

COMMENTARY

Limits of Hamilton's rule

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The evolution of cooperation is a fundamental problem in evolutionary biology. Over the last decades a wealth of models and mechanisms have been proposed for explaining how cooperators can thrive under Darwinian selection. At the same time, discussions of the conceptual connections between the different approaches have often been neglected. The synthesis proposed by Lehmann & Keller (2006) is therefore a welcome contribution to the literature on the evolution of cooperation. Their framework for understanding the evolution of cooperative traits is based on the fitness gradient. A particular mechanism is said to favour cooperation if it generates a positive fitness gradient towards higher values of the cooperative trait. The proposed framework is based on an extension of Hamilton's rule that is obtained by adjusting and reinterpreting costs, benefits and genetic relatedness. While such an approach may be useful in many circumstances, we would like to point out that if selection on cooperation is frequency-dependent, the classification given by Lehmann & Keller (2006) is not applicable in an interesting class of evolutionary scenarios.

When fitness gradients are determined entirely by processes that are not affected by the current state of the population, they remain constant as long as the environment stays the same, and hence evolution can only come to a halt due to exhaustion of genetic variation. However, when selection is frequency-dependent, fitness gradients depend on the current state of the population and hence change as the population evolves. In this case, the evolutionary dynamics generally converges to points in phenotype space where fitness gradients are zero. Such points are called singular points in the framework of adaptive dynamics (Dieckmann & Law, 1996; Metz *et al.*, 1996; Geritz *et al.*, 1998). After convergence to a singular point, the further development of the evolutionary process is determined by the second derivative of the fitness function (since the first derivative, i.e. the fitness gradient, is zero at the singular point). In particular, if the second derivative is positive, the singular point represents a fitness minimum, and evolutionary branching, that is, a splitting of the evolving population into two diverging phenotypic clusters, is a possible outcome. It has been shown that such conver-

gence to fitness minima and subsequent evolutionary branching is a generic outcome of frequency-dependent selection in many different types of models (e.g. Metz *et al.*, 1996; Geritz *et al.*, 1998; Doebeli & Dieckmann, 2000; Kisdi & Gyllenberg, 2005).

If evolutionary branching occurs in cooperative traits, this would imply that if the population is at the evolutionary branching point (i.e. at the singular point at which the fitness function has a minimum), mutants with both more cooperative and less cooperative traits can invade. Therefore, the classification suggested by Lehmann & Keller (2006) cannot be applied in such situations. Their classification applies to directional scenarios, in which a particular mechanism is either conducive to the evolution of cooperation, in which case more cooperative mutants can invade and less cooperative mutants cannot, or it is not conducive to cooperation, in which case more cooperative mutants cannot invade while less cooperative mutants can. In contrast, mechanisms that generate evolutionary branching are conducive to both more and less cooperation at the same time, and hence do not appear to be captured in the framework of Lehmann & Keller (2006).

To illustrate the evolutionary branching in cooperative traits, we present two examples from opposite ends of the spectrum of mechanisms envisaged by Lehmann & Keller (2006). In the first example, cooperative investments yield direct benefits to the cooperator, but there are no iterated interactions and no kin selection [this corresponds to the category 'direct benefits' in Table 3 of Lehmann & Keller (2006)]. In the second example there is only kin selection, but no direct benefits and no iterated interactions [corresponding to the category 'kin selection' in Table 3 of Lehmann & Keller (2006)].

The first example is taken from Doebeli *et al.* (2004). Consider a situation where cooperative investments x have costs, but yield a benefit to both the individual making the investment and to others it is interacting with. Then, when an individual with trait x plays against a y -individual, the payoff to x is $P(x,y) = B(x+y) - C(x)$, where B and C are monotonically increasing benefit and cost functions with $B(0) = C(0) = 0$. Thus, the payoff to x is the benefit obtained from the sum of the investments $x + y$, minus the cost of x , reflecting the fact that x not only benefits from the partner's investment y , but also from its own investment. The evolutionary dynamics of the trait x is determined by the selection gradient $D(x) = B'(2x) - C'(x)$ (Doebeli *et al.*, 2004) and the cooperative trait increases as long as $D(x) > 0$. It is important to note that this condition is formulated in terms of derivatives of the benefit and cost functions, and not in terms of the absolute payoff P . Thus, contrary to what seems to be implied in Lehmann & Keller (2006), whether individuals receive net direct benefits from the act of cooperation, i.e. positive payoffs P , is not the determinant of whether cooperation is favoured.

