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Resident-invader dynamics and the coexistence of similar strategies

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Abstract. We study the resident-invader dynamics for a given class of models of unstructured populations of finite-dimensional strategies. We prove various results on the existence and uniqueness of ω -limit sets in the interior of the resident-invader population state space, and we classify the generically possible types of dynamics in terms of the invasion conditions when the resident and invader strategies are similar to one another.

1. Introduction

If an initially rare strategy y can invade a resident population of strategy x , but not *vice versa*, does this mean that y will actually take over the population and become the new resident itself? It is known that in general this need not happen, as illustrated by examples of unprotected coexistence and the “resident strikes back” phenomenon (Figure 1; also see [4, 16]). Is it possible, then, to say anything at all about the outcome of an invasion event on the basis of invasion considerations alone, i.e., without looking into the interior of the resident-invader population state space?

Previously [5], we have proven the *Tube Theorem*, which, for a large class of ecological models, gives conditions such that the resident-invader dynamics develops inside a “tube” in which the sum of the invader and resident population sizes stays close to the former resident attractor (i.e., before the invader came along) whenever the invader and resident strategies are sufficiently similar. The *Tube Theorem* rules out various types of resident-invader dynamics, including most cases of the “resident strikes back”, but the possibility of unprotected coexistence inside the tube remains (Figure 1). Neither does the *Tube Theorem* say anything about the number or type of ω -limit sets inside the tube.

In this paper we prove various results on the existence and uniqueness of ω -limit sets in the interior of the resident-invader population state space, and we classify the generically possible types of dynamics in terms of the invasion conditions when the resident and invader strategies are similar to one another. To this end we first define the context to which these results apply. The initial setup is somewhat more

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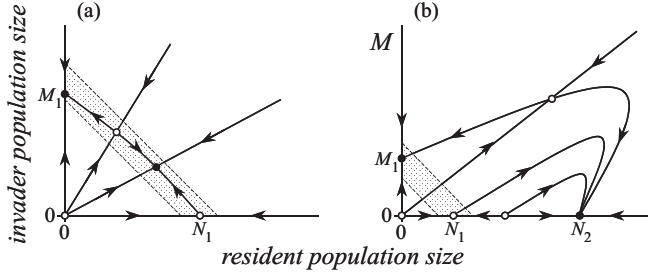


Fig. 1. Examples of resident-invader dynamics. (a) Unprotected coexistence: invasion of the resident at the steady state N_1 leads to coexistence even though invasion at M_1 under reversal of roles (i.e., with the resident as invader) is not possible. (b) The resident strikes back: invasion of the resident at the steady state N_1 causes the resident to switch to N_2 that cannot be invaded. Under the *Tube Theorem* orbits starting close to N_1 stay inside the shaded strip or “tube”, so that the “resident strikes back” scenario in (b) is not possible, but unprotected coexistence inside the tube (a) cannot *a priori* be excluded.

general than is strictly necessary, but this is done in order to show how the present work fits within the more general adaptive dynamics framework [3, 6, 7, 13, 14].

2. Preliminaries

Let \mathcal{X} denote the strategy space, \mathcal{N} the space of non-negative population sizes and \mathcal{I} the space of environmental conditions. Each of these spaces is assumed to be a subset of a normed vector space. Let further $\mathcal{T} = \mathbb{Z}^+$ or \mathbb{R}^+ , depending on whether time is discrete or continuous. An environment is a map $I : \mathcal{T} \rightarrow \mathcal{I}$ describing how the environmental condition varies over time. We take time to be continuous.

Consider a population of strategy x in environment I , and suppose the population dynamics is given by

$$\dot{N}(t) = L(x, I(t))N(t), \quad (1)$$

where $L(x, I(t))$ is a linear operator, which itself is a function of x and $I(t)$, and which acts on the population vector $N(t)$. The invasion fitness of x in I is defined as

$$\rho(x, I) = \lim_{t \rightarrow \infty} \frac{1}{t} \log \|N(t)\|, \quad (2)$$

provided the limit exists and is the same for every positive initial population vector $N(0)$ [14]. Strategy x can invade environment I if, and only if, $\rho(x, I) > 0$. We say that x is singular with respect to I if $D_1 \rho(x, I)$ exists and is equal to zero.

A population may affect the very environment in which it is growing. How this happens is described by the so-called environmental feedback loop [8, 12, 15]. Consider a population of strategies x_1, \dots, x_k and corresponding population vectors N_1, \dots, N_k . As environmental feedback loop we take

$$I(t) = \sum_{i=1}^k G(x_i)N_i(t), \quad (3)$$

where $G(x_i)$ is a bounded linear operator, which itself is a function of x_i , and which acts on $N_i(t)$. One possible interpretation is that $G(x_i)$ describes by how much different types of resources are reduced due to the presence of a single individual with strategy x_i . Consequently, $I(t)$ gives the total impact of the entire population on the abundance of the various resources. Alternatively, by allowing the environmental condition to be infinite-dimensional, we can also incorporate into the formalism terms that are traditionally interpreted as describing direct interactions between individuals. Two concrete examples of this are given in Section 4 where the environmental condition at any given point in time is a function of strategy and where $L(x, I(t))$ involves the evaluation of $I(t)$ in x .

From (1) and (3) it follows that the dynamics of a population of a single strategy x is given by

$$\begin{aligned}\dot{N}(t) &= L(x, I(t))N(t) \\ I(t) &= G(x)N(t).\end{aligned}\tag{4}$$

Suppose that $\widehat{N}(x)$ is a steady state of (4) with corresponding environmental condition $\widehat{I}(x) = G(x)\widehat{N}(x)$, and define

$$s(y, x) = \rho(y, \widehat{I}(x))\tag{5}$$

as the invasion fitness of y in a resident population of x at the steady state. Notice that in (5) we use $\widehat{I}(x)$ to indicate the constant environment (i.e., the environment $I(t) = \widehat{I}(x)$ for all t) rather than the environmental condition at a particular point in time.

