

S.A.H. Geritz · M. Gyllenberg · F.J.A. Jacobs · K. Parvinen

## **Invasion dynamics and attractor inheritance**

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**Abstract.** We study the dynamics of a population of residents that is being invaded by an initially rare mutant. We show that under relatively mild conditions the sum of the mutant and resident population sizes stays arbitrarily close to the initial attractor of the monomorphic resident population whenever the mutant has a strategy sufficiently similar to that of the resident. For stochastic systems we show that the probability density of the sum of the mutant and resident population sizes stays arbitrarily close to the stationary probability density of the monomorphic resident population. Attractor switching, evolutionary suicide as well as most cases of “the resident strikes back” in systems with multiple attractors are possible only near a bifurcation point in the strategy space where the resident attractor undergoes a discontinuous change. Away from such points, when the mutant takes over the population from the resident and hence becomes the new resident itself, the population stays on the same attractor. In other words, the new resident “inherits” the attractor from its predecessor, the former resident.

### **1. Introduction**

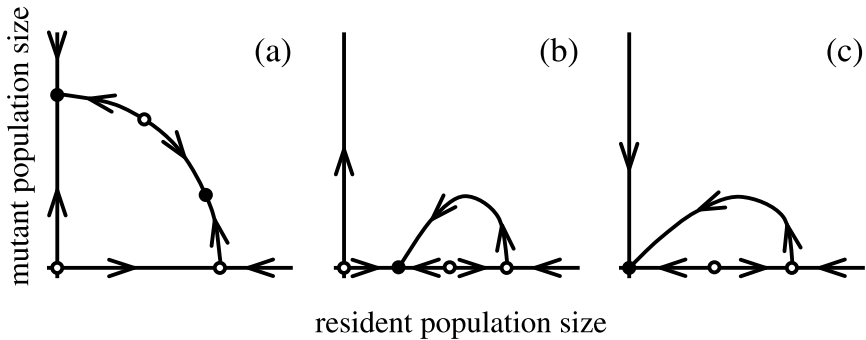
The notion of invasion of a population by a new and initially rare mutant plays a central role in evolutionary theory. Within the theoretical framework of adaptive dynamics (Metz *et al.* 1996; Dieckmann and Law 1996; Geritz *et al.* 1997, 1998; but also see Hammerstein 1996; Matessi and Di Pasquale 1996; Weissing 1996; Eshel 1997, 1998) it is commonly assumed that if a mutant can invade a resident population, while invasion under reversal of roles (i.e., with the resident as invader) is not possible, then the mutant will go to fixation, i.e., the mutant will oust the resident and become the new resident itself. The succession of a great number of such invasion-fixation events, each time by a different mutant, causes the population to change on an evolutionary time scale (Eshel 1983; Taylor 1989; Metz *et al.* 1992; Hammerstein 1996). A second common assumption is that if the mutant can invade, and invasion under reversal of roles is also possible, then the resident is protected against extinction by a positive growth rate when rare and therefore cannot be

S.A.H. Geritz, M. Gyllenberg, K. Parvinen: Department of Mathematics, University of Turku, FIN-20014 Turku, Finland

F.J.A. Jacobs: Institute of Evolutionary and Ecological Sciences, University of Leiden, NL-2311 GP Leiden, The Netherlands

Correspondence to S.A.H. Geritz (stefan.geritz@utu.fi)

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**Fig. 1.** Examples of resident-mutant dynamics with multiple demographic attractors: (a) unprotected dimorphism, (b) the resident strikes back, and (c) evolutionary suicide. The axes may represent finite- or infinite-dimensional spaces.

ousted, so that the mutant and the resident will coexist as a protected dimorphism. Similar assumptions have been used in population genetics to establish criteria for allele substitution and protected polymorphism (e.g., Roughgarden 1979).

