

# Supporting Online Material:

## Adaptive Dynamics of Continuous Games

Michael Doebeli<sup>1</sup>, Christoph Hauert<sup>1,2</sup> & Timothy Killingback<sup>3</sup>

<sup>1</sup> Departments of Mathematics and Zoology, University of British Columbia, Vancouver BC V6T 1Z4, Canada.

<sup>2</sup> Present address: Program for Evolutionary Dynamics, Harvard University, One Brattle Square, Cambridge MA 02138, USA.

<sup>3</sup> Ecology and Evolution, ETH Zürich, 8092 Zürich, Switzerland.

### 1 Adaptive Dynamics

The evolution of a continuous trait  $x$  under mutation and selection can be analyzed using the mathematical framework of adaptive dynamics ( $S1, S2, S3$ ). The central concept is that of *invasion fitness*  $f_x(y)$ , which denotes the growth rate of a rare mutant  $y$  in a resident population that is monomorphic for trait  $x$ . The adaptive dynamics of the trait  $x$  is then governed by the selection gradient  $D(x) = \partial f_x / \partial y|_{y=x}$ , so that  $\dot{x} = D(x)$ . For a detailed discussion of the underlying assumptions of this dynamic equation we refer to ( $S1, S2, S3$ ). Note that in general,  $\dot{x} = mD(x)$ , where  $m$  depends on population size and reflects the mutational process providing the raw material for evolutionary change. For constant population sizes,  $m$  is simply a parameter that scales time, and one can set  $m = 1$  without loss of generality.

Singular points of the adaptive dynamics are given by solutions of  $D(x^*) = 0$ . If there is no such solution, the trait  $x$  either always increases or decreases evolutionarily, depending on the sign of  $D(x)$ . If a singular trait  $x^*$  exists, it is convergent stable – and hence an attractor for the adaptive dynamics – if  $dD/dx|_{x=x^*} < 0$ . If this inequality is reversed,  $x^*$  is a repellor, i.e. the trait  $x$  evolves to ever lower values if the initial trait of the population  $x_0$  is  $x_0 < x^*$ , and to ever higher values if  $x_0 > x^*$ .

Very interesting evolutionary dynamics can occur because convergence stability does not imply evolutionary stability. Generically, a convergent stable singular point  $x^*$  is either a

maximum or a minimum of the invasion fitness  $f_x(y)$  (S2, S3). If  $x^*$  is a maximum, i.e., if  $\partial^2 f_{x^*} / \partial y^2|_{y=x^*} < 0$ , then  $x^*$  is evolutionarily stable, i.e., it cannot be invaded by any mutant. If, however,  $x^*$  is a minimum, i.e., if  $\partial^2 f_{x^*} / \partial y^2|_{y=x^*} > 0$ , then a population that is monomorphic for  $x^*$  can be invaded by mutants with trait values on either side of  $x^*$ . In this case, the population first converges evolutionarily towards  $x^*$ , but subsequently splits into two distinct and diverging phenotypic clusters. This phenomenon is called evolutionary branching, and the singular point is called an evolutionary branching point.

## 1.1 Continuous Snowdrift Game

In the Continuous Snowdrift game, the quantitative trait  $x$  represents the level of cooperative investments. The growth rate of a rare mutant strategy  $y$  in a monomorphic resident  $x$  is determined by replicator dynamics (S4), and the invasion fitness of the rare mutant  $y$  is given by  $f_x(y) = P(y, x) - P(x, x)$ , where  $P(y, x)$  is the payoff of  $y$  playing against  $x$ , and  $P(x, x)$  is the payoff of  $x$  playing against itself. In the Continuous Snowdrift game the payoff is given by  $P(x, y) = B(x + y) - C(x)$  where  $B(x)$  and  $C(x)$  are the benefit and cost functions.

The adaptive dynamics of the continuous trait  $x$  is then given by  $\dot{x} = D(x) = B'(2x) - C'(x)$ , and singular strategies are solutions of  $B'(2x^*) = C'(x^*)$ . If a singular strategy  $x^*$  exists, it is convergent stable if  $dD/dx|_{x=x^*} = 2B''(2x^*) - C''(x^*) < 0$ , and it is evolutionarily unstable if  $\partial^2 f_{x^*} / \partial y^2|_{y=x^*} = B''(2x^*) - C''(x^*) > 0$ . Consequently,  $x^*$  is a branching point if  $2B''(2x^*) < C''(x^*) < B''(2x^*) < 0$ . Note that adaptive dynamics never maximizes the monomorphic population payoff given by  $B(2x) - C(x)$ , because maximizing this payoff would yield the gradient dynamics  $2B'(2x) - C'(x)$ , which is different from the adaptive dynamics given above.

