

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

38 the same game and the phenotypes are different (see Cressman and Garay
39 2003a,b; Garay 2007) or interaction parameters between resident and mutant
40 phenotypes are not so different. This contrasts to models in invasion ecology
41 where the phenotypic similarity between exotic and native species cannot be
42 assumed. One well-known example of dissimilar phenotypes is from Australi-
43 a, when the invasive mammals substitute for the native marsupials. However,
44 Hutchinson (1965) has already emphasized that biotic evolution cannot be
45 separated from ecology, since ecological factors (like competition and feed-
46 ing) have a curtailing effect on the evolutionary success of all mutants and/or
47 species.

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

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

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

76 *substitution*” has occurred.

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

83 Our investigation is based on the dynamics of evolving population sizes for
84 the resident and mutant phenotypes of the N –species evolutionary ecology
85 system that assumes these dynamics are of Lotka-Volterra (LV) type.¹ This
86 extends the work of Garay and Varga (2000) and Cressman and Garay
87 (2003a) who investigated resident stability/invadability in such LV systems
88 rather than substitution/replacement. In particular, the monomorphic model
89 of Cressman and Garay (2003a) examines the invadability of the resident
90 system when there is a single mutant phenotype in each species. As we
91 will see, the methods developed there are also essential to our results on
92 evolutionary substitution and replacement.

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

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

¹Here 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 successfully invade. Adaptive dynamics also questions whether invasion leads to substitution/replacement (O-ba and Kigami, 2018).

108 the dominance concept of Section 3. However, if the successful invasions occur through a sequence of evolutionary substitutions that does not depend on
 109 whether a rare mutant first appears in species one or in species two (which we
 110 call “*historically independent replacement*”), then evolutionary replacement
 111 ensues (see Theorem 4 there). The biological importance of this concept is
 112 illustrated at the end of Section 5. This final section also discusses other
 113 results of the paper from a biological perspective.
 114

115 2 Evolutionary Substitution and Replacement 116 in Single Species LV Systems

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

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

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

123 where ρ_1 is the resident density, r_1 is the intrinsic growth rate and m_{11}^{RR} is
 124 the interaction parameter. Clearly, this system has a stable equilibrium with
 125 $\rho_1^* > 0$ (i.e. with the resident species present) if and only if the intrinsic
 126 growth is positive and the interaction term is negative (in which case, the
 127 equilibrium is $\rho_1^* = -r_1/m_{11}^{RR}$).²

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

²The 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.

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

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

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

137 We say that general LV systems of the form (2) exhibit evolutionary sub-
138 stitution if (i) the one-dimensional resident system and mutant system respec-
139 tively each have a stable equilibrium with positive density; (ii) the resident
140 (respectively, mutant) equilibrium is unstable (respectively, stable) since it
141 can be invaded by the mutant phenotype (respectively, cannot be invaded
142 by the resident phenotype) in the two-dimensional resident-mutant system
143 (2); and (iii) after the mutant successfully invades the resident, the system e-
144 volves to the mutant equilibrium. In fact, these two-dimensional LV systems
145 exhibit evolutionary substitution if and only if $r_1 > 0, m_{11}^{RR} < 0, m_{11}^{II} < 0$
146 (i.e. the resident system and the mutant system each have a globally stable
147 equilibrium) and $m_{11}^{IR} \geq m_{11}^{RR}, m_{11}^{II} \geq m_{11}^{RI}$ with strict inequality in at least
148 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 s-
strategy (ESS). That is, in addition to ecological stability, we have evolution-
ary stability of the mutant phenotype since it is an ESS of the evolutionary
game given by the 2×2 payoff matrix (or interaction matrix)

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

149 In game-theoretic terms (Apaloo, 2006), the final condition for evolutionary
150 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

³That 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.

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

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

- 158 (i) there is ecological stability in the resident system and in the mutant
 159 system
- 160 (ii) the resident phenotype cannot invade the mutant phenotype (i.e. the
 161 mutant phenotype is an ESS of the interaction matrix for the resident-mutant
 162 evolutionary game), and
- 163 (iii) the mutant phenotype can invade the resident phenotype (i.e. the
 164 mutant phenotype is a NIS of the resident phenotype for this interaction
 165 matrix).

166 3 Evolutionary Substitution in N -Species

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

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

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

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

178 Garay, 2003a). Then m_{kl}^{RR} (respectively, m_{kl}^{RI}) is the payoff to a resident
 179 phenotype (or strategy) in species k when interacting with a resident pheno-
 180 type in species l (respectively, the intruder or mutant phenotype).⁴ Similarly,
 181 m_{l1}^{IR} and m_{l1}^{II} are payoffs to the mutant phenotype. That is, the superscripts
 182 denote the phenotypes and the subscripts are the species in the interaction
 183 where the first superscript and subscript specify the phenotype and species
 184 of the individual receiving the payoff, respectively

185 The first requirement for evolutionary substitution is that this resident
 186 system is stable in the absence of mutants. In particular, from the biological
 187 perspective, this means that there is species coexistence in the residence
 188 system. Mathematically, there is a locally asymptotically stable equilibrium
 189 $\rho^* = (\rho_1^*, \dots, \rho_N^*)$ with all components positive (i.e. $\rho^* \in R_{>0}^N$) for the resident
 190 system

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

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

202 The next requirement is that the mutant phenotype can invade. That
 203 is, $(\rho^*, 0)$ is not a locally asymptotically stable equilibrium of the resident-
 204 mutant system (3). $(\rho^*, 0)$ will be unstable in the resident-mutant system
 205 if the *invasion fitness* $\lambda_1^I \equiv r_1 + \sum_{l=1}^N m_{l1}^{IR} \rho_l^*$ of the mutant phenotype at

⁴In 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.

