



Unfolding the resident–invader dynamics of similar strategies



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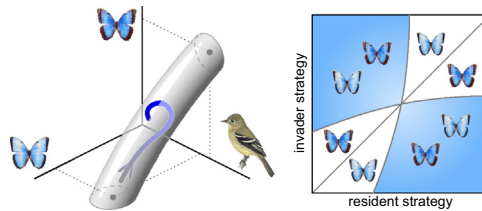
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HIGHLIGHTS

- We unravel the competition between two similar unstructured populations.
- We revisit the invasion–substitution theorem on which Adaptive Dynamics is grounded.
- We complete the classification of singular strategies, including degenerate cases.
- We show that unprotected coexistence is possible close to nearly degenerate singularities.
- Our approach works at any level of degeneracy resulting from the modeling assumptions.

GRAPHICAL ABSTRACT



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ABSTRACT

We investigate the competition between two groups of similar agents in the restricted, but classical context of unstructured populations varying in continuous time in an isolated, homogeneous, and constant abiotic environment. Individual behavioral and phenotypic traits are quantified by one-dimensional strategies and intra- as well as inter-specific interactions are described in the vicinity of a stationary regime. Some known results are revisited: invasion by a new strategy generically implies the substitution of the former resident; and resident–invader coexistence is possible close to singular strategies—the stationary points of the invasion fitness—and is generically protected—each of the two competing groups can invade the other. An (almost known) old conjecture is shown true: competition close to a singular strategy is “essentially Lotka–Volterra”—dominance of one strategy, protected coexistence at an intermediate equilibrium, and mutual exclusion are the generic outcomes. And the unfolding of the competition scenarios is completed with the analysis of three degenerate singular strategies—characterized by vanishing second-order fitness derivatives—near which resident–invader coexistence can be unprotected. Our approach is based on the series expansion of a generic demographic model, w.r.t. the small strategy difference between the two competing groups, and on known results on time-scale separation and bifurcation theories. The analysis is carried out up to third order and is extendable to any order. For each order, explicit genericity conditions under which higher orders can be neglected are derived and, interestingly, they are known prior to invasion. An important result is that degeneracies up to third-order are required to have more than one stable way of coexistence. Such degeneracies can be due to particular symmetries in the model formulation, and breaking the genericity

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conditions provides a direct way to draw biological interpretations. The developed body of theory is exemplified on a model for the evolution of cannibalism and on Lotka–Volterra competition models.
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1. Introduction

Many systems, both natural and artificial, are regulated by the competition between groups of similar agents. E.g., the struggle for life between a resident and a similar mutant phenotype for the same environmental niche is the basis of the Darwinian concept of natural selection (Mayr, 1982; Maynard-Smith, 1993); marginal innovations characterize the battle for market share in many economic sectors (Grossman and Helpman, 1991; Ziman, 2000); similar strategies produced by imperfect imitation, learning or cultural transmission challenge each other in both real-life and virtual social networks and define the behavioral schemes of artificial intelligence (Sutton and Barto, 1998; Gintis, 2000; Hofbauer and Sigmund, 2003).

The performance of an invader strategy x_2 against a resident strategy x_1 is universally called the invasion fitness of the invader and is typically quantified by a function, that we denote $\lambda(x_1, x_2)$, measuring the initial rate of growth shown by the invader population when introduced at very small density (Metz et al., 1992). Positive/negative fitness thus indicates invasion/extinction of the invader. Typically, the best performing strategy takes over the others (Gause, 1934; Hardin, 1960; Geritz, 2005; Meszéna et al., 2005; Dercole and Rinaldi, 2008) (see Fig. 1a and b). This leads to evolutionary steps in the resident strategy in the direction of the invasion fitness gradient $\partial_{x_2} \lambda(x_1, x_2)|_{x_2=x_1}$ (Metz et al., 1996; Dieckmann and Law, 1996), i.e., in the direction that is advantageous for the invader (Fig. 1b). However, there are singular strategies x near which selection is not directional and allows the coexistence of similar strategies (Fig. 1c), the prerequisite for evolutionary branching (Metz et al., 1996; Geritz et al., 1997, 1998). These are strategies x where the fitness gradient vanishes at $x_1 = x$ and the resident–invader dynamics are ruled by the “curvatures” of the fitness landscape (i.e., by the fitness second-derivatives w.r.t. resident and invader strategies).