### 1.1.1 Quadratic Cost and Benefit Functions

If the cost and benefit functions  $B(x)$  and  $C(x)$  are linear, the gradient  $D(x)$  is constant and the evolution of the trait  $x$  is always directional, either leading to ever higher or ever lower investments (except in the degenerate case where  $x$  is a neutral trait). However, richer dynamics are already observed for quadratic cost and benefit functions  $C(x) = c_2 x^2 + c_1 x$  and  $B(x) =$

$b_2x^2 + b_1x$ , for which the adaptive dynamics are given by  $\dot{x} = 4b_2x + b_1 - 2c_2x - c_1$ . The singular strategy (if it exists) is given by  $x^* = \frac{c_1 - b_1}{2(2b_2 - c_2)}$  and is convergent stable if  $2b_2 - c_2 < 0$  and evolutionarily stable if  $b_2 - c_2 < 0$ .

The existence of a positive  $x^*$  requires either (i)  $4b_2 - 2c_2 > c_1 - b_1 > 0$  or (ii)  $4b_2 - 2c_2 < c_1 - b_1 < 0$ . In the first case,  $x^*$  is always a repellor. Whether the repellor is evolutionarily stable or not is irrelevant as this state is never reached from generic initial conditions. In the second case  $x^*$  is always convergent stable. If, in addition,  $b_2 - c_2 < 0$ , then  $x^*$  is evolutionarily stable strategy (ESS). In this case, the population evolves towards the evolutionary end state  $x^*$  in which all individuals make intermediate cooperative investments. If, however,  $b_2 - c_2 > 0$ , then  $x^*$  is an evolutionary branching point, and after converging towards  $x^*$ , the population splits into two distinct and diverging phenotypic clusters.

### 1.1.2 Adaptive Dynamics after Branching

After evolutionary branching, the adaptive dynamics can be calculated based on the equilibrium frequencies of the two co-existing strategies  $x > x^* > y$  (where  $x^*$  is the branching point). According to traditional replicator dynamics (S4) the equilibrium frequency  $p^*$  of strategy  $x$  is the solution of  $p^*P(x, x) + (1 - p^*)P(x, y) = p^*P(y, x) + (1 - p^*)P(y, y)$ . With quadratic cost and benefit functions, this yields  $p^* = \frac{c_1 - b_1 + x(c_2 - b_2) + y(c_2 - 3b_2)}{2b_2(x - y)}$ . The invasion fitness of a mutant  $v$  with respect to the two resident branches  $x$  and  $y$  is then given by  $f_{x,y}(v) = p^*P(v, x) + (1 - p^*)P(v, y) - \bar{P}(x, y)$  where  $\bar{P}(x, y) = p^*P(x, x) + (1 - p^*)P(x, y) = p^*P(y, x) + (1 - p^*)P(y, y)$  denotes the average population payoff. Adaptive dynamics in the two branches is then given by  $\dot{x} = m_1(x, y) \frac{\partial f_{x,y}(v)}{\partial v} \Big|_{v=x}$  and  $\dot{y} = m_2(x, y) \frac{\partial f_{x,y}(v)}{\partial v} \Big|_{v=y}$ , respectively, where  $m_1(x, y) \propto p^*$  and  $m_2(x, y) \propto 1 - p^*$  are positive quantities describing the mutational process in the two branches (S2, S3). For the quadratic cost and benefit functions one finds  $\dot{x} = m_1(x, y)(b_2 - c_2)(x - y)$  and  $\dot{y} = -m_2(x, y)(b_2 - c_2)(x - y)$ . This implies that after branching, evolution is always directional and drives the trait values in the two branches to the boundaries of the strategy range. With more complicated cost and benefit functions, such as those used for Fig. 3 (see main text), analytical solutions for  $p^*$ , and hence for the 2-dimensional adaptive dynamics, can in general not be obtained.