In systems with multiple demographic attractors, these assumptions need not be satisfied. For example, unprotected coexistence may occur at an attractor inside the interior of the population state space of the combined resident-mutant dynamics in spite of the resident not being able to invade a population of the mutant (Fig. 1a). Moreover, if there are multiple attractors for the resident population, then the initially successful invasion by a mutant may trigger the resident to switch to another attractor at which the mutant cannot invade, so that the mutant disappears again (Fig. 1b). The latter scenario has been dubbed “the resident strikes back” (Diekmann *et al.* 1999, Mylius *et al.* 2001a,b) and has been found by other authors as well (Doebeli 1998; Parvinen 1999). A special case of “the resident strikes back” is “evolutionary suicide” (a term coined by Ferrière, 2000) where the invasion of a mutant leads to the demise of both the resident and the mutant (Fig. 1c). Evolutionary suicide has also been studied by Matsuda and Abrams (1994), Cadet (1998), Gyllenberg *et al.* (2000) and Gyllenberg and Parvinen (2001).

Multiple demographic attractors occur in many ecological models owing to Allee-effects, functional responses, delayed feedback, or metapopulation structure (e.g., Gilpin and Case 1976; May 1977; Gyllenberg and Hanski 1992; Gyllenberg *et al.* 1993; Hastings 1993; Matsuda and Abrams 1994; Jansen 1995; Van Dooren and Metz 1998; Briggs *et al.* 1999; Gyllenberg *et al.* 1999). Whenever there are multiple attractors it is generally not possible to predict the outcome of an invasion event on the basis of invasion criteria alone. Instead, the full dynamics of the resident-mutant population must be taken into account. The existence of multiple attractors can also have important long-term evolutionary consequences, because the selective environment at different attractors need not be the same, i.e., the set of potentially invading mutants need not be the same (Rand *et al.* 1994; Van Dooren and Metz 1998). Switching between alternative attractors during the course of evolution can give rise to evolutionary phenomena that do not occur in systems

with only a single attractor, such as evolutionary cycles (Doebeli and Ruxton 1997) and evolutionary suicide (Matsuda and Abrams 1994; Cadet 1998; Ferrière 2000; Gyllenberg *et al.* 2000; Gyllenberg and Parvinen 2001).

Important questions for understanding evolution with multiple demographic attractors are the following: (1) Under what conditions does an initially rare and successfully invading mutant replace the resident, coexist with the resident, or eventually go extinct as in the case of “the resident strikes back”? (2) If the mutant ousts the resident and thus becomes the new resident itself, then under what conditions does the new resident population stay on the same attractor (i.e., the new resident “inherits” the attractor from its predecessor) or switch to another attractor? (3) How does a bifurcation in the resident attractor affect the long-term course of evolution? In this paper our focus is on the question of attractor inheritance versus attractor switching, but in addition we obtain some partial answers to the other questions as well. To this end we study the general dynamics in discrete time of a population of residents that is being invaded by an initially rare mutant.

The structure of the paper is as follows. In Section 2 we review some of the mathematical concepts used in this paper. In Section 3 we show that under relatively mild conditions (i.e., conditions that are readily satisfied in ecologically realistic models) the sum of the mutant and resident population sizes stays arbitrarily close to the attractor of the monomorphic resident population whenever the mutant has a strategy sufficiently similar to that of the resident. In Section 4, we show that if the population state is a probability density over all possible population sizes, then the probability density of the sum of the mutant and resident population sizes stays arbitrarily close to the stationary probability density of the monomorphic resident population. In Section 5 we conclude that attractor switching, evolutionary suicide as well as most cases of “the resident strikes back” can happen only near a bifurcation point in the strategy space where the resident attractor undergoes an abrupt change. Away from such points, with each invasion-fixation event the mutant inherits the attractor from its predecessor, the former resident. The long-term evolutionary consequence is that if only mutants slightly different from the resident can occur, then the population will stay on the same attractor during the course of evolution.

## 2. Preliminaries

We begin with a brief review of the main concepts used in this paper, largely following Gyllenberg *et al.* (1996) and Easton (1998). Throughout this section,  $X$  is a metric space with metric  $d$ , and  $f : X \rightarrow X$  is a continuous function.

**Definition 2.1.** Any ordered set  $\{x_0, x_1, \dots, x_{n-1}\} \in X^n$  of length  $n \geq 2$  is an  $\varepsilon$ -chain if  $d(x_{t+1}, f(x_t)) \leq \varepsilon$  for each  $t \in \{0, 1, \dots, n-2\}$ .