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

206 this equilibrium is greater than the fitness of the resident phenotype $r_1 +$
 207 $\sum_{l=1}^N m_{1l}^{RR} \rho_l^* = 0$ (i.e. if $\lambda_1^I > 0$). On the other hand, $(\rho^*, 0)$ is locally
 208 asymptotically stable if $\lambda_1^I < 0$. In the intermediate case where $\lambda_1^I = 0$, the
 209 mutant phenotype is initially *selectively neutral* when invading the resident
 210 equilibrium. This case was analyzed by Cressman and Garay (2003a, 2003b)
 211 who showed that, for Lotka-Volterra systems, $(\rho^*, 0)$ is invadable if and only
 212 if $M^{II} - M^{IR} (M^{RR})^{-1} M^{RI} \geq 0$.

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

220 The question arises whether hyperbolic stability of ρ^* and $(\hat{\rho}_2, \dots, \hat{\rho}_N, \hat{\mu}_1)$
 221 in their respective N - dimensional Lotka-Volterra systems (which we as-
 222 sume from now on) implies evolutionary substitution if the mutant phenotype
 223 can invade $(\rho^*, 0)$ but the resident phenotype of species one cannot invade
 224 $(0, \hat{\rho}_2, \dots, \hat{\rho}_N, \hat{\mu}_1)$. Such an implication would generalize the evolutionary sub-
 225 stitution in a single species discussed in Section 2. Our first result (Theorem
 226 1) implies that a unique coexistence equilibrium is impossible in this case.

227 **Theorem 1** *Suppose that $E_1 \equiv (\rho^*, 0)$ and $E_2 \equiv (0, \hat{\rho}_2, \dots, \hat{\rho}_N, \hat{\mu}_1)$ are equi-*
 228 *libria of the N -species resident-mutant LV system (3) with all species present*
 229 *(i.e. $\rho_i^* > 0$ for $i = 1, 2, \dots, N$ and $\hat{\rho}_j > 0$ for $j = 2, \dots, N$ and $\hat{\mu}_1 > 0$). Also*
 230 *assume that E_1 and E_2 are locally asymptotically stable equilibria for system*
 231 *(3) restricted to their respective N -dimensional boundary face and that the*
 232 *mutant phenotype can invade E_1 but the resident phenotype of species one*
 233 *cannot invade E_2 .⁷ Then there is no isolated interior equilibrium⁸ for the*
 234 *$N + 1$ dimensional LV system.*

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

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

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

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

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

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

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

$$x_i^* = - \frac{|A^i|}{|A|} (r_i + (Ax^i)_i) \quad (5)$$

239 whenever the principal submatrix A^i of A formed by deleting the i^{th} row and
 240 column is nonsingular and, apart from the i -th coordinate which is then taken
 241 as $x_i^i = 0$, the remaining coordinates of $x^i = (x_1^i, \dots, x_{i-1}^i, 0, x_{i+1}^i, \dots, x_{N+1}^i)$
 242 are defined as the coordinates of the unique solution to the linear system
 243 $r_j + (Ax)_j = 0$ 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 $|A^1|$ and $|A^{N+1}|$ 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

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

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

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

$$|A| x_i^* = - |A^i| (r_i + (Ax^i)_i). \quad (6)$$

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

⁹The 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.

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

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

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

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

265 It is readily checked that the conditions of Theorem 1 are satisfied for
266 $N = 2$, equilibria $E_1 = (\rho_1^*, \rho_2^*, 0) = (1, 1, 0)$, $E_2 = (0, \widehat{\rho}_2, \widehat{\mu}_1) = (0, 1, 1)$ and
267 $\lambda_1^I = -4 + 7 = 3 > 0$, $\lambda_1^R = -4 + 7 - 4 = -1 < 0$. The equilibria of (7) are
268 the origin $O = (0, 0, 0)$, $P_+ = E_2$ (which are asymptotically stable¹⁰) and the
269 saddle points $P_- = E_1$ and $S = (0, \frac{1}{2}, 0)$.

270 The global dynamics of (7) as well as the dynamics of the resident sub-
271 system

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

¹⁰Since $0 < \rho_2 < \frac{1}{2}$ 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 .

272 and of the mutant subsystem

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

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

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

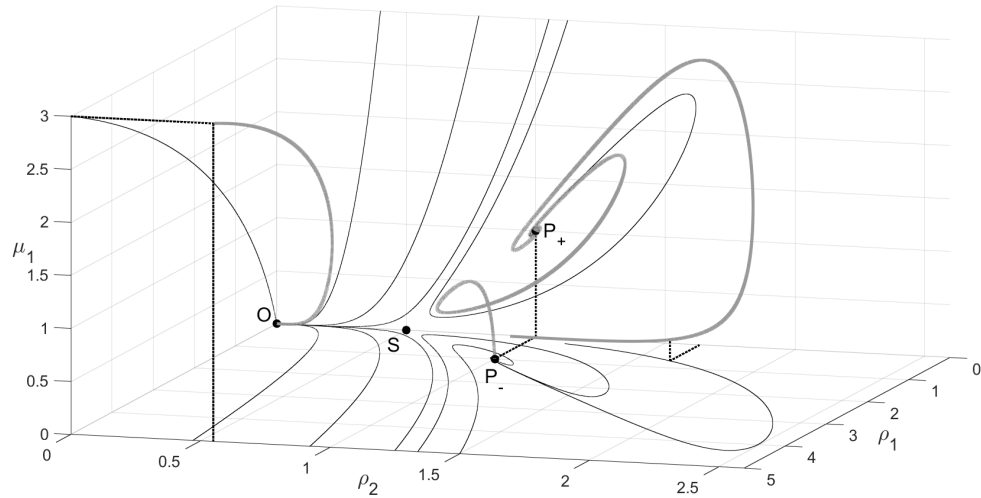


Figure 1: Phase portrait of the replicator system (7).