The dynamics of a population of two strategies x and y and corresponding population vectors N and M is given by

$$\begin{aligned}\dot{N}(t) &= L(x, I(t))N(t) \\ \dot{M}(t) &= L(y, I(t))M(t) \\ I(t) &= G(x)N(t) + G(y)M(t).\end{aligned}\tag{6}$$

We are interested in the dynamics of (6) when y is close to x and with initial conditions close to $(\widehat{N}(x), 0)$, where $\widehat{N}(x)$ is a strictly positive hyperbolic attracting steady state of (4). Such conditions are representative for an initially rare mutant strategy y attempting to invade a resident population with strategy x near its steady state.

Throughout this paper we adhere to the notation and definitions given in this section. In addition, we also assume the following.

H 1 $\mathcal{N} = \mathbb{R}^+$.

H 2 $D_1L(x, I)$, $D_2L(x, I)$ and $DG(x)$ exist for all $x \in \mathcal{X}$ and $I \in \mathcal{I}$, and $D_2L(x, I)$ is a continuous function of I .

H 3 $\mathcal{X} \subset \mathbb{R}^n$ ($n \geq 1$) is open and such that for every $x \in \mathcal{X}$ there exists a strictly positive hyperbolic attracting steady state $\widehat{N}(x)$ of (4), i.e., $D_2L(x, G(x)\widehat{N}(x))G(x) \neq 0$, and $\widehat{N}(x)$ is a differentiable function of x .

H4 $D_{112}L(x, I)$ and $D^2G(x)$ exist for all $x \in \mathcal{X}$ and $I \in \mathcal{I}$, and $D_2L(x, I)$ is a continuous function of I .

Notice that under H1, $L(x, I)$ is just a number so that by (1), (2) and (5)

$$s(y, x) = L(y, G(x)\widehat{N}(x)). \quad (7)$$

Continuity of $D_2L(x, I)$ in H2 ensures existence and uniqueness of solutions to (6). Although H2 is implied by H4, for our first result we only need the weaker assumptions of H2. Finally, for arbitrary $\varepsilon > 0$ and $\mathcal{A} \subset \mathcal{N}$ define the ε -tube of \mathcal{A} as the set

$$T_\varepsilon(\mathcal{A}) = \{(N, M) \in \mathcal{N}^2 : d(N + M, \mathcal{A}) \leq \varepsilon\}, \quad (8)$$

where $d(N + M, \mathcal{A})$ is the point-to-set distance between $N + M$ and \mathcal{A} .

3. Results

Our first result gives conditions under which a successfully invading mutant will actually oust the former resident and become the new resident itself. In the population genetics literature the invader is then said to “go to fixation”. The proof of the proposition is given in the Appendix.

Proposition 1. (“Invasion implies fixation theorem”) *Suppose that H1, H2 and H3 are satisfied. Then for every $x \in \mathcal{X}$ and every $\gamma > 0$ there exists an $\varepsilon > 0$ and a $\delta > 0$ such that every orbit of (6) starting in the interior of $T_\varepsilon(\widehat{N}(x))$ converges to $(0, \widehat{N}(y))$ as $t \rightarrow \infty$ whenever $s(y, x) > 0$, $\|y - x\| < \delta$ and $|D_1s(x, x)(y - x)| > \gamma\|y - x\|$. \square*

If $\mathcal{X} \subset \mathbb{R}^1$, then there exists a $\gamma > 0$ such that $|D_1s(x, x)(y - x)| > \gamma\|y - x\|$ is true for every non-singular x and every $y \neq x$. For one-dimensional strategies we thus recover the *Invasion Implies Substitution Theorem* of Dercole [1] (pp. 46–47). If x is singular, then $|D_1s(x, x)(y - x)| > \gamma\|y - x\|$ cannot be satisfied for any y . Indeed, examples abound in the adaptive dynamics literature where invasion of a singular strategy by an arbitrarily similar mutant strategy leads to coexistence rather than to fixation. In particular, this happens if x is a so-called branching point [6, 7, 13].

If $\mathcal{X} \subset \mathbb{R}^n$ with $n \geq 2$ and x is not singular, then the condition $|D_1s(x, x)(y - x)| > \gamma\|y - x\|$ for given $\gamma > 0$ means that $(y - x)/\|y - x\|$ has to stay bounded away from the null-set of the linear form $\xi \mapsto D_1s(x, x)\xi$. Geometrically, y has to be inside a cone whose apex is located at x and whose axis is parallel to the vector $D_1s(x, x)$ (Figure 2a). As γ decreases, the cone becomes wider and at the same time δ may have to be taken smaller. The set of invader strategies y to which the conclusion of the proposition applies, therefore, locally looks like two paraboloid-shaped bodies touching one another at x and tangent to the orthogonal complement of $D_1s(x, x)$ at their point of contact (Figure 2b). If we confine y to a smooth one-dimensional manifold through x and orthogonal to $D_1s(x, x)$, then x is singular in this one-dimensional restriction of the strategy space, and hence (see previous paragraph) invasion may lead to coexistence rather than to fixation.

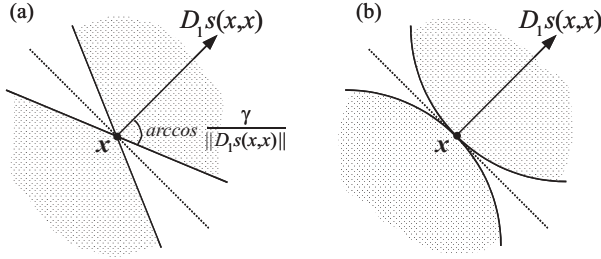


Fig. 2. (a) The set of strategies y (shaded) such that $(y - x)/\|y - x\|$ stays bounded away from the null-set (dotted lines) of the linear form $\xi \mapsto D_1s(x, x)\xi$. (b) The local geometry of the set of strategies y (shaded) to which the conclusion of Proposition 1 applies.