For  $A, B \subset X$  we use  $ch(A, B, \varepsilon)$  to denote the set of points of all  $\varepsilon$ -chains of arbitrary length starting in  $A$  and ending in  $B$ .

**Definition 2.2.** A set  $A \subset X$  is *invariant* if  $f(A) = A$ .

**Definition 2.3.** A compact invariant set  $A \subset X$  is

1. **stable** if for every open neighbourhood  $U$  of  $A$  there exists an open neighbourhood  $V$  of  $A$  such that  $f^t(V) \subset U$  for all  $t \geq 0$ ;
2. an **attractor** if it is stable and if there exists an open neighbourhood  $V$  of  $A$  such that for every  $x \in V$  and every open neighbourhood  $U$  of  $A$  there exists a  $T \geq 0$  such that  $f^t(x) \in U$  for all  $t \geq T$ ;
3. **chain stable** if for every open neighbourhood  $U$  of  $A$  there is an  $\varepsilon > 0$  such that  $ch(A, X, \varepsilon) \subset U$ .

An equivalent way of defining chain stability is to require that for every open neighbourhood  $U$  of  $A$  there exists an  $\varepsilon > 0$  and an  $\varepsilon$ -neighbourhood  $V_\varepsilon$  of  $A$  such that  $ch(V_\varepsilon, X, \varepsilon) \subset U$ . Indeed, if  $\{y_0, y_1, \dots, y_t\}$  is an  $\varepsilon$ -chain with  $y_0 \in V_\varepsilon$ , then there exist points  $x_0 \in A$  with  $d(x_0, y_0) \leq \varepsilon$  and  $x_{-1} \in A$  with  $f(x_{-1}) = x_0$ , so that  $\{x_{-1}, y_0, y_1, \dots, y_t\}$  is an  $\varepsilon$ -chain starting in  $A$ .

Our definition of an attractor was adopted from Gyllenberg *et al.* (1996) and is equivalent to an asymptotically stable compact invariant set as defined by Easton (1998).

**Theorem 2.4.** Every attractor is chain stable.

A proof of this theorem can be found in Easton (1998; chapter 4).

### 3. Invasion dynamics; deterministic systems

Throughout this section, let  $X$  be the set of all non-negative population sizes as a subset of some finite- or infinite-dimensional normed space, and let  $S$  be the strategy space (i.e., the set of admissible strategies) equipped with a metric  $d$ . Consider a monomorphic resident population with strategy  $r \in S$  and population size  $x_t \in X$  at time  $t \geq 0$ , and let the population dynamics be given by

$$x_{t+1} = f(x_t, r) \tag{3.1}$$

for some continuous mapping  $f : X \times S \rightarrow X$ .

Also consider a population of residents and mutants with population sizes  $x_t, y_t \in X$  and strategies  $r, s \in S$ , respectively, and let their population dynamics be given by

$$\begin{cases} x_{t+1} = g(x_t, y_t, r, s) \\ y_{t+1} = h(x_t, y_t, r, s) \end{cases} \tag{3.2}$$

for given mappings  $g, h : X^2 \times S^2 \rightarrow X$ .

We assume that  $f, g$  and  $h$  satisfy the following consistency relations:

$$\begin{cases} f(x, r) = g(x, 0, r, s) \\ f(x + y, r) = g(x, y, r, r) + h(x, y, r, r) \\ g(x, y, r, s) = h(y, x, s, r) \end{cases} \tag{3.3}$$

for each  $x, y \in X$  and  $r, s \in S$ . The ecological interpretation of (3.3) is that (i) if the mutants population size is zero, then the population is effectively monomorphic; (ii) If the resident and the mutant have the same strategy so that they are

ecologically identical, then the population is again effectively monomorphic so that the sum of the resident and mutant population sizes has the same dynamics as of a monomorphic resident population; (iii) Since the only difference between a mutant and a resident is their strategy, the right hand sides of (3.2) can be swapped, provided that we swap the corresponding population sizes and strategies inside the functions  $g$  and  $h$  as well. Below we use only properties (ii) and (iii).