283 [ROSS: Please check that footnote 10 is placed where Barnabas intended
 284 it and that the figure is okay. The difference between the gray and black
 285 curves is not that great. Maybe the gray ones could be some other color

286 (red?) instead? I have inserted the sentence on orientation into the text
 287 since figure 1 does not have arrows on the trajectories.]

288 By Example 1, the invasion criteria of Theorem 1 do not imply evolution-
 289 ary substitution for two-species LV systems. On the other hand, if the LV
 290 system has more structure, the invasion criteria of Theorem 1 can be equiv-
 291 alent to evolutionary substitution. The following discusses two such systems
 292 of biological importance.

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

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

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

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

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

¹¹Here, 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”.

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

317 By Theorem 1 and Remark 1, (10) has no interior equilibria. Moreover,
 318 $E_1 \equiv (\rho_1^*, \rho_2^*, 0)$ corresponds to a saddle point on the x_1x_2 edge whose stable
 319 manifold is this edge and $E_2 \equiv (0, \hat{\rho}_2, \hat{\mu}_1)$ corresponds to a stable equilibrium
 320 on the x_2x_3 edge of the triangle. Thus, of the 33 possible classes of dynamic
 321 behavior classified by Zeeman (1993), the dynamics on the triangle is given
 322 by one of classes 9 to 12 depending on the behavior on the x_1x_3 edge. In all
 323 four classes, the equilibrium corresponding to E_2 is globally asymptotically
 324 stable. ■

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

331 **Theorem 3** *As in Theorem 1, let $E_1 \equiv (\rho^*, 0)$ and $E_2 \equiv (0, \hat{\rho}_2, \dots, \hat{\rho}_N, \hat{\mu}_1)$
 332 be equilibria of the N -species resident-mutant LV system (3) with all species
 333 present (i.e. $\rho_i^* > 0$ for $i = 1, 2, \dots, N$ and $\hat{\rho}_j > 0$ for $j = 2, \dots, N$ and
 334 $\hat{\mu}_1 > 0$). Furthermore, assume that all forward trajectories of (3) are bound-
 335 ed¹² and that E_2 is globally asymptotically stable equilibrium for system (3)
 336 restricted to its N -dimensional boundary face. If the mutant phenotype is
 337 always more fit than the resident phenotype of species one, then there is no
 338 interior equilibrium, the resident phenotype of species one goes extinct and
 339 E_2 is a locally asymptotically stable equilibrium for system (3). Moreover,
 340 if no interior trajectories converge to the boundary of the N -dimensional
 341 boundary face containing E_2 , then evolutionary substitution occurs.*

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

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

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

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

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

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

355 for all $(\rho_1, \rho_2, \dots, \rho_N, \mu_1)$ where ρ_1 and μ_1 are both positive. The final in-
 356 equality follows from (11). Thus, $\frac{\rho_1}{\mu_1}$ is a strictly decreasing function a-
 357 long every trajectory where ρ_1 and μ_1 are initially both positive. For the
 358 given interior trajectory, define $\lim_{t \rightarrow \infty} \frac{\rho_1(t)}{\mu_1(t)} = C \geq 0$. If $C = 0$, then
 359 $\lim_{t \rightarrow \infty} \rho_1(t) = 0$ since $\mu_1(t)$ is bounded. Suppose that ρ_1 does not converge
 360 to 0 (i.e. $\limsup_{t \rightarrow \infty} \rho_1(t) > 0$). Thus, $C > 0$ and there exists a limit point
 361 of the given trajectory with ρ_1 and μ_1 both positive. Any trajectory that
 362 is initially at this limit point is also in the limit set of the given trajectory.
 363 Since $\frac{\rho_1}{\mu_1}$ is strictly decreasing at this initial point, $\lim_{t \rightarrow \infty} \frac{\rho_1(t)}{\mu_1(t)} < C$, a
 364 contradiction. Since the resident phenotype ρ_1 goes extinct, there can be no
 365 interior equilibrium.

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

375 words, evolutionary substitution occurs. ■

376 **Remark 2.** The condition in Theorem 3 that E_2 is globally asymptotical-
 377 ly stable equilibria for system (3) restricted to its N -dimensional boundary
 378 face is necessary for the conclusion that evolutionary substitution occurs. To
 379 see this, consider Example 1 again. In it, we have that the mutant fitness
 380 $-4 + 7\rho_2 - 3\mu_1$ is always greater than the fitness $-4 - 3\rho_1 + 7\rho_2 - 4\mu_1$ of
 381 the resident phenotype of species one when ρ_1 and μ_1 are positive. However,
 382 evolutionary substitution does not occur in Example 1 since $(0, 0, 0)$ is local-
 383 ly asymptotically stable. Note that Theorem 3 also makes the biologically
 384 reasonable assumption that the density of each species must be bounded.

385 4 Evolutionary Replacement

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

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

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

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

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

404 **Example 2** Consider the resident-mutant system

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

405 The intrinsic growth rates of species one and two are $r_1 = 2$ and $r_2 = 3$
 406 respectively. This has an interior equilibrium at $(\rho_1, \rho_2, \mu_1, \mu_2) = (1, 1, 1, 1)$
 407 that is locally asymptotically stable since the only eigenvalue of the corre-
 408 sponding 4×4 Jacobian matrix is -1 (with multiplicity 4). The resident
 409 system has a globally asymptotically stable equilibrium at $(\rho_1^*, \rho_2^*) = (2, 3)$
 410 and the mutant system also has a globally asymptotically stable equilibrium
 411 at $(\mu_1^*, \mu_2^*) = (2, 3)$. Moreover, to analyze whether (ρ_1^*, ρ_2^*) can be invaded, we
 412 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
 413 analyze whether (μ_1^*, μ_2^*) can be invaded, we calculate $\lambda_1^R = 2 - \mu_1^* = 0$ and
 414 $\lambda_2^R = 3 - 2\mu_1^* = -1 < 0$.