Proposition 1 does not apply if x is singular, but also in a neighborhood of a singular strategy it loses its usefulness, because there is no lower bound on the maximal distance between x and y as x approaches the singular strategy. The following proposition does not have this limitation. It gives a classification of the generically possible types of dynamical behavior in terms of invasion criteria when the invader strategy is close to that of the resident. The proof is given in the Appendix.

Proposition 2. (“Classification theorem”) *Suppose that H1, H2 and H4 are satisfied. Then, concerning the dynamics of (6), for every $x \in \mathcal{X}$ and every $\gamma > 0$ there exists an $\varepsilon > 0$ and a $\delta > 0$ such that the following holds whenever $\|y - x\| < \delta$ and $|(y - x)^\top D_{12}s(x, x)(y - x)| > \gamma\|y - x\|^2$.*

1. If $s(y, x) > 0$ and $s(x, y) < 0$, then the interior of $T_\varepsilon(\widehat{N}(x))$ contains no ω -limits, and every orbit starting in the interior of $T_\varepsilon(\widehat{N}(x))$ converges to $(0, \widehat{N}(y))$;
2. If $s(y, x) < 0$ and $s(x, y) > 0$, then the interior of $T_\varepsilon(\widehat{N}(x))$ contains no ω -limits, and every orbit starting in the interior of $T_\varepsilon(\widehat{N}(x))$ converges to $(\widehat{N}(x), 0)$;
3. If $s(y, x) > 0$ and $s(x, y) > 0$, then the interior of $T_\varepsilon(\widehat{N}(x))$ contains one and only one ω -limit, which is a stable node, and every orbit starting in the interior of $T_\varepsilon(\widehat{N}(x))$ converges to this node;
4. If $s(y, x) < 0$ and $s(x, y) < 0$, then the interior of $T_\varepsilon(\widehat{N}(x))$ contains one and only one ω -limit, which is a saddle, and every orbit starting in the interior of $T_\varepsilon(\widehat{N}(x))$ but not on the saddle itself or on its stable manifolds converges either to $(0, \widehat{N}(y))$ or to $(\widehat{N}(x), 0)$. \square

If $\mathcal{X} \subset \mathbb{R}^1$, then there exists a $\gamma > 0$ such that $|(y - x)^\top D_{12}s(x, x)(y - x)| > \gamma\|y - x\|^2$ is satisfied for every x with $D_{12}s(x, x) \neq 0$ and every $y \neq x$, and therefore the condition is not restrictive whatsoever. In the general classification of singular strategies [6, 7, 13], the case $D_{12}s(x, x) = 0$ is non-generic, and may hint at the existence of a maximization principle underlying the evolutionary model [6, 11].

If $\mathcal{X} \subset \mathbb{R}^n$ with $n \geq 2$, then the condition $|(y - x)^\top D_{12}s(x, x)(y - x)| > \gamma\|y - x\|^2$ for given $\gamma > 0$ means that $(y - x)/\|y - x\|$ has to stay bounded away from the null-set of the quadratic form $\xi \mapsto \xi^\top D_{12}s(x, x)\xi$ (Figure 3a). If

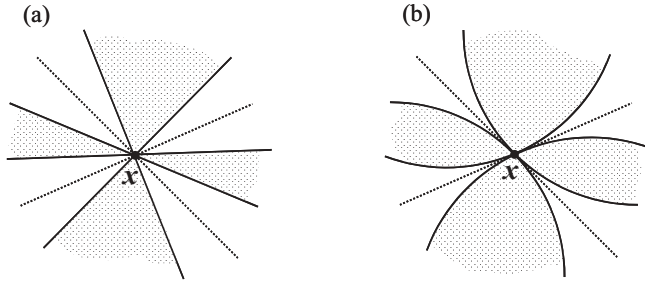


Fig. 3. (a) The set of strategies y (shaded) such that $(y - x)/\|y - x\|$ stays bounded away from the null-set (dotted lines) of the quadratic form $\xi \mapsto \xi^\top D_{12}s(x, x)\xi$. (b) The local geometry of the set of strategies y (shaded) to which the conclusions of Proposition 2 apply.

the (symmetric part of the) matrix $D_{12}s(x, x)$ is definite, then there exists a $\gamma > 0$ for which this is true for all $y \neq x$. As γ approaches zero, δ has to be taken smaller as well, so that the set of invader strategies y to which the conclusions of the proposition apply is like in Figure 3b.

The combination of Propositions 1 and 2 gives the following result.

Proposition 3. (“Strong invasion-fixation theorem”) *Suppose that H1, H2 and H4 are satisfied, and let $x \in \mathcal{X}$ be such that there does not exist a $\xi \in \mathbb{R}^n \setminus \{0\}$ that satisfies both $D_1s(x, x)\xi = 0$ and $\xi^\top D_{12}s(x, x)\xi = 0$. Then there exists an $\varepsilon > 0$ and a $\delta > 0$ such that every orbit of (6) starting in the interior of $T_\varepsilon(\widehat{N}(x))$ converges to $(0, \widehat{N}(y))$ as $t \rightarrow \infty$ whenever $s(y, x) > 0$, $s(x, y) < 0$ and $\|y - x\| < \delta$. \square*

Indeed, if $D_1s(x, x)\xi \neq 0$ or $\xi^\top D_{12}s(x, x)\xi \neq 0$ for every $\xi \neq 0$, then there exists a $\gamma > 0$ such that $|D_1s(x, x)(y - x)| > \gamma\|y - x\|$ or $|(y - x)^\top D_{12}s(x, x)(y - x)| > \gamma\|y - x\|^2$ for every $y \neq x$, and hence Proposition 1 or Proposition 2 (case 1) applies.