Resident–invader coexistence between nearly singular strategies is typically protected—each of the two types can invade the other, so that no one can take over the other (Fig. 1c). This is well known since from the first classification of singular strategies (Metz et al., 1996; Geritz et al., 1997, 1998), though the arrangement of the internal attractors of the resident–invader dynamics has been poorly investigated. Restricting to stationary coexistence, we show that competition between similar strategies works as in the classical model of Lotka (1920) and Volterra (1926): either one type dominates and leads to a stable monomorphic equilibrium (Fig. 1a and b), or coexistence is protected, with a unique stable internal equilibrium (Fig. 1c), or the two types mutually exclude each other, with a unique internal saddle equilibrium separating the basins of attraction of the two monomorphic equilibria (Fig. 1d).

Although this result may seem rather intuitive and has been surmised since Metz et al. (1996) and Geritz et al. (1997, 1998) (see also Durinx et al., 2008, where the result is shown for a particular class of single-species physiologically structured population models), its formal derivation is rather involved, as will be seen in the next sections, and its implications are broad. If, for example, an innovative strategy is able to coexist with the established ones, then we know a priori that, generically (the genericity condition turns out to be the nonvanishing fitness cross-derivative, see Fig. 1c), it cannot take over the similar residents, even if its relative abundance is arbitrarily increased. Moreover, the coexistence

equilibrium being unique, there is only one way in which evolution can proceed after branching.

Resident–invader unprotected coexistence—coexistence that is stable together with at least one of the monomorphic equilibria—is possible close to a singular strategy characterized by degeneracies in the curvatures of the fitness landscape. The two most simple configurations are depicted in Fig. 1e and f. We show that these are the only possible competition scenarios if fitness degeneracies do not involve the third-order derivatives at the singular strategy. Note that in Fig. 1f there is only one stable equilibrium of

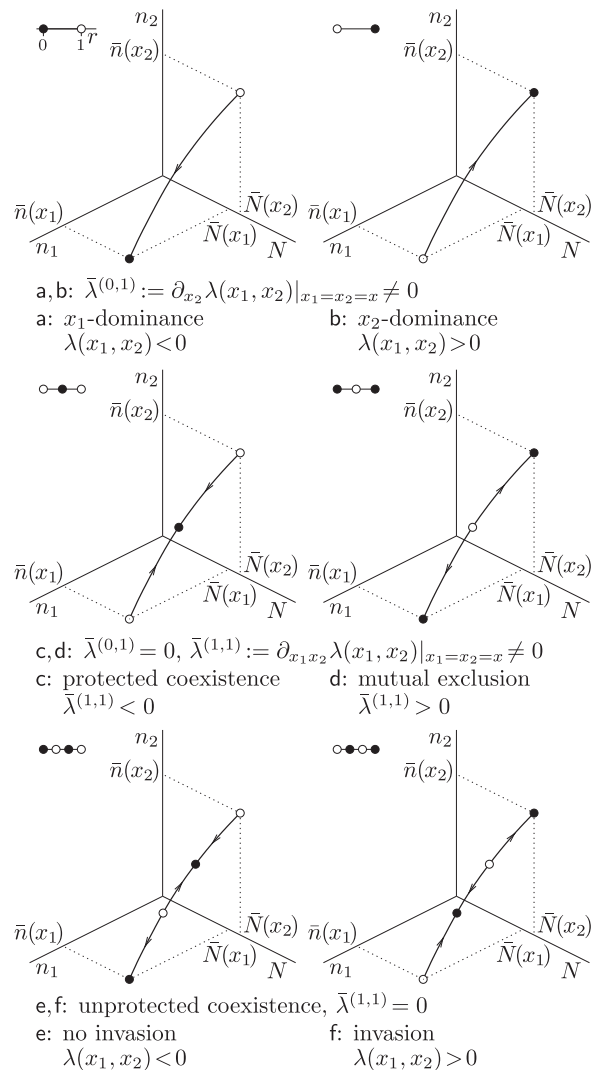


Fig. 1. Competition scenarios of the resident–invader dynamics between two similar strategies x_1 (resident, density n_1) and x_2 (invader, density n_2), possibly interacting with other resident populations (densities in vector N , graphically represented as one-dimensional). Strategies x_1 and x_2 are thought to be close to a reference strategy x , that is nonsingular in cases a and b, and singular (i.e., $\bar{\lambda}^{(0,1)} = 0$) in cases c–f. The singular strategy x is generic in cases c and d (i.e., $\bar{\lambda}^{(1,1)} \neq 0$), and degenerate in cases e and f. In the absence of invader, the resident populations coexist at the stable equilibrium $(\bar{n}(x_1), \bar{N}(x_1))$. After resident substitution, the new residents coexist at $(\bar{n}(x_2), \bar{N}(x_2))$. The dynamics of the relative density of the invader, $r := n_2/(n_1 + n_2)$, are schematically represented in the top-left of each panel. The sketches of the r -dynamics will be used to identify the six scenario in Section 4.

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