The following theorem gives conditions that imply that if the mutant has a strategy similar to that of the resident, and if the mutant is introduced at a low initial frequency in a monomorphic resident population near its attractor, then the orbits of (3.2) will stay inside a narrow tube in the resident-mutant population state space where the sum of the population densities of the resident and the mutant are close to the resident densities of the monomorphic resident attractor. For this reason we call the following theorem the Tube Theorem.

**Theorem 3.1** (*Tube Theorem*). *For given  $r \in S$ , let  $f(\cdot, r) : X \rightarrow X$  be continuous, and let  $A \subset X$  be an attractor of (3.1). Assume further that  $g : X^2 \times S^2 \rightarrow X$  in (3.2) is uniformly continuous, and that (3.3) is satisfied. Then, for every  $\varepsilon > 0$  there exists a  $\delta > 0$  such that  $x_t + y_t$  in (3.2) stays inside an  $\varepsilon$ -neighbourhood of  $A$  for all  $t \geq 0$  provided  $x_0 + y_0$  is inside a  $\delta$ -neighbourhood of  $A$  and  $d(r, s) < \delta$ .*

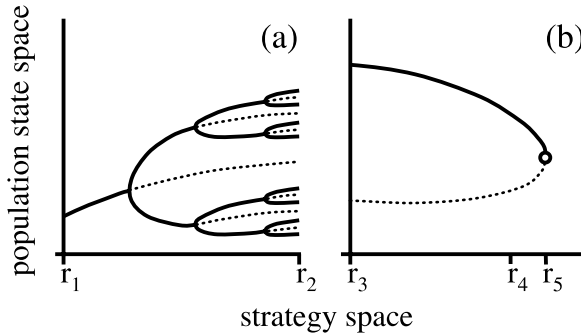
*Proof.* We show that for every  $\varepsilon' > 0$  there exists a  $\delta > 0$  such that for all  $t > 0$ ,  $\{x_0 + y_0, \dots, x_t + y_t\}$  is an  $\varepsilon'$ -chain for (3.1) whenever  $d(r, s) < \delta$ . The present theorem then follows from Theorem 2.4. Indeed, from (3.2) we have  $x_{t+1} + y_{t+1} = f(x_t + y_t, r) + \lambda_t$  where  $\lambda_t = g(x_t, y_t, r, s) + h(x_t, y_t, r, s) - f(x_t + y_t, r)$ , which by (3.3) can be written as  $\lambda_t = (g(x_t, y_t, r, s) - g(x_t, y_t, r, r)) + (g(y_t, x_t, s, r) - g(y_t, x_t, r, r))$ . Since  $g$  is uniformly continuous,  $\|\lambda_t\|$  can be made arbitrarily small by choosing  $s$  sufficiently close to  $r$ , independently of  $t$ , which completes the proof.  $\square$

The Tube Theorem applies only point-wise with respect to  $r \in S$ , because the value of  $\delta$  may still depend on  $r$ . The reason for this lack of uniformity with respect to the resident's strategy is due to  $\varepsilon'$ , which in the proof should be small depending on the attractor  $A$ , which in turn depends on  $r$ . Next, we formulate a version of the Tube Theorem that applies uniformly to every  $r$  in a compact strategy space. To this end, we first define a notion of continuity of the resident attractor as a function of the resident's strategy.

**Definition 3.2.** *Let  $S$  be compact, and for each  $r \in S$ , let  $A(r) \subset X$  be an attractor of (3.1). We say that  $A(r)$  **varies continuously as a function of  $r$  on  $S$**  if the set  $\{(x, r) : x \in A(r), r \in S\}$  is compact in  $X \times S$  equipped with the metric  $d'((x, r), (y, s)) = \|x - y\| + d(r, s)$ .*

The above notion of continuity is intuitively appealing: for example, period doublings, supercritical pitch-fork as well as supercritical Hopf bifurcations are allowed on  $S$ , but saddle-node bifurcations typically are not (Fig. 2).