### 1.1.3 Groups of $N$ Interacting Individuals

The Continuous Snowdrift can be generalized to groups of  $N > 2$  interacting individuals, in which the  $N$  individuals make cooperative investments  $x_1, \dots, x_N$  towards a common good. There are a number of ways in which this can be done, but perhaps the most straightforward approach is to assume that the payoff to the  $i$ -th player is  $\frac{1}{N}B(\sum_{j=1}^N x_j) - C(x_i)$ , reflecting the fact that the benefit accrued from the sum of the individual investments is equally shared among the  $N$  interacting players. In principle, the factor  $1/N$  can be incorporated into the benefit function, but explicitly retaining it facilitates comparison of results for different group sizes  $N$  (see below). The payoff of a mutant  $y$  in a monomorphic resident population with strategy  $x$  is  $P(y, x) = \frac{1}{N}B((N-1)x + y) - C(y)$ . Using similar arguments as above, this yields the adaptive dynamics  $\dot{x} = \frac{1}{N}B'(Nx) - C'(x)$ . Singular strategies  $x^*$  are now given as solutions of  $\frac{1}{N}B'(Nx^*) - C'(x^*) = 0$ . A singular strategy is convergent stable if  $B''(Nx^*) - C''(x^*) < 0$ , and it is evolutionarily stable if  $\frac{1}{N}B''(Nx^*) - C''(x^*) < 0$ . The condition for evolutionary branching becomes  $B''(Nx^*) < C''(x^*) < \frac{1}{N}B''(Nx^*) < 0$ .

With quadratic cost and benefit functions, the singular strategy for  $N$ -player games is thus given by  $x^* = \frac{c_1 - \frac{1}{N}b_1}{2(b_2 - c_2)}$ . In complete analogy to pairwise interactions, the existence of  $x^*$  requires either (i)  $2(b_2 - c_2) > c_1 - \frac{1}{N}b_1 > 0$  or (ii)  $2(b_2 - c_2) < c_1 - \frac{1}{N}b_1 < 0$ . In the first case,  $x^*$  is again a repellor. In the second case it is an ESS if  $b_2 - c_2 < 0$ , while  $x^*$  is an evolutionary branching point if  $b_2 < c_2 < \frac{1}{N}b_2 < 0$ . It follows that the range of parameters generating evolutionary branching increases with group size  $N$ .

## 2 Individual-Based Simulations

The analytical predictions derived from adaptive dynamics can be illustrated and verified through individual-based simulations of the Continuous Snowdrift game in finite populations of fixed size  $N_{\text{pop}}$  (S5). These simulations emulate replicator dynamics in populations in which individuals are characterized by their investment strategy  $x$ . The population is updated asynchronously by sequentially choosing a random focal individual  $x$  to be replaced by an offspring as follows. The payoff of the focal individual,  $P_x = P(x, z)$ , is determined through a single interaction

with a random member  $z$  of the population.  $P_x$  is then compared to the payoff of another randomly chosen individual  $y$ , whose payoff  $P_y$  is also obtained through a random interaction. With a probability  $w$  proportional to the payoff difference,  $w = (P_y - P_x)/\alpha$  (where  $\alpha = \max_{x,y,u,v} |P(x,y) - P(u,v)|$  ensures  $w \leq 1$ ), the offspring replacing the focal individual has  $y$  as parent; otherwise the parent is the focal individual itself (which is also the case if  $P_y < P_x$ ). The offspring inherits the parental strategy, except if a mutation occurs (which happens with probability  $\mu$ ), in which case the offspring strategy is drawn from a Gaussian distribution with the parental strategy as mean and a small standard deviation  $\sigma$ . This numerical scheme implements the deterministic replicator dynamics in the limit of large population sizes  $N_{\text{pop}}$  (S6). Our individual-based models of the Continuous Snowdrift game can be explored interactively at <http://www.univie.ac.at/virtuallabs>.

## References and Notes

- S1. U. Dieckmann, R. Law, *J. Math. Biol.* **34**, 579 (1996).
- S2. S. A. H. Geritz, E. Kisdi, G. Meszina, J. A. J. Metz, *Evol. Ecol.* **12**, 35 (1998).
- S3. J. A. J. Metz, S. A. H. Geritz, G. Meszina, F. J. A. Jacobs, J. S. van Heerwaarden, *Stochastic and Spatial Structures of Dynamical Systems*, S. J. van Strien, S. M. Verduyn Lunel, eds. (North Holland, Amsterdam, 1996), pp. 183–231.
- S4. J. Hofbauer, K. Sigmund, *Evolutionary Games and Population Dynamics* (Cambridge University Press, Cambridge, 1998).
- S5. C. Hauert, Virtuallabs: Interactive tutorials on evolutionary game theory, <http://www.univie.ac.at/virtuallabs> (2004).
- S6. C. Hauert, M. Doebeli, *Nature* **428**, 643 (2004).