415 Since the eigenvalue λ_2^I is zero (respectively, $\lambda_1^R = 0$), it is not imme-
 416 diately clear whether $(\rho_1^*, \rho_2^*, 0, 0) = (2, 3, 0, 0)$ (respectively, $(0, 0, \mu_1^*, \mu_2^*) =$
 417 $(0, 0, 2, 3)$) can be invaded. To avoid the use of B-matrix methods for these
 418 neutral invasion coefficients (Cressman and Garay, 2003a), we consider in-
 419 stead the slightly perturbed system

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

420 with some $\varepsilon > 0$. The new interior equilibrium $\left(\frac{1-5\varepsilon}{1-2\varepsilon}, \frac{1-6\varepsilon}{1-2\varepsilon}, \frac{1}{1-2\varepsilon}, \frac{1+4\varepsilon-6\varepsilon^2}{1-2\varepsilon}\right)$
 421 will still be locally asymptotically stable when ε is sufficiently small. More-
 422 over, the equilibrium of the resident system remains unchanged at $(\rho_1^*, \rho_2^*, 0, 0) =$
 423 $(2, 3, 0, 0)$ as does the equilibrium for the mutant system $(0, 0, \mu_1^*, \mu_2^*) = (0, 0, 2, 3)$.

424 However, it is now clear that both invader phenotypes can invade $(\rho_1^*, \rho_2^*, 0, 0)$,
 425 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
 426 $(0, 0, \mu_1^*, \mu_2^*)$, neither resident phenotype can invade since $\lambda_1^R = 2 - (1 + \varepsilon)\mu_1^* =$
 427 $-2\varepsilon < 0$ and $\lambda_2^R = 3 - 2\mu_1^* = -1 < 0$.

428 By Example 2, it is clear that more conditions are needed besides our inva-
 429 sion criteria in order to guarantee evolutionary replacement. One possibility
 430 is to assume that the mutant phenotype “dominates” the resident phenotype
 431 in each species as in Theorem 3 (i.e. the mutant phenotype is always more
 432 fit than the resident phenotype in each species). Keeping the boundedness
 433 assumption on forward trajectories, we see that all interior trajectories of
 434 the $2N$ –dimensional resident-mutant system converge to nonempty compact
 435 subsets of the N –dimensional mutant system. In particular, there are no in-
 436 terior equilibria. Moreover, the proof of Theorem 3 easily extends to show
 437 that there will be evolutionary replacement when the N –dimensional mutant
 438 system has a globally asymptotically stable equilibrium $(\mu_1^*, \mu_2^*, \dots, \mu_N^*)$ with
 439 all species present if interior trajectories do not converge to the boundary of
 440 the N –dimensional mutant system.¹³

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

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

¹³Specifically, by the dominance assumption, ρ_i/μ_i for $i = 1, 2, \dots, N$ 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 $\lim_{t \rightarrow \infty} \rho_i(t) = 0$ 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 $(\mu_1^*, \mu_2^*, \dots, \mu_N^*)$ 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.

¹⁴To 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.

449 N -dimensional mutant system.

450 **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 (e.g. $x_1 = \rho_1/(\rho_1 + \rho_2 + \mu_1 + \mu_2)$) 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

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

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

456 In Example 3, notice that the equilibrium of the resident system $(1/7, 1/7)$
 457 for (14) can be invaded by both mutant phenotypes since $\lambda_1^I = \lambda_2^I = 1 - 3/7 -$
 458 $1/7 > 0$ whereas the equilibrium of the mutant system $(1/5, 1/5)$ cannot be

459 invaded by either resident phenotype since $\lambda_1^R = \lambda_2^R = 1 - 2/5 - 5/5 < 0$.
460 On the other hand, these equilibria are unstable in their respective two-
461 dimensional system since the determinant of the linearization is negative in
462 both cases. This leaves open the possibility that combining dominance with
463 conditions that these boundary equilibria are locally asymptotically stable
464 in their respective two-dimensional system implies evolutionary replacement.
465 As we will see in the following section, this is indeed the case for two-species
466 competitive systems in biologically significant scenarios where dominance
467 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

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

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

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

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

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

477 The mutant phenotypes invade the resident system but the residents can-
478 not invade the mutants. Furthermore, all interior trajectories of (15) that

479 start close to the resident equilibrium evolve to the equilibrium of the mutant
480 system. That is, the mutant phenotypes have replaced the residents.

481 **4.1 Historically independent replacement**

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

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

- (i) $\rho_1\rho_2$ can be invaded by both μ_1 and μ_2
 - (ii) $\mu_1\rho_2$ can be invaded by μ_2 but not by ρ_1
 - (iii) $\rho_1\mu_2$ can be invaded by μ_1 but not by ρ_2
 - (iv) $\mu_1\mu_2$ cannot be invaded by ρ_1 or by ρ_2 .
- (16)

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

495 The sequence of evolutionary substitutions given by rare mutations can
496 then serve as a model of punctuated equilibrium based on the fossil record
497 in paleontology, a concept suggested by Eldredge and Gould (1972). This
498 theory claims that during a short geological time, new species arrive in rapid
499 succession and contribute revolutionary morphological changes. Following
500 these speciation events, an evolutionary stable ecosystem rapidly evolves,
501 where lineages are in stasis. We have previously demonstrated that, in a
502 two-species coevolutionary model, successful invasion is quickly followed by
503 evolutionary changes in behavior, leading to a sequence of punctuated equi-
504 librium (Cressman and Garay 2006). Historically independent replacement
505 implies that the final outcome for the ecosystem can be predicted without
506 knowing the sequence of mutations and their intermediate stasis events.