**Theorem 3.3** (*Uniform Tube Theorem*). *Let  $S$  be compact, and for each  $r \in S$ , let  $f(\cdot, r) : X \rightarrow X$  be continuous, and let  $A(r) \subset X$  be an attractor of (3.1) such*



**Fig. 2.** Examples of a continuously varying resident attractor as a function of the resident’s strategy. (a) The resident attractor undergoes a number of period doublings as the resident’s strategy varies through the strategy space. The set  $\{(x, r) : x \in A(r), r \in S\}$  (bold line) with  $S = [r_1, r_2]$  is an attractor for the mapping  $k : X \times S \rightarrow X \times S$ . (b) The resident attractor undergoes a saddle-node bifurcation at  $r_5$  where it ceases to exist. The set  $\{(x, r) : x \in A(r), r \in S\}$  (bold line) is an attractor for  $k$  if  $S = [r_3, r_4]$  (any  $r_4 < r_5$ ), but not if  $S = [r_3, r_5]$ . The unstable fixed points or periodic orbits are represented by dotted lines.

that  $A(r)$  varies continuously as a function of  $r$  on  $S$  in the sense of Definition 3.2. Assume further that  $g : X^2 \times S^2 \rightarrow X$  in (3.2) is uniformly continuous, and that (3.3) is satisfied. Then, for every  $\varepsilon > 0$  there exists a  $\delta > 0$  such that  $x_t + y_t$  in (3.2) stays inside an  $\varepsilon$ -neighbourhood of  $A(r)$  for all  $t \geq 0$  and all  $r \in S$ , provided  $x_0 + y_0$  is inside a  $\delta$ -neighbourhood of  $A(r)$  and  $d(r, s) < \delta$ .

*Proof.* The set  $\{(x, r) : x \in A(r), r \in S\}$  is an attractor for the mapping  $k : X \times S \rightarrow X \times S$  defined as  $k(x, r) = (f(x, r), r)$ . By Theorem 2.4 it is sufficient to show that for every  $\varepsilon' > 0$  there exists a  $\delta > 0$  such that for all  $t > 0$ ,  $\{(x_0 + y_0, r), \dots, (x_t + y_t, r)\} \in (X \times S)^{t+1}$  is an  $\varepsilon'$ -chain for  $k$  whenever  $d(r, s) < \delta$ , which can be done in essentially the same way as in the proof of the Tube Theorem (Theorem 3.1).  $\square$

#### 4. Invasion dynamics; stochastic systems

In this section we formulate a version of the Tube Theorem (Theorem 3.1) for stochastic systems where the population state is a probability density over all possible population sizes. To this end, let  $X$  and  $S$  be defined as in Section 3, and let  $F \subset L^1(X)$  be the set of all probability densities over  $X$ , i.e.,  $f \geq 0$  and  $\|f\|_1 = 1$  for all  $f \in F$ . Consider a monomorphic resident population with strategy  $r \in S$  and probability density  $f_t \in F$  at time  $t \geq 0$ , and suppose that the dynamics of  $f_t$  is given by

$$f_{t+1}(x) = \int_X \varphi(x, x', r) f_t(x') dx' \tag{4.1}$$

for all  $x \in X$ , where  $\varphi(\cdot, x', r) \in F$  is the probability density of population sizes given that the population size one time step before was  $x'$ .

Next, let  $G \subset L^1(X^2)$  be the set of all probability densities over  $X^2$ , and consider a population of residents and mutants with strategies  $r, s \in S$ , respectively, and with probability density  $g_t \in G$  at time  $t \geq 0$ . Suppose that the dynamics of  $g_t$  is given by

$$g_{t+1}(x, y) = \int_{X^2} \gamma(x, y, x', y', r, s) g_t(x', y') dx' dy' \tag{4.2}$$

for all  $x, y \in X$ , where  $\gamma(\cdot, \cdot, x', y', r, s) \in G$  is the probability density of the population sizes of the resident and the mutant given that one time step before the population sizes were  $x'$  and  $y'$ , respectively.

