii). If $y_{11} < 1$ and $y_{13} < 1$, then we can take $(x^*, y^*) = (1, 1)$ (i.e. the mutant phenotype of species 1 dominates its resident phenotype).

If $y_{11} \geq 1$, both the existence of x_{11} and inequality $0 < x_{11} \leq 1$ are implied by $y_{01} < 1 \leq y_{11}$. As a by–product, we obtain that $\text{Slope}(L_1) > 0$. Recall that $0 < x_{14} < x_{13}$. The argument we used in *Case* 1(i) leads to $x_{14} < x_{11}$ again. In what follows we distinguish two cases according as $\text{Slope}(L_2) > 0$ or $\text{Slope}(L_2) = 0$. Suppose that $\text{Slope}(L_2) > 0$. Then $y_{01} < y_{02} < y_{12}$ and $y_{11} < y_{12}$ give rise both to the existence of x_{12} and to inequality $x_{12} < x_{11}$. Since $0 < \max\{1, y_{13}\} < y_{12}$ and $x_{02} < x_{03}$ $\big($i.e. $\frac{-\mathbf{b}_{42}}{b_{32}-\mathbf{b}_{42}} < 1 - \frac{b_{23}}{b_{43}}$ by (20d) when $b_{32} - \mathbf{b}_{42} > 0$ which is equivalent to $\text{Slope}(L_2) > 0\big)$ with $x_{03} < 1$, also inequality $x_{12} < x_{13}$ holds true. All in all, we arrived at the chain of inequalities $1 \geq \min\{x_{11}, x_{13}\} > \max\{0, x_{12}, x_{14}\}$ and can take $(x^*, y^*) = (\min\{x_{11}, x_{13}\} - \varepsilon, 1)$. In the degenerate case $\text{Slope}(L_2) = 0$, we have $0 < x_{11} \leq 1$, $x_{14} < x_{11}$ and $0 < x_{14} < x_{13}$. In particular, $0 < x_{14} < \min\{x_{11}, x_{13}\} \leq 1$. Given $x \in [0, x_{11})$ arbitrarily, $(x, 1)$ is (strictly) below L_2 and above L_1. For $x \in (x_{14}, x_{13})$, $(x, 1)$ is to the left of L_3 and to the right of L_4. Thus the choice $(x^*, y^*) = (\min\{x_{11}, x_{13}\} - \varepsilon, 1)$ is still possible.

If $y_{11} < 1$ and $y_{13} \geq 1$, consider first the special case $\text{Slope}(L_1) \geq 0$ and $\text{Slope}(L_2) = 0$. Since $y_{11} < 1 < y_{12}$, all points on the top edge of the unit square (i.e. for $0 \leq x \leq 1$ and $y = 1$) are (strictly) below L_2 and above

L_1. Combining inequalities $0 < x_{14} < x_{13}$ and $y_{03} < 1 \le y_{13}$, we arrive at $0 < x_{14} < x_{13} \le 1$. In particular, we can take $(x^*, y^*) = (x_{13} - \varepsilon, 1)$. Now we turn our attention to the special case $\text{Slope}(L_1) > 0$ and $\text{Slope}(L_2) > 0$. Thus $\ell_1, \ell_2, \ell_3, \ell_4$ are strictly increasing functions. This implies the existence of the intersection points $x_{11}, x_{12}, x_{13}, x_{14}$. Clearly $0 < x_{14} < x_{13} \le 1$. The derivation of inequalities $x_{14} < x_{11}$ and $x_{12} < x_{13}$ is exactly the same as in the case $y_{11} \ge 1$ above. The remaining inequality $x_{12} < x_{11}$ follows from the chains of inequalities $y_{01} < y_{02} < y_{12}$, $y_{01} < y_{11} < 1 < y_{12}$ via an easy geometric argument. Depending on the relative position of y_{02}, y_{11} and 1 in the open interval (y_{01}, y_{12}), we have to consider three separate subcases, namely $y_{11} < 1 \le y_{02}$, $y_{02} \le y_{11} < 1$ or $y_{11} \le y_{02} \le 1$. (If $y_{11} \le y_{02} \le 1$, then one of the inequalities should be strict.) In each of the three subcases, we arrive at inequality $x_{12} < 1 < x_{11}$. Again, an appropriate choice in the unit square is $(x^*, y^*) = (\min\{x_{11}, x_{13}\} - \varepsilon, 1)$. Finally, consider now the remaining special case $\text{Slope}(L_1) = 0$ and $\text{Slope}(L_2) > 0$. As before, $0 < x_{14} < x_{13} \le 1$ and $x_{12} < x_{13}$ (and $y_{11} < 1$, $y_{12} > 1$). For $x \in (x_{14}, x_{13})$, $(x, 1)$ is to the left of L_3 and to the right of L_4. Given $x \in (x_{12}, 1]$ arbitrarily, $(x, 1)$ is (strictly) below L_2 and above L_1. Thus the choice $(x^*, y^*) = (x_{13} - \varepsilon, 1)$ is appropriate.

Case 2(iii). If $\text{Slope}(L_1) < 0$ and $\text{Slope}(L_2) = 0$, then $1 > y_{01} > y_{11}$ and $y_{02} > y_{12} > 1$. Thus all points on the top edge of the unit square are (strictly) above L_1 and below L_2. Since $0 < x_{14} < x_{13}$ and $x_{14} < 1$ (by using $y_{14} > 1$ and $\text{Slope}(L_4) > 0$), we can take $(x^*, y^*) = (x_{14} + \varepsilon, 1)$. If $\text{Slope}(L_1) < 0$ and $\text{Slope}(L_2) > 0$, then x_{12} exists and (by using $y_{12} > 1$) satisfies $x_{12} < 1$. Similarly, $x_{14} < 1$ and $x_{11} < 0$. As in the proof of *Case* 1(iii), inequalities $x_{02} < x_{03} < 1$ and $\max\{1, y_{13}\} < y_{12}$ imply via some geometry that $x_{12} < x_{13}$. In view of $0 < x_{14} < x_{13}$, we can take $(x^*, y^*) = (\max\{x_{12}, x_{14}\} + \varepsilon, 1)$. Note that the choice $(x^*, y^*) = (\min\{1, x_{13}\} - \varepsilon, 1)$ is also possible.

Case 3(iii). Since $\text{Slope}(L_2) < 0$, we have $y_{02} > y_{12}$. As a trivial consequence of assumption $y_{12} > 1$, all points on the top edge of the unit square are (strictly) below L_2. In addition, $x_{12} > 1$. Similarly, assumption $y_{14} > 1$ implies that $x_{14} < 1$. Recall that, from (27), $0 < x_{14} < x_{13}$. Last but not least, the proof of inequality $x_{14} < x_{11}$ in *Case* 1(i) with $\text{Slope}(L_1) > 0$ can be repeated and leads to $(x^*, y^*) = (x_{14} + \varepsilon, 1)$. If $\text{Slope}(L_1) = 0$, then $y_{01} < 1$ implies that the choice $(x^*, y^*) = (x_{14} + \varepsilon, 1)$ is still possible.

Case 4(iii). Every point on the top edge of the unit square is (strictly) above L_1 and below L_2. Recall that $0 < x_{14} < x_{13}$ and note that $x_{14} < 1$ by assumption $y_{14} > 1$. As above, we can take $(x^*, y^*) = (x_{14} + \varepsilon, 1)$. ■