Notice that if x is not singular and $D_{12}s(x, x)$ is not zero, then the condition that $D_1s(x, x)\xi \neq 0$ or $\xi^\top D_{12}s(x, x)\xi \neq 0$ for every $\xi \neq 0$ is readily satisfied, because the null-space of the linear form $\xi \mapsto D_1s(x, x)\xi$ and the null-space of the quadratic form $\xi \mapsto \xi^\top D_{12}s(x, x)\xi$ generically have only the origin in common. If (the symmetric part of) $D_{12}s(x, x)$ is definite, then $\xi^\top D_{12}s(x, x)\xi \neq 0$ for every $\xi \neq 0$, and consequently the conclusion of Proposition 3 applies to every x .

4. Examples

4.1. Example 1

Gyllenberg & Parvinen [9] studied the phenomenon of evolutionary suicide (i.e., the evolution towards self-extinction) in a model in which the dynamics of a population of strategies x_1, \dots, x_k and corresponding population sizes N_1, \dots, N_k is given by

$$\dot{N}_i(t) = N_i(t) \left(a\rho(x_i) \frac{\bar{N}(t)}{1 + \bar{N}(t)} - b - c \sum_{j=1}^k \alpha(x_i, x_j) N_j(t) \right) \quad (9)$$

with $\bar{N}(t) = \sum_{j=1}^k N_j(t)$ and $a, b, c > 0$ and given positive functions ρ and α .

We first show that (9) belongs to the class of models considered in this paper, i.e., models of the form specified in (1) and (3). To this end, let \mathcal{I} be the set of all functions $v : \mathcal{X} \rightarrow \mathbb{R}^2$ of the form

$$v(y) = \sum_{j=1}^k n_j \begin{pmatrix} 1 \\ \alpha(y, x_j) \end{pmatrix} \quad (10)$$

for $n_j \geq 0$, $x_j \in \mathcal{X}$ and $k \in \mathbb{N}$. Then \mathcal{I} is a subset of the linear vector space \mathcal{V} consisting of functions of the same form but where the n_j also take negative values. Clearly, \mathcal{V} can be normalized if the functions $y \mapsto \alpha(y, x)$ belong to a given normed function space. For every $x \in \mathcal{X}$, define the linear operator $G(x) : \mathcal{N} \rightarrow \mathcal{I}$ by

$$\left(G(x)N \right)(y) = \begin{pmatrix} N \\ \alpha(y, x)N \end{pmatrix}. \quad (11)$$

Writing $v = (v_1, v_2)$ for every $v \in \mathcal{I}$, define the map $L : \mathcal{X} \times \mathcal{I} \rightarrow \mathbb{R}$ by

$$L(y, v) = a\rho(y) \frac{v_1(y)}{1 + v_1(y)} - b - cv_2(y). \quad (12)$$

Then (9) can be written as

$$\begin{aligned} \dot{N}_i(t) &= L(x_i, I(t))N_i(t) \\ I(t) &= \sum_{j=1}^k G(x_j)N_j(t), \end{aligned} \quad (13)$$

which is of the form specified in (1) and (3). The derivatives $D_1L(x, I)$, $D_2L(x, I)$ and $DG(x)$ exist whenever ρ and α are differentiable, and $D_{112}L$ and D^2G exist whenever ρ and α are at least twice differentiable.

Gyllenberg & Parvinen [9] showed that for one-dimensional strategies and their specific choice of the parameters a , b and c and differentiable functions ρ and α , there exists a finite interval (x_{low}, x_{high}) such that a population of a single strategy x in this interval has a hyperbolic attracting steady state $\hat{N}(x) > 0$, which vanishes at the endpoints of the interval through a saddle-node bifurcation. The interval was shown to be free of singular strategies, so that from Proposition 1 with $\mathcal{X} = (x_{low}, x_{high})$ we conclude that every successfully invading y in a sufficiently small neighborhood of x will also takeover the population. A sequence of such invasion events causes the population to evolve to one of the endpoints of the interval. Since $\hat{N}(x)$ at the endpoint is non-hyperbolic, we cannot use any of our results there. What happens is that close to x_{low} or x_{high} an invader may come along that triggers a switch in the resident attractor from $\hat{N}(x)$ to the extinct population state $N = 0$, which is readily shown to be stable for all x . In other words, the population evolves towards self extinction, also called evolutionary suicide (for details, see [9]).

Here we consider a different case of (9) with $\mathcal{X} \subset \mathbb{R}^n$ for $n \geq 1$. Assume that ρ and α are twice differentiable and that $\alpha(x, x) = 1$ for all x and $\alpha(y, x) < 1$ for all $y \neq x$. This may be interpreted as a case of symmetric competition. Then $D_1\alpha(x, x) = D_2\alpha(x, x) = 0$ and $D_{12}\alpha(x, x)$ is positive-definite for every x . Assume further that ρ has a local maximum at $x = x^*$ with $\rho(x^*) > (b + c + 2\sqrt{bc})/a$. Then for every population with a single strategy x in a neighborhood of x^* there exists a hyperbolic attracting steady state $\widehat{N}(x) > 0$ that moreover is a differentiable function of x . One readily shows that x^* is singular so that we cannot usefully apply Proposition 1. Instead we apply Proposition 2. A straightforward calculation then shows that $D_{12}s(x^*, x^*)$ is negative-definite, and hence, by continuity, $D_{12}s(x, x)$ is negative-definite for all x sufficiently close to x^* . Thus, there exists a $\gamma > 0$ such that the condition $|(y - x)^\top D_{12}s(x, x)(y - x)| > \gamma \|y - x\|^2$ is satisfied for every x and y sufficiently close to x^* . The classification of possible types of dynamical behavior listed in Proposition 2 therefore applies to all x and y in a neighborhood of x^* .