507 **Theorem 4** Suppose a two-species competitive system exhibits historically
508 independent replacement. In other words, the four two-dimensional faces
509 $\rho_1\rho_2$, $\rho_2\mu_1$, $\rho_1\mu_2$ and $\mu_1\mu_2$ have globally asymptotically stable interior equi-
510 libria that satisfy (16). Then there is no interior equilibrium where mutants
511 and residents coexist. Moreover, the equilibrium $(0, 0, \mu_1^*, \mu_2^*)$ with both mu-
512 tants present is globally asymptotically stable for the resident-mutant system
513 (12) with $N = 2$. That is, evolutionary replacement occurs.

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

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

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

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

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

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

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

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

524 (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
525 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
526 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
527 asymptotically stable on its two-dimensional face for system (18). Finally,
528 $(0, 0, \mu_1^*, \mu_2^*)$ can be invaded by the resident phenotype of species 1 for system
529 (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
530 and only if $(0, 0, \mu_1^*, \mu_2^*)$ can be invaded by the resident phenotype of species
531 1 for system (18).
532

533 By Hofbauer and Sigmund (1998, Exercise 7.5.2), the dynamics of system
534 (18) is the “same” as the replicator equation on the three-dimensional strategy
535 simplex $\Delta^4 \equiv \{(x_1, x_2, x_3, x_4) \mid x_i \geq 0, \sum x_i = 1\}$ with payoff matrix
536 $-\widehat{A}$. Moreover, this replicator equation is also given by a payoff matrix of
537 the form B where

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

538 by subtracting the diagonal entry of $-\widehat{A}$ from all entries in its column. We
539 want to show the assumptions that the four two-dimensional faces $\rho_1\rho_2$, $\rho_2\mu_1$,
540 $\rho_1\mu_2$ and $\mu_1\mu_2$ have globally asymptotically stable interior equilibria that
541 satisfy (16) imply that this matrix game has no equilibrium in the interior
542 of Δ^4 .

543 First, globally asymptotic stability of interior equilibria on the four two-
544 dimensional faces implies that $b_{12}, b_{14}, b_{21}, b_{23}, b_{32}, b_{34}, b_{41}, b_{43}$ are all positive.
545 The other entries in B , indicated by boldface in (19), may be positive or nega-
546 tive. The invasion assumptions correspond to the following eight inequalities
547 in (20). For instance, the interior resident equilibrium for the replicator e-
548 quation 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
549 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

550 listed (i.e. $\mathbf{b}_{31}b_{12} + b_{32}b_{21} > b_{12}b_{21}$).

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

551 By Akin (1980), there is no equilibrium in the interior of Δ^4 if and only if
552 there is some dominance relation among the four strategies. In fact, we show
553 in Appendix A3 that a convex combination of the two mutant strategies
554 dominates a convex combination of the two resident strategies. That is,
555 for matrix B , we show dominance of the form $y(\text{row}_1) + (1 - y)(\text{row}_2) <$
556 $x(\text{row}_3) + (1 - x)(\text{row}_4)$ for some $x, y \in [0, 1]$. Thus, the replicator equation
557 has no interior equilibrium and so neither does (17).

558 Given an interior trajectory of (17), the dominance in matrix B means
559 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 con-
560 verges to the carrying simplex of the competitive system (and so is bounded
561 as well as bounded away from the origin), the method of proof of Theorem 3
562 generalizes to show that $\lim_{t \rightarrow \infty} \rho_1 \rho_2 = 0$. Thus, there can be no limit point
563 in the interior of a three-dimensional face since this face must include the
564 $\mu_1 \mu_2$ plane in which case the only limit point is $(0, 0, \mu_1^*, \mu_2^*)$. That is, if the
565 trajectory does not converge to $(0, 0, \mu_1^*, \mu_2^*)$, then all its limit points must be
566 in the four curves of the carrying simplex contained in the $\rho_1 \mu_1$, $\rho_1 \mu_2$, $\rho_2 \mu_1$,
567 $\rho_2 \mu_2$ planes. The trajectory cannot converge to an equilibrium point on any
568 of these four curves since all such points have an unstable manifold of at
569 least one-dimension. That is, either the trajectory converges to $(0, 0, \mu_1^*, \mu_2^*)$
570 or else to a heteroclinic cycle around these four curves (in analogy to Exam-
571 ple 3). This latter scenario is impossible due to the locally asymptotically
572 stable equilibrium for the curve in the $\rho_1 \mu_2$ plane (or the $\rho_2 \mu_1$ plane). In
573 summary, every interior trajectory converges to $(0, 0, \mu_1^*, \mu_2^*)$, which is then
574 globally asymptotically stable. ■

575 5 Conclusion

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

599 Simultaneous invasion by two species occurs naturally as the following
600 example shows. When an invasive species appears, it is usually introduced
601 at a low density. An important question is whether the invasive species can or
602 cannot substitute for the native species. For instance, Grey squirrels (*Sciurus*
603 *carolinensis*) originated in North America and are a vector for a smallpox
604 virus that evolved there. Grey squirrels (and this virus) have been introduced
605 in many places throughout the world (e.g. England and continental Europe)
606 where they do not need large numbers to start a new population. In Great
607 Britain, grey squirrels have been able to spread 17-25 times faster through
608 competitive exclusion (Bertolino et al. 2008) of the red squirrel (*Sciurus*
609 *vulgaris*) due to increased mortality of reds from the squirrelpox virus which
610 was not resident in Europe (Sandro, 2008; Strauss, 2012). Grey squirrels do
611 not die from this virus but the virus can spread from them and infect red

612 squirrels, causing death. Clearly, in this case, two species (i.e. grey squirrels
613 and its virus) simultaneously invade into the European ecosystems, and the
614 interactions in the whole ecosystem determine the success of grey squirrels.