Define the set  $\Gamma(z) = \{(x, y) \in X^2 : x + y = z\}$ . We assume that  $\varphi$  and  $\gamma$  satisfy the consistency relation

$$\varphi(z, z', r) = \int_{\Gamma(z)} \gamma(x, y, x', y', r, r) dx dy \tag{4.3}$$

for every  $r \in S, z, z' \in X$  and  $(x', y') \in \Gamma(z')$ . The ecological interpretation of (4.3) is that if the resident and the mutant have the same strategy so that they are ecologically identical, then the population is effectively monomorphic so that the sum of the mutant and resident population sizes must have the same transition probabilities as in a monomorphic resident population.

The following version of the Tube Theorem gives conditions that imply that the probability density of the sum of the mutant and resident population sizes stays arbitrarily close (with respect to the  $L^1$ -norm) to the probability density of the monomorphic resident population, provided the mutant is introduced at a sufficiently low initial population density, and provided that the strategy of the mutant is sufficiently similar to that of the resident.

**Theorem 4.1** (*Stochastic Tube Theorem*). *For given  $r \in S$ , let  $A \subset F$  be an attractor of (4.1). Assume that  $\gamma : X^4 \times S^2 \rightarrow [0, \infty)$  is uniformly continuous, and that the support of  $\gamma(\cdot, \cdot, x', y', r, s)$  is bounded, uniformly in  $x', y' \in X$  and  $r, s \in S$ . Also assume that (4.3) is satisfied. Let further  $h_t \in F$  denote the probability density of the sum of mutant and resident population sizes in (4.2), i.e.,*

$$h_t(z) = \int_{\Gamma(z)} g_t(x, y) dx dy. \tag{4.4}$$

*Then, for every  $\varepsilon > 0$  there exists a  $\delta > 0$  such that  $h_t$  stays inside an  $\varepsilon$ -neighbourhood of  $A$  (with respect to the  $L^1$ -norm) for all  $t \geq 0$ , provided  $h_0$  is inside a  $\delta$ -neighbourhood of  $A$  and  $d(r, s) < \delta$ .*

*Proof.* Because of Theorem 2.4, it is sufficient to show that for every  $\varepsilon' > 0$  there exists a  $\delta > 0$  such that for all  $t > 0$ ,  $\{h_0, \dots, h_t\}$  is an  $\varepsilon'$ -chain for (4.1) whenever  $d(r, s) < \delta$ . Indeed, from (4.2) and (4.3) we have  $h_{t+1}(z) =$

$\int_X \varphi(z, z', r) h_t(z') dz' + \lambda_t(z)$ , where  $\lambda_t(z) = \int_{\Gamma(z)} \int_{X^2} (\gamma(x, y, x', y', r, s) - \gamma(x, y, x', y', r, r)) g_t(x', y') dx' dy' dx dy$ . Since  $\gamma$  is uniformly continuous and has a uniformly bounded support,  $\|\lambda_t\|_1 \rightarrow 0$  as  $d(r, s) \rightarrow 0$ , uniformly with respect to  $t$ , which completes the proof.  $\square$

Next we formulate a version of Theorem 4.1 that applies uniformly with respect to all resident strategies in a compact strategy space.

**Theorem 4.2** (*Uniform Stochastic Tube Theorem*). *Let  $S$  be compact, and for each  $r \in S$ , let  $A(r) \subset F$  be an attractor of (4.1) such that  $A(r)$  varies continuously as a function of  $r$  on  $S$  in the sense of Definition 3.2. Assume further that  $\gamma : X^4 \times S^2 \rightarrow [0, \infty)$  is uniformly continuous, and that the support of  $\gamma(\cdot, \cdot, x', y', r, s)$  is bounded, uniformly in  $x', y' \in X$  and  $r, s \in S$ . Also assume that (4.3) is satisfied, and let  $h_t \in F$  be defined as in (4.4). Then, for every  $\varepsilon > 0$  there exists a  $\delta > 0$  such that  $h_t$  stays inside an  $\varepsilon$ -neighbourhood of  $A(r)$  (with respect to the  $L^1$ -norm) for all  $t \geq 0$  and all  $r \in S$ , provided  $h_0$  is inside a  $\delta$ -neighbourhood of  $A(r)$  and  $d(r, s) < \delta$ .*