4.2. Example 2

Dercole *et al.* [2] studied evolutionary cycles in a model in which the dynamics of strategies x_1, \dots, x_k and corresponding population sizes N_1, \dots, N_k is given by

$$\dot{N}_i(t) = N_i(t) \left(a\rho(x_i) - \frac{b\bar{N}(t)}{1 + \bar{N}(t)^2} - c \sum_{j=1}^k \alpha(x_i, x_j) N_j(t) \right) \quad (14)$$

with $\bar{N}(t) = \sum_{j=1}^k N_j(t)$ and $a, b, c > 0$ and given positive functions ρ and α . To show that (14) belongs to the class of models considered in this paper, let \mathcal{I} be defined as in Example 1, $G(x)$ as in (11), and let $L(x, v)$ be given by

$$L(y, v) = a\rho(y) - \frac{bv_1(y)}{1 + v_1(y)^2} - cv_2(y) \quad (15)$$

instead of (12). Then (14) can be written as (13), which is of the form specified in (1) and (3). Like previously, $D_1L(x, I)$, $D_2L(x, I)$ and $DG(x)$ exist whenever ρ and α are differentiable, and $D_{12}L$ and D^2G exist whenever ρ and α are at least twice differentiable.

Dercole *et al.* [2] showed that for one-dimensional strategies and their specific choice of the parameters a, b and c and differentiable functions ρ and α , there exists an interval (x_{low}, x_{high}) such that for a population of a single strategy x in this interval there exist two strictly positive hyperbolic attracting steady states, $\widehat{N}_1(x)$ and $\widehat{N}_2(x)$, where $\widehat{N}_1(x)$ vanishes at x_{low} and $\widehat{N}_2(x)$ at x_{high} through a saddle-node bifurcation. The interval (x_{low}, x_{high}) was moreover shown to be free of singular strategies, so that from Proposition 1 it follows that every successfully invading y in a sufficiently small neighborhood of x will also takeover the population. The proposition moreover guarantees that there will be no switch from one attracting steady state to the other as long as the population stays away from the endpoints of the interval. Evolution is directed to the endpoint where the current resident attractor undergoes a saddle-node bifurcation. Near the bifurcation point an invader will

come along that triggers a switch in the resident population from one attractor to the other, while the invader itself goes extinct. This is an example of the “resident strikes back” phenomenon referred to in the Introduction. After the attractor switch, the direction of evolution reverses, giving rise to long term evolutionary cycles (for details, see [2]).

Here we consider a different case of (14) with $\mathcal{X} \subset \mathbb{R}^n$ for $n \geq 1$. Assume that ρ and α are twice differentiable and that $\alpha(x, x) = 1$ for all x and $\alpha(y, x) < 1$ for all $y \neq x$. Then $D_1\alpha(x, x) = D_2\alpha(x, x) = 0$ and $D_{12}\alpha(x, x)$ is positive-definite for every x . Suppose further that that ρ has a local maximum at $x = x^*$ and that there exist a hyperbolic attracting steady state $\widehat{N}(x)$ for all x in a neighborhood of x^* . Then x^* is singular strategy and $D_{12}s(x, x)$ is negative-definite for all x in a neighborhood of x^* . Like in Example 1, the classification of possible types of dynamical behavior listed in Proposition 2 therefore applies to all x and y in a neighborhood of x^* .

5. Discussion

Proposition 1 implies that an arbitrarily large fraction of all strategies y in a sufficiently small neighborhood of a non-singular resident strategy x at a hyperbolic attracting steady state $\widehat{N}(x)$ will actually replace the resident and become the new resident itself whenever it can invade. For one-dimensional strategies this result reduces to the *Invasion Implies Substitution Theorem* of Dercole [1] (pp. 46–47). It should be pointed out, however, that while our results have been proven for resident populations consisting of only a single (multi-dimensional) strategy, Dercole’s theorem also applies to populations consisting of an arbitrary number of (one-dimensional) resident strategies.

Concerning the biological significance of multi-dimensional strategies, we note that individuals are typically characterized by many traits. If two traits mutate independently of one another, mutants with variations in both traits are very unlikely to appear. If the two traits are strongly correlated, they always mutate according to some strict relationship, so that one can define a one-dimensional equivalent trait. One might expect, however, that most cases are intermediate such that a single mutation affects several traits simultaneously according to some multi-variate probability distribution. In such situations strategies are in an essential way multi-dimensional.

Proposition 2 gives a classification of the generically possible types of dynamics of the resident-invader population in terms of the invasion conditions when the resident and invader strategies are very similar to one another. In particular, the proposition states that in the interior of the tube $T_\varepsilon(\widehat{N}(x))$, there can be at most one ω -limit, which is either a saddle or a stable node. To appreciate this result, notice that if $y = x$, then every point (N, M) with $N + M = \widehat{N}(x)$ is a steady state of the resident-invader dynamics. It is not *a-priori* obvious why, as y becomes different from x , the continuum of neutrally stable steady states does not break up into two or more isolated steady states. In contrast to the first proposition, Proposition 2 also applies if x is singular.

Proposition 3 is a strong version of Proposition 1. It implies that generically every y (as opposed to an arbitrarily large fraction of all y as in the case of Proposition 1) in a sufficiently small neighborhood of a non-singular x at a hyperbolic attracting steady state will takeover the population and will become the new resident, whenever it can invade and invasion under reversal of roles (i.e., with x as the invader) is not possible.

Our results apply to the resident-invader dynamics given by (6). The form of the environmental feedback seems appropriate whenever there is competition for a finite, countable or even uncountable number of different resources. By allowing the environmental condition to be infinite-dimensional, we can also incorporate into the formalism terms that are traditionally interpreted as describing direct interactions between individuals. Two concrete examples of this are given in Section 4. Using different techniques, Proposition 1 is readily generalized to include structured populations as well as more complicated resident attractors (Geritz *in prep.*). Propositions 2 and 3, however, we are unable to generalize beyond the confines of (6).