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

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714 Appendix A1. Remark 1

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

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

715 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)
716 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

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

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

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

717 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

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

718 In other words, condition $|W_1| \neq 0$ implies formula (6) for $i = 1$ and $N = 2$.
 719 If $|W_1| = 0$, there are two cases depending on the (non)singularity of A . If A
 720 is nonsingular, then Cramer's Rule applies to $Ax^* = -r$ and yields $x_1^* = 0$.
 721 By using $|W_1| = |A^1| (r_1 + (Ax^1)_1)$ again, the nonsingularity of A^1 implies
 722 the $x_1^* = 0 = (r_1 + (Ax^1)_1)$ special case of (6). In the second case where A
 723 is singular, then $|A| = 0$ and, as before, $(r_1 + (Ax^1)_1) = 0$ and we are done.
 724 ■

725 Appendix A2. Example 1

726 *Discussion of Example 1 (continued).* To describe the global phase portrait
 727 of the three-dimensional (3D) LV system (7) investigated in Example 1, we
 728 pass to the associated 4D replicator system¹⁵ (Bomze, 1983; Hofbauer and
 729 Sigmund, 1998)

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

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

730 is the payoff matrix, $\mathbf{x} \cdot \mathbf{Ax}$ is the dot product $\sum_i x_i (\mathbf{Ax})_i$ of the column
 731 vectors \mathbf{x} and \mathbf{Ax} , and

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

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

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

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

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

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

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

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

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

732 where \mathbf{a}_j is the j th column of \mathbf{A} . Eigenvectors which are not perpendicular
 733 to the normal vector of the 3D plane of equation $x_1 + x_2 + x_3 + x_4 = 1$ have
 734 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 $R_{\geq 0}^3$, 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,

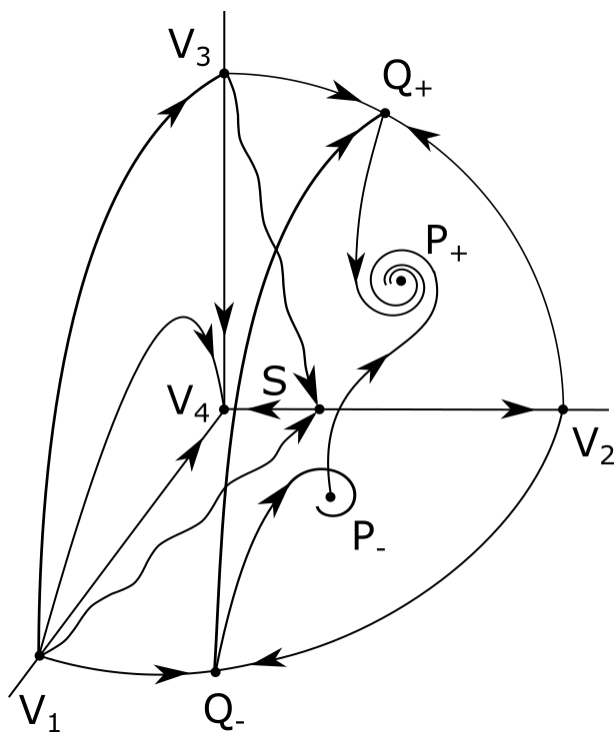


Figure 2: Schematic phase portrait of the replicator system (21).

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

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

735 valid for trajectories of systems (21) and (7) with $x_1, x_3 \in (0, 1)$ and $\rho_1, \mu_1 >$
 736 0 , respectively.¹⁶

¹⁶The local phase portraits in the vicinity of the nine equilibria are clearly visible in Figure 2. Note that V_1 is a repeller, 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

737 **Appendix A3. Theorem 4**

738 *Proof of Theorem 4 (continued).* It is left to point out that a convex combi-
 739 nation of the two mutant strategies dominates a convex combination of the
 740 two resident strategies.

741

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

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

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

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

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

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

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

747 respectively. The line of equation $y = \ell_i(x)$ will be denoted by L_i , $i =$
 748 $1, 2, 3, 4$. Please note that all denominators are positive (for $i = 3$ and $i = 4$,
 749 recall that $b_{23} > \mathbf{b}_{13}$ by (20c0) and $b_{14} > \mathbf{b}_{24}$ by (20e0)). As a by-product,
 750 both L_3 and L_4 have positive slopes.

751

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

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.

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

756

757 Note that L_2 is always strictly above L_1 for $0 \leq x \leq 1$ since $(0, 1 - \frac{b_{41}}{b_{21}})$
 758 and $(1, 1 - \frac{b_{31}}{b_{21}})$ are points on L_1 , $(0, \frac{b_{42}}{b_{12}})$ and $(1, \frac{b_{32}}{b_{12}})$ are points on L_2 and
 759 $1 - \frac{b_{41}}{b_{21}} < \frac{b_{42}}{b_{12}}$ by (20b) and $1 - \frac{b_{31}}{b_{21}} < \frac{b_{32}}{b_{12}}$ by (20a). Similarly, note that L_3
 760 is strictly to the right of L_4 for $0 \leq y \leq 1$ since $(1 - \frac{b_{23}}{b_{43}}, 0)$ and $(1 - \frac{b_{13}}{b_{43}}, 1)$
 761 are points on L_3 , $(\frac{b_{24}}{b_{34}}, 0)$ and $(\frac{b_{14}}{b_{34}}, 1)$ are points on L_4 , and $1 - \frac{b_{23}}{b_{43}} > \frac{b_{24}}{b_{34}}$ by
 762 (20h) and $1 - \frac{b_{13}}{b_{43}} > \frac{b_{14}}{b_{34}}$ by (20g). A major consequence is that geometrically,
 763 our task is to find a point (x^*, y^*) in the unit square $[0, 1]^2$ that is (strictly)
 764 above L_1 , below L_2 , to the left of L_3 , and to the right of L_4 .