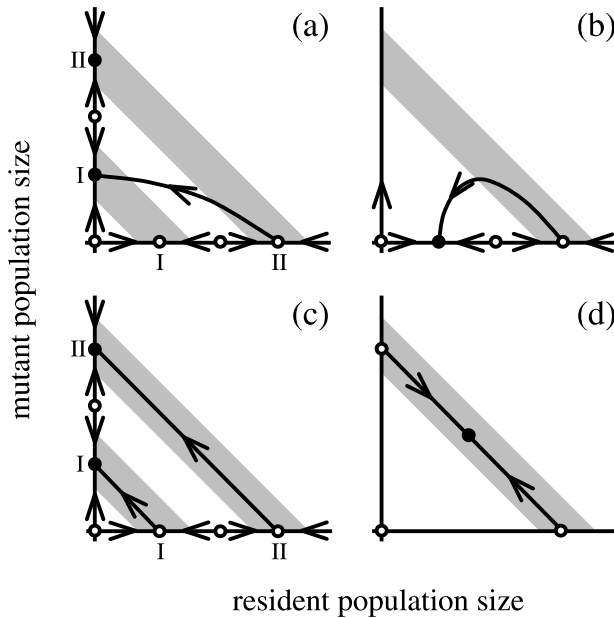
*Proof.* The set  $\{(f, r) : f \in A(r), r \in S\}$  is an attractor for the mapping  $k : F \times S \rightarrow F \times S$  defined as  $k(f, r)(x) = \left( \int_X \varphi(x, x', r) f(x') dx', r \right)$ . By Theorem 2.4 it is sufficient to show that for every  $\varepsilon' > 0$  there exists a  $\delta > 0$  such that for all  $t > 0$ ,  $\{(h_0, r), \dots, (h_t, r)\} \in (F \times S)^{t+1}$  is an  $\varepsilon'$ -chain for  $k$  whenever  $d(r, s) < \delta$ , which is done in a completely analogous way as in the proof of Theorem 4.1.  $\square$

### 5. Discussion

Our main result in this paper is Theorem 3.1, which states that if a mutant enters a population of residents near a demographic attractor, and if the strategy of the mutant is sufficiently similar to that of the residents, then the sum of the population sizes of the resident and the mutant stays arbitrarily close to the resident attractor. This result holds under fairly mild conditions on the functions describing the population dynamics, and which are satisfied in a great majority of ecological models studied to date. Since by the theorem the dynamics of the mixed population of residents and mutants is confined to interior of a “tube” in the resident-mutant population state space, we refer to this result as the Tube Theorem.

Attractor switching, evolutionarily suicide as well as most cases of “the resident strikes back” require that the resident-mutant population leaves the “tube” (Fig. 3a,b) and therefore can be excluded as possible outcomes of the invasion dynamics provided the mutation step size is sufficiently small. The only remaining possibilities are that the mutant takes over the population while staying on the same attractor (a process referred to as “attractor inheritance”), or the mutant coexists with the resident as a protected or unprotected dimorphism inside the “tube” (Fig. 3c,d). A special case of “the resident strikes back” occurring inside the “tube” is discussed below in the context of resident attractors with chaotic dynamics. For





**Fig. 3.** Impossibilities and possibilities under the Tube Theorem. (a) Attractor switching (from II to I), and (b) ‘the resident strikes back’ are not possible, because for that the orbit of the resident-mutant dynamics has to leave the ‘tube’ (indicated by a grey strip). However, (c) attractor inheritance (from I to I and from II to II), and (d) coexistence are possible, because for these the orbits do not have to leave the ‘tube’. The axes may represent finite- or infinite-dimensional spaces.

specific examples of models illustrating attractor inheritance see, e.g., Matsuda and Abrams (1994), Doebeli and Ruxton (1997), Van Dooren and Metz (1998) and Gyllenberg *et al.* (2000).