Referring back to an issue raised in the Introduction, the present results show that if the resident and invader strategies are sufficiently similar to one another, then unprotected coexistence (Figure 1a) can readily be excluded. This result, also in combination with the *Tube Theorem*, shows how the outcome of an invasion event can generically be predicted on the basis of invasion considerations alone, i.e., without looking into the interior of the resident-invader population state space.

6. Appendix

6.1. Proof of Proposition 1

Lemma 1. *Suppose that H1, H2 and H3 are satisfied. Then for every $x \in \mathcal{X}$ there exist $\varepsilon > 0$ and $\delta > 0$ such that if $\|y - x\| < \delta$, then $T_\varepsilon(\widehat{N}(x))$ is forward invariant. Moreover, orbits cross the boundary of $T_\varepsilon(\widehat{N}(x))$ at $N + M = \widehat{N}(x) \pm \varepsilon$ at a non-vanishing speed from the outside to the interior as shown in Figure 4.*

Proof. For $\|x - y\| < |N + M - \widehat{N}(x)|^2$ we have from (6)

$$\begin{aligned} (\dot{N} + \dot{M})/(N + M) &= D_2L(x, G(x)\widehat{N}(x))G(x)(N + M - \widehat{N}(x)) \\ &\quad + o(1)|N + M - \widehat{N}(x)|. \end{aligned} \quad (16)$$

Let $\varepsilon > 0$ and $\delta = \varepsilon^2$ be so small that if $|N + M - \widehat{N}(x)| = \varepsilon$ and $\|x - y\| < \delta$, then $\dot{N} + \dot{M}$ and $D_2L(x, G(x)\widehat{N}(x))G(x)(N + M - \widehat{N}(x))$ have the same sign. Since $\widehat{N}(x)$ is a hyperbolic attracting steady state of (4), we have

$$D_2L(x, G(x)\widehat{N}(x))G(x)\widehat{N}(x) < 0. \quad (17)$$

Hence, if $N + M - \widehat{N}(x) = \varepsilon$, then $\dot{N} + \dot{M} < 0$, and if $N + M - \widehat{N}(x) = -\varepsilon$, then $\dot{N} + \dot{M} > 0$. The flow across the boundary of $T_\varepsilon(\widehat{N}(x))$ at $N + M = \widehat{N}(x) \pm \varepsilon$ is thus as claimed, and by implication $T_\varepsilon(\widehat{N}(x))$ is forward invariant. \square

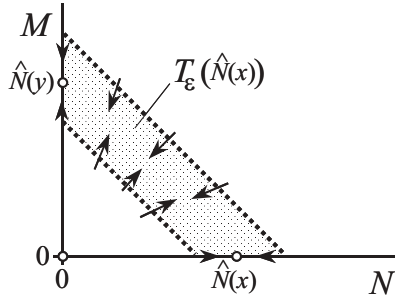


Fig. 4. The flow of (6) in relation to the forward invariant tube $T_\varepsilon(\widehat{N}(x))$.

Lemma 2. *Suppose that H1, H2 and H3 are satisfied. Then for every $x \in \mathcal{X}$ there exist $\varepsilon > 0$ and $\delta > 0$ such that if $\|y - x\| < \delta$, then $T_\varepsilon(\widehat{N}(x))$ does not contain a periodic orbit.*

Proof. The divergence of the flow of (6) is

$$L(x, I) + L(y, I) + D_2L(x, I)G(x)N + D_2L(y, I)G(y)M \quad (18)$$

where $I = G(x)N + G(y)M$. As $y \rightarrow x$ and $N + M \rightarrow \widehat{N}(x)$, then (18) converges to (17). Thus, there exist $\varepsilon > 0$ and $\delta > 0$ such that if $\|x - y\| < \delta$, then (18) is strictly negative for all $(N, M) \in T_\varepsilon(\widehat{N}(x))$. It then follows directly from *Bendixson-Dulac Theorem* (see, e.g., [17] p. 133) that there exists no periodic orbit in $T_\varepsilon(\widehat{N}(x))$. \square

Lemma 3. *Suppose that H1, H2 and H3 are satisfied. Then for every $x \in \mathcal{X}$ and every $\gamma > 0$ there exist $\varepsilon > 0$ and $\delta > 0$ such that if $\|y - x\| < \delta$ and $|D_1s(x, x)(y - x)| > \gamma\|y - x\|$, then the interior of $T_\varepsilon(\widehat{N}(x))$ does not contain a steady state.*

Proof. To reach a contradiction, suppose the lemma is not true. Then there exists a $\gamma > 0$ and a sequence of strategies (y_1, y_2, \dots) and a sequence of strictly positive steady states $((N_1, M_1), (N_2, M_2), \dots)$ with corresponding environmental states $I_i = G(x)N_i + G(y_i)M_i$ such that $y_i \rightarrow x$ and $N_i + M_i \rightarrow \widehat{N}(x)$ as $i \rightarrow \infty$ and such that $|D_1s(x, x)(y_i - x)| > \gamma\|y_i - x\|$ for all i . Since \mathcal{X} is finite-dimensional, we may, without loss of generality, assume that there exists a $\xi \in \mathbb{R}^n$ such that $(y_i - x)/\|y_i - x\| \rightarrow \xi$ as $i \rightarrow \infty$. Hence

$$|D_1s(x, x)\xi| \geq \gamma > 0. \quad (19)$$

Since (N_i, M_i) is a steady state of (6) we have $L(x, I_i) = 0$ and $L(y_i, I_i) = 0$ for all i . Hence

$$D_1s(x, x)\xi = \lim_{i \rightarrow \infty} \frac{L(y_i, I_i) - L(x, I_i)}{\|y_i - x\|} = 0, \quad (20)$$

which contradicts with (19), and which completes the proof. \square

Proof of Proposition 1. For given $x \in \mathcal{X}$ and $\gamma > 0$, let $\varepsilon > 0$ and $\delta > 0$ be such that the conclusions of Lemmas 1-3 hold, and such that $(\widehat{N}(x), 0)$ and $(0, \widehat{N}(y))$ are the only ω -limits in $T_\varepsilon(\widehat{N}(x))$. If $s(y, x) > 0$, then $(\widehat{N}(x), 0)$ is a saddle whose stable manifold lies in the boundary of the resident-invader population state space and therefore cannot be the ω -limit of any orbit starting in the interior of $T_\varepsilon(\widehat{N}(x))$. All orbits starting in the interior must therefore converge to the remaining ω -limit $(0, \widehat{N}(y))$. \square