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

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

770 Observe that L_2 and L_4 both have positive height at $x = 1$ (i.e. $y_{12} =$
 771 $\frac{b_{32}}{b_{12}} > 0$ and $y_{14} = \frac{b_{23} - b_{24}}{b_{14} - b_{24}} > 0$ by (20h0) and (20e0)) and that the heights
 772 of L_1 and L_3 are both less than 1 at $x = 0$ (i.e. $y_{01} = 1 - \frac{b_{41}}{b_{21}} < 1$ and
 773 $y_{03} = \frac{b_{23} - b_{43}}{b_{23} - b_{13}} < 1$ by (20c0) and (20g0)):

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

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

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

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

$$y_{12} > \max\{y_{11}, y_{13}\} > 0. \quad (28)$$

776 Note that $y_{14} > 0$ is equivalent to $x_{04} < 1$ and $y_{14} \leq 1$ is equivalent to
 777 $x_{14} \geq 1$. There are several equivalencies of the types above, e.g. the equiva-
 778 lence between $x_{13} > 0$ and $y_{03} < 1$ etc.

779

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

782

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

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

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

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

787

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

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

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

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

789 In view of inequality (28) and assumption $0 < y_{14} \leq 1$ (for (i)) or assumptions
 790 $0 < y_{12} \leq 1$ and $y_{14} > 1$ (for (ii)), (x^*, y^*) is above L_1 , below L_2 and to the
 791 right of L_4 . Thus, the mutant strategy of species 1 will dominate a convex
 792 combination of the two resident strategies if (x^*, y^*) is to the left of L_3 . That
 793 is, it remains to check that

$$y_{14} > \max\{y_{11}, y_{13}\}. \quad (29)$$

794 *Case* 1(i). Recall that $y_{14} \leq 1$ is equivalent to $x_{14} \geq 1$. With the help
 795 of a little plane geometry, $y_{14} > y_{13}$ is implied¹⁷ by $x_{04} < x_{03} < 1$ and
 796 $1 \leq x_{14} < x_{13}$. In order to prove inequality $y_{14} > y_{11}$, the cases $\text{Slope}(L_1) > 0$
 797 and $\text{Slope}(L_1) = 0$ will be considered separately. Note that the lines L_2 , L_3 ,
 798 and L_4 are already fixed. If $\text{Slope}(L_1) > 0$, then x_{11} is defined and satisfies
 799 $x_{14} < x_{11}$. In fact, $x_{14} = \frac{b_{14}}{b_{34}} < \frac{b_{41}}{b_{41}-b_{31}} = x_{11}$ follows directly from assump-
 800 tion $b_{41} > b_{31}$ and (20f). Combining $1 \leq x_{14} < x_{11}$ and $y_{01} < y_{04} < 1$ (the
 801 second chain of inequalities in (27)), inequality $y_{14} > y_{11}$ follows by an ele-
 802 mentary geometric argument for two lines in the plane. The degenerate case
 803 $\text{Slope}(L_1) = 0$ is easier. Then x_{11} does not exist but $y_{11} = y_{01} < y_{04} < y_{14}$
 804 and we are done.

805

¹⁷Note that a purely algebraic proof of inequality $y_{14} = \frac{b_{34}-b_{24}}{b_{14}-b_{24}} > \frac{b_{23}}{b_{23}-b_{13}} = y_{13}$ 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).

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

809
810 The proof of inequality $y_{14} > y_{11}$ in *Case 1(i)* above works also in *Case*
811 *3(i)*. For the remaining *Cases 2(i)* and *4(i)*, the slope of L_1 is negative
812 (and the slope of L_4 is positive). Thus $y_{14} > y_{11}$ is a direct consequence of
813 inequality $y_{01} < y_{04}$ in (27). Fortunately, the proofs of inequality $y_{14} > y_{13}$
814 are the same in *Cases 1(i)*, *2(i)*, *3(i)*, and *4(i)*. Moreover, the proof in *Case*
815 *1(ii)* can be repeated in *Cases 2(ii)*, *3(ii)*, and *4(ii)*, too. Absolutely no
816 modifications are needed.

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

822
823 *Case 1(iii)*. If $y_{11} < 1$ and $y_{13} < 1$, then we can take $(x^*, y^*) = (1, 1)$ (i.e.
824 the mutant phenotype of species 1 dominates its resident phenotype).

825 If $y_{11} \geq 1$, both the existence of x_{11} and inequality $0 < x_{11} \leq 1$ are implied
826 by $y_{01} < 1 \leq y_{11}$. As a by-product, we obtain that $\text{Slope}(L_1) > 0$. Recall
827 that $0 < x_{14} < x_{13}$. The argument we used in *Case 1(i)* leads to $x_{14} < x_{11}$
828 again. In what follows we distinguish two cases according as $\text{Slope}(L_2) > 0$
829 or $\text{Slope}(L_2) = 0$. Suppose that $\text{Slope}(L_2) > 0$. Then $y_{01} < y_{02} < y_{12}$
830 and $y_{11} < y_{12}$ give rise both to the existence of x_{12} and to inequality $x_{12} <$
831 x_{11} . Since $0 < \max\{1, y_{13}\} < y_{12}$ and $x_{02} < x_{03}$ (i.e. $\frac{-b_{42}}{b_{32}-b_{42}} < 1 - \frac{b_{23}}{b_{43}}$
832 by (20d) when $b_{32} - b_{42} > 0$ which is equivalent to $\text{Slope}(L_2) > 0$) with
833 $x_{03} < 1$, also inequality $x_{12} < x_{13}$ holds true. All in all, we arrived at
834 the chain of inequalities $1 \geq \min\{x_{11}, x_{13}\} > \max\{0, x_{12}, x_{14}\}$ and can take
835 $(x^*, y^*) = (\min\{x_{11}, x_{13}\} - \varepsilon, 1)$. In the degenerate case $\text{Slope}(L_2) = 0$, we
836 have $0 < x_{11} \leq 1$, $x_{14} < x_{11}$ and $0 < x_{14} < x_{13}$. In particular, $0 < x_{14} <$
837 $\min\{x_{11}, x_{13}\} \leq 1$. Given $x \in [0, x_{11})$ arbitrarily, $(x, 1)$ is (strictly) below L_2
838 and above L_1 . For $x \in (x_{14}, x_{13})$, $(x, 1)$ is to the left of L_3 and to the right
839 of L_4 . Thus the choice $(x^*, y^*) = (\min\{x_{11}, x_{13}\} - \varepsilon, 1)$ is still possible.