The Tube Theorem applies only point-wise in the strategy space, i.e., the required degree of similarity between the mutant and resident strategies generally depends on the resident strategy. In Theorem 3.3 we formulate the Uniform Tube Theorem, which states that on a compact (subset of the) strategy space where the resident attractor varies continuously in the sense of Definition 3.2, there exists a sufficient degree of similarity between the mutant and resident strategies that is independent of the resident strategy. In other words, in a finite-dimensional strategy space, and as long as the population stays away from points where the resident attractor undergoes an abrupt change, there exists a uniformly small mutation step size that guarantees that with each invasion-fixation event the new resident inherits the attractor from its predecessor, and hence the population stays on the same attractor during the course of evolution. Various authors have used the idea of attractor inheritance to explain certain behaviour in their models (e.g. Matsuda and Abrams 1994; Doebeli and Ruxton 1997; Van Dooren and Metz 1998), but until now without any rigorous mathematical underpinning. Notice that a period doubling, a

supercritical pitch-fork as well as a supercritical Hopf bifurcation are continuous in the sense of Definition 3.2, and therefore are not considered as an abrupt change in the resident attractor.

Close to points in the strategy space where the resident attractor undergoes an abrupt change, the required degree of similarity between the resident and mutant strategies may become biologically unrealistic, so that it is no longer reasonable to use the Tube Theorem to predict the outcome of an invasion event. For example, if, as a consequence of evolution, the population approaches a saddle-node bifurcation where the resident attractor will cease to exist altogether, then the Tube Theorem requires smaller and smaller mutation steps such that the population always stays on the same side of the bifurcation point. In reality, however, it becomes increasingly likely that a mutant comes along whose strategy is on the other side of the bifurcation point. With small evolutionary steps, attractor switching, evolutionary suicide and “the resident strikes back” are possible only near strategies where the resident attractor undergoes a sudden change. For examples in specific models see, e.g., Matsuda and Abrams (1994), Doebeli (1998), Gyllenberg *et al.* (2000) and Gyllenberg and Parvinen (2001). In the models studied by Diekmann *et al.* (1999), Mylius *et al.* (2001) and Mylius and Diekmann (2001) “the resident strikes back” because of a discrete strategy space in which small evolutionary steps are not possible.

Sudden changes in the resident attractor due to arbitrary small changes in resident strategy are common in chaotic systems, but chaotic systems pose problems for the application of the Tube Theorem for other reasons as well. Due to basin riddling (Alexander *et al.* 1992; Sommerer and Ott 1993), for every initial mutant density that drives the mutant to extinction there may exist an initial mutant density arbitrarily nearby that leads to invasion (De Feo and Ferrière 2000). Moreover, the invader may experience recurrent outburst punctuating periods of arbitrarily low mutant densities for arbitrary periods of time. During such periods of low density, the mutant faces a high probability of extinction due to demographic stochasticity (De Feo and Ferrière 2000). While the outbursts occur inside the ‘tube’ implied by the Tube Theorem, the effect is the same as when ‘the resident strikes back’.

We suspect that in many cases the problems with chaotic resident dynamics may be structurally unstable in the sense that they disappear with the addition of a small amount of environmental noise. This then would allow for a formulation of the invasion dynamics where the population state is a probability density over all possible population sizes. In that case the probability density of the sum of the population sizes of the mutant and the resident stays arbitrarily close to the stationary probability density of the monomorphic resident population whenever the mutant and resident strategies are sufficiently similar (Theorem 4.1 and Theorem 4.2).

In this paper we considered the invasion of a monomorphic resident population. Extension of the theory to polymorphic resident populations is straight forward but involves more extensive notation without introducing any new insight or new result.

Our results were derived using the theory of chain recurrence of Conley (1978). Similar results can be obtained using singular perturbation theory (Jacobs *et al.* in prep.), applying theorems proven by Hoppensteadt (1966). One advantage of using singular perturbation theory is that it directly gives information about whether or

not the resident and mutant can coexist, possibly as an unprotected dimorphism. The results of Jacobs *et al.* (in prep.), however, have been proven only for one-dimensional strategy spaces and one-dimensional population state spaces (i.e., unstructured populations). The strength of the present approach is its full generality with respect to the dimensionality of both the strategy space and the population state space.

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