6.2. Proof of Proposition 2

Lemma 4. *Suppose that H1, H2 and H4 are satisfied. Then for every $x \in \mathcal{X}$ and every $\gamma > 0$ there exist $\varepsilon > 0$ and $\delta > 0$ such that if $\|y - x\| < \delta$ and $|(y - x)^\top D_{12}s(x, x)(y - x)| > \gamma\|y - x\|^2$, then every steady state in the interior of $T_\varepsilon(\widehat{N}(x))$ has real and non-zero eigenvalues. Specifically,*

1. *if $(x - y)^\top D_{12}s(x, x)(x - y) > \gamma\|x - y\|^2$, then every steady state in the interior of $T_\varepsilon(\widehat{N}(x))$ is a saddle with one strictly negative and one strictly positive eigenvalue;*
2. *if $(x - y)^\top D_{12}s(x, x)(x - y) < -\gamma\|x - y\|^2$, then every steady state in the interior of $T_\varepsilon(\widehat{N}(x))$ is an attracting node with two strictly negative eigenvalues.*

Proof. Let (N, M) be a steady state of (6), and let J denote the Jacobi matrix of (6) at (N, M) , i.e.,

$$J = \begin{pmatrix} D_2L(x, I)G(x)N & D_2L(x, I)G(y)N \\ D_2L(y, I)G(x)M & D_2L(y, I)G(y)M \end{pmatrix} \quad (21)$$

where $I = G(x)N + G(y)M$. The determinant of J converges to zero and its trace to (17) as $y \rightarrow x$ and $N + M \rightarrow \widehat{N}(x)$. Hence there exist an $\varepsilon > 0$ and a $\delta > 0$ such that if $\|x - y\| < \delta$ and $(N, M) \in T_\varepsilon(\widehat{N}(x))$, then J has one eigenvalue close to zero and one eigenvalue that is strictly negative. In particular, both eigenvalues are real. That no eigenvalue is equal to zero follows from the particular claims 1 and 2 of the lemma, which we prove next.

To arrive at a contradiction, suppose that claim 1 of the lemma is not true. Then there exist a $\gamma > 0$ and a sequence of strategies (y_1, y_2, \dots) and corresponding strictly positive steady states $((N_1, M_1), (N_2, M_2), \dots)$ such that $y_i \rightarrow x$ and $N_i + M_i \rightarrow \widehat{N}(x)$ as $i \rightarrow \infty$, and such that $(y_i - x)^\top D_{12}s(x, x)(y_i - x) > \gamma\|y_i - x\|^2$, and such that the Jacobi matrix of (6) at (N_i, M_i) has one negative eigenvalue and one eigenvalue that is not positive. Thus,

$$\det J_i \geq 0 \quad (22)$$

for all i , where J_i is the Jacobi matrix of (6) at the steady state (N_i, M_i) . Without loss of generality we may further assume that there exists a $\xi \in \mathbb{R}^n$ such that $(y_i - x)/\|y_i - x\| \rightarrow \xi$ as $i \rightarrow \infty$. Then

$$\xi^\top D_{12}s(x, x)\xi \geq \gamma > 0 \quad (23)$$

and, as will be shown later,

$$\lim_{i \rightarrow \infty} \frac{\widehat{N}(x) \det J_i}{N_i M_i \|y_i - x\|^2} = \left(D_2 L(x, G(x) \widehat{N}(x)) G(x) \right) \left(\xi^\top D_{12} s(x, x) \xi \right) \geq 0. \quad (24)$$

That the limit in (24) is not smaller than zero follows from (22). Because of (17) it follows from (24) that $\xi^\top D_{12} s(x, x) \xi \leq 0$, which contradicts with (23). Although this is the contradiction that we were after in order to prove claim 1 of the lemma, it still has to be proven that the limit in (24) is correct. This is done after the next paragraph.

The proof of claim 2 is similar: to reach a contradiction, suppose the claim is not true. Then there exist a $\gamma > 0$ and a sequence of strategies (y_1, y_2, \dots) and corresponding sequence of strictly positive steady states $((N_1, M_1), (N_2, M_2), \dots)$ as before, but now with $(y_i - x)^\top D_{12} s(x, x) (y_i - x) < -\gamma \|y_i - x\|^2$ and such that J_i has one negative eigenvalue and one eigenvalue that is not negative. (We know from the first part of the proof of the lemma that at least one eigenvalue is strictly negative.) The ordering with respect to zero in (23) and in (24) is then reversed, which again gives a contradiction that proves that claim 2 is true.

We now show that the limit in (24) is correct. After a somewhat tedious but otherwise straight-forward calculation one finds

$$\begin{aligned} \lim_{i \rightarrow \infty} \frac{\widehat{N}(x) \det J_i}{N_i M_i \|y_i - x\|^2} &= \left(D_2 L(x, G(x) \widehat{N}(x)) G(x) \right) \left(D_{12} L(x, G(x) \widehat{N}(x)) \xi D G(x) \xi \right) \\ &\quad - \left(D_2 L(x, G(x) \widehat{N}(x)) D G(x) \xi \right) \left(D_{12} L(x, G(x) \widehat{N}(x)) \xi G(x) \right). \end{aligned} \quad (25)$$

This result may be easiest obtained by Taylor-expanding $D_2 L(y_i, I_i)$ and $G(y_i)$ (as they occur in the expression of $\det J_i$) as functions of y_i , and only retaining terms up to second order in $(y_i - x)$. The environmental condition $I_i = G(x) N_i + G(y_i) M_i$ then can stay as it is, and need not be expanded as a function of y_i . It is during this calculation that we explicitly use the linear form of the feedback environment given in (3) to eliminate various terms that do no longer occur in (25).