840 If $y_{11} < 1$ and $y_{13} \geq 1$, consider first the special case $\text{Slope}(L_1) \geq 0$ and
841 $\text{Slope}(L_2) = 0$. Since $y_{11} < 1 < y_{12}$, all points on the top edge of the unit
842 square (i.e. for $0 \leq x \leq 1$ and $y = 1$) are (strictly) below L_2 and above

843 L_1 . Combining inequalities $0 < x_{14} < x_{13}$ and $y_{03} < 1 \leq y_{13}$, we arrive at
844 $0 < x_{14} < x_{13} \leq 1$. In particular, we can take $(x^*, y^*) = (x_{13} - \varepsilon, 1)$. Now
845 we turn our attention to the special case $\text{Slope}(L_1) > 0$ and $\text{Slope}(L_2) > 0$.
846 Thus $\ell_1, \ell_2, \ell_3, \ell_4$ are strictly increasing functions. This implies the existence
847 of the intersection points $x_{11}, x_{12}, x_{13}, x_{14}$. Clearly $0 < x_{14} < x_{13} \leq 1$. The
848 derivation of inequalities $x_{14} < x_{11}$ and $x_{12} < x_{13}$ is exactly the same as in
849 the case $y_{11} \geq 1$ above. The remaining inequality $x_{12} < x_{11}$ follows from the
850 chains of inequalities $y_{01} < y_{02} < y_{12}$, $y_{01} < y_{11} < 1 < y_{12}$ via an easy geo-
851 metric argument. Depending on the relative position of y_{02} , y_{11} and 1 in the
852 open interval (y_{01}, y_{12}) , we have to consider three separate subcases, namely
853 $y_{11} < 1 \leq y_{02}$, $y_{02} \leq y_{11} < 1$ or $y_{11} \leq y_{02} \leq 1$. (If $y_{11} \leq y_{02} \leq 1$, then one of
854 the inequalities should be strict.) In each of the three subcases, we arrive at
855 inequality $x_{12} < 1 < x_{11}$. Again, an appropriate choice in the unit square is
856 $(x^*, y^*) = (\min\{x_{11}, x_{13}\} - \varepsilon, 1)$. Finally, consider now the remaining special
857 case $\text{Slope}(L_1) = 0$ and $\text{Slope}(L_2) > 0$. As before, $0 < x_{14} < x_{13} \leq 1$ and
858 $x_{12} < x_{13}$ (and $y_{11} < 1$, $y_{12} > 1$). For $x \in (x_{14}, x_{13})$, $(x, 1)$ is to the left of
859 L_3 and to the right of L_4 . Given $x \in (x_{12}, 1]$ arbitrarily, $(x, 1)$ is (strictly)
860 below L_2 and above L_1 . Thus the choice $(x^*, y^*) = (x_{13} - \varepsilon, 1)$ is appropriate.

861
862 *Case 2(iii)*. If $\text{Slope}(L_1) < 0$ and $\text{Slope}(L_2) = 0$, then $1 > y_{01} > y_{11}$ and
863 $y_{02} > y_{12} > 1$. Thus all points on the top edge of the unit square are (strictly)
864 above L_1 and below L_2 . Since $0 < x_{14} < x_{13}$ and $x_{14} < 1$ (by using $y_{14} > 1$
865 and $\text{Slope}(L_4) > 0$), we can take $(x^*, y^*) = (x_{14} + \varepsilon, 1)$. If $\text{Slope}(L_1) < 0$
866 and $\text{Slope}(L_2) > 0$, then x_{12} exists and (by using $y_{12} > 1$) satisfies $x_{12} < 1$.
867 Similarly, $x_{14} < 1$ and $x_{11} < 0$. As in the proof of *Case 1(iii)*, inequalities
868 $x_{02} < x_{03} < 1$ and $\max\{1, y_{13}\} < y_{12}$ imply via some geometry that $x_{12} < x_{13}$.
869 In view of $0 < x_{14} < x_{13}$, we can take $(x^*, y^*) = (\max\{x_{12}, x_{14}\} + \varepsilon, 1)$. Note
870 that the choice $(x^*, y^*) = (\min\{1, x_{13}\} - \varepsilon, 1)$ is also possible.

871
872 *Case 3(iii)*. Since $\text{Slope}(L_2) < 0$, we have $y_{02} > y_{12}$. As a trivial conse-
873 quence of assumption $y_{12} > 1$, all points on the top edge of the unit square
874 are (strictly) below L_2 . In addition, $x_{12} > 1$. Similarly, assumption $y_{14} > 1$
875 implies that $x_{14} < 1$. Recall that, from (27), $0 < x_{14} < x_{13}$. Last but not
876 least, the proof of inequality $x_{14} < x_{11}$ in *Case 1(i)* with $\text{Slope}(L_1) > 0$ can
877 be repeated and leads to $(x^*, y^*) = (x_{14} + \varepsilon, 1)$. If $\text{Slope}(L_1) = 0$, then $y_{01} < 1$
878 implies that the choice $(x^*, y^*) = (x_{14} + \varepsilon, 1)$ is still possible.

879
880 *Case 4(iii)*. Every point on the top edge of the unit square is (strictly)

881 above L_1 and below L_2 . Recall that $0 < x_{14} < x_{13}$ and note that $x_{14} < 1$ by
882 assumption $y_{14} > 1$. As above, we can take $(x^*, y^*) = (x_{14} + \varepsilon, 1)$. ■