The following steps are to simplify the above expression and to show that the limits in (24) and (25) are identical. To this end, first notice that since $\widehat{N}(x)$ is a steady state of (4), we have $L(x, G(x) \widehat{N}(x)) = 0$ for all x . Differentiation with respect to x gives

$$D_1 L(x, G(x) \widehat{N}(x)) + D_2 L(x, G(x) \widehat{N}(x)) (D G(x) \widehat{N}(x) + G(x) D \widehat{N}(x)) = 0. \quad (26)$$

Next, since (N_i, M_i) is a steady state of (6) for all i , we have $L(x, I_i) = 0$ and $L(y_i, I_i) = 0$ where $I_i = G(x) N_i + G(y_i) M_i$. Hence

$$D_1 L(x, G(x) \widehat{N}(x)) \xi = \lim_{i \rightarrow \infty} \frac{L(y_i, I_i) - L(x, I_i)}{\|y_i - x\|} = 0. \quad (27)$$

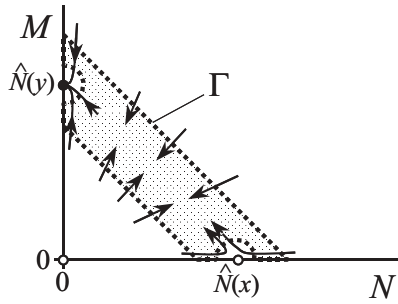


Fig. 5. The flow of (6) in relation to the closed curve Γ .

Application of (26) to ξ then gives

$$D_2L(x, G(x)\widehat{N}(x)) DG(x)\xi \widehat{N}(x) + D_2L(x, G(x)\widehat{N}(x)) G(x) D\widehat{N}(x)\xi = 0, \quad (28)$$

which we can use to eliminate $D_2L(x, G(x)\widehat{N}(x)) DG(x)\xi$ from (25). This gives

$$\begin{aligned} & \lim_{i \rightarrow \infty} \frac{\widehat{N}(x) \det J_i}{N_i M_i \|y_i - x\|^2} \\ &= \left(D_2L(x, G(x)\widehat{N}(x)) G(x) \right) \left\{ \left(D_{12}L(x, G(x)\widehat{N}(x)) \xi DG(x)\xi \right) \widehat{N}(x) \right. \\ & \quad \left. + \left(D_{12}L(x, G(x)\widehat{N}(x)) \xi G(x) \right) \left(D\widehat{N}(x)\xi \right) \right\}. \end{aligned} \quad (29)$$

By differentiating (5) we find that the expression between curly brackets in (29) is equal to the quadratic form $\xi^\top D_{12}s(x, x)\xi$, which shows that the limits in (24) and (25) are identical. This completes the proof of the lemma. \square

Proof of Proposition 2. For given $x \in \mathcal{X}$ and given $\gamma > 0$, let $\varepsilon > 0$ and $\delta > 0$ be such that the conclusions of Lemmas 1,2 and 4 hold, and such that $(\widehat{N}(x), 0)$ and $(0, \widehat{N}(y))$ are the only ω -limits on the boundary of \mathcal{N}^2 that are also in $T_\varepsilon(\widehat{N}(x))$.

We first consider case 1 of Proposition 2, i.e., suppose that $s(y, x) > 0$ and $s(x, y) < 0$. Then $(0, \widehat{N}(y))$ is a stable node, and $(\widehat{N}(x), 0)$ is a saddle. Construct the closed curve Γ as in Figure 5. Thus, Γ largely coincides with the boundary of $T_\varepsilon(\widehat{N}(x))$, except close to the neighborhoods of the two boundary steady states. Then by construction, the Poincaré index of Γ with respect to the flow of (6) is zero. By the *Poincaré-Bendixon Theorem*, any ω -limit in the interior of $T_\varepsilon(\widehat{N}(x))$ is either a limit cycle or contains at least one steady state. Limit cycles are not possible because of Lemma 2. We now show that the interior can also not contain a steady state. From Lemma 4 it follows that any such steady state is hyperbolic, and if there is more than one steady state, then they are all of the same type, i.e., they are all saddles or they are all stable nodes. A saddle has a Poincaré index of -1 and a node of $+1$. Consequently, by the *Poincaré-Hopf Theorem* (see, e.g., [10] p. 157),

the index of Γ is either negative or positive, which is a contradiction, because by construction the index of Γ is zero. All orbits starting in the interior of $T_\varepsilon(\widehat{N}(x))$ must therefore have ω -limits on the boundary of $T_\varepsilon(\widehat{N}(x))$. By choice of ε and δ , the only ω -limits on the boundary are $(\widehat{N}(x), 0)$ and $(0, \widehat{N}(y))$. Since $(\widehat{N}(x), 0)$ is a saddle whose stable manifold lies on the boundary, all orbits starting in the interior of $T_\varepsilon(\widehat{N}(x))$ must converge to $(0, \widehat{N}(y))$ as $t \rightarrow \infty$.

Case 2 is identical to case 1 with the roles of x and y reversed. Case 3 is proven in a similar way, but now the boundary fixed-points are both saddles and the index of Γ is -1 . Limit cycles are excluded by Lemma 2, and from Lemma 3 and by adding up the indices of the steady states enclosed by Γ , it follows that the interior of $T_\varepsilon(\widehat{N}(x))$ contains one and only one steady state which necessarily is a stable node. In case 4, the boundary fixed-points are both stable nodes and the index of Γ is $+1$, and one shows in a similar way that the interior of $T_\varepsilon(\widehat{N}(x))$ contains one and only one steady state which is a saddle. This completes the proof of Proposition 2. \square

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