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Using the framework of adaptive dynamics for the continuous Snowdrift game, it can be shown analytically that for certain classes of nonlinear cost and benefit functions, the cooperative trait first converges to an intermediate singular point and then undergoes evolutionary branching because the attracting singular point is a fitness minimum. This is illustrated in Fig. 1. A detailed analysis of this model can be found in Doebeli *et al.* (2004). The point we want to make here is that when the population is at the evolutionary branching point, both higher investing mutants and lower investing mutants can invade, and hence there is selection for both more cooperation and less cooperation at the same time. Even though more cooperative behaviour is clearly favoured in this situation, it would be futile to say that any particular mechanism (e.g. the fact that the benefits of one's own investments outweigh costs) is responsible for the evolution of cooperation, because whatever the mechanism that generates selection for more cooperative behaviour, it is also the mechanism that selects for less cooperative behaviour. Thus, it is impossible to establish a one-to-one relationship between cause and effect with regard to the evolution of cooperation, and hence the classification proposed in Lehmann & Keller (2006) breaks down. One might argue that this is a special case due to the particular setup of the continuous Snowdrift game, in which sufficient nonlinearity of the cost and benefit functions

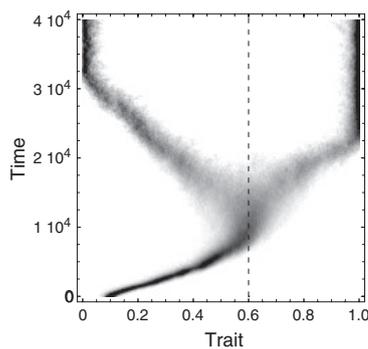


Fig. 1 Evolutionary branching of cooperative investment levels into two distinct phenotypic clusters of high and low investors in the continuous Snowdrift game with quadratic cost and benefit functions $C(x) = c_2x^2 + c_1x$ and $B(x) = b_2x^2 + b_1x$. The figure shows the time evolution of the trait distribution in individual based simulations. In the adaptive dynamics analysis, the fitness of a rare mutant y in a resident population x is given by $f_x(y) = P(y,x) - P(x,x)$. First, the system experiences directional selection following the selection gradient $D(x) = d/dy f_x(y)|_{y=x} = B'(2x) - C'(x)$ until it reaches a singular point at $x^* = (c_1 - b_1)/(4b_2 - 2c_2)$ (dashed vertical line), which is convergent stable, i.e. $dD(x)/dx|_{x=x^*} = 2B''(2x^*) - C''(x^*) < 0$. As x^* represents a fitness minimum [$d^2/dy^2 f_x(y)|_{y=x^*} = B''(2x^*) - C''(x^*) > 0$] the system undergoes evolutionary branching, and two distinct phenotypic clusters of high and low investors emerge. Parameters: $b_2 = -1.4$, $b_1 = 6$, $c_2 = -1.6$, $c_1 = 4.56$, population size 10 000, Gaussian mutations with probability 0.01 and standard deviation 0.005. The results can be verified using the VirtualLabs (Hauert, 2005).

is built in to yield evolutionary branching points. However, the next example shows that the same type of situation can occur in scenarios in which benefits and costs are linear, and in which - according to the framework of Lehmann & Keller (2006) - the only possible mechanism facilitating the evolution of cooperation is kin selection.

The starting point for the second example is similar to the previous one, but we now assume that cooperative investments do not confer a benefit to the cooperating individual. Accordingly, the payoff to x when playing against y is $P(x,y) = B(y) - C(x)$, i.e. equal to the benefit accrued to the partner's investment minus the cost due to the own investment. This is a continuous version of the Prisoner's Dilemma game (Killingback *et al.*, 1999). Because investments only affect costs of the investing individual, but not benefits, it is clear that in well-mixed populations with random interactions, the trait x always evolves to zero. Things turn out to be different in spatially structured populations (C. Hauert & M. Doebeli, unpublished data), in which individuals occupy sites of a lattice and interact only with individuals occupying neighbouring sites. It is well known that such spatial structure can promote cooperation (Nowak & May, 1992; Killingback *et al.*, 1999; Hauert, 2002; but see Hauert & Doebeli, 2004), essentially because spatial structure can lead to positive assortment between cooperators (Fletcher and Doebeli, this volume). This effect is classified under kin selection by Lehmann & Keller (2006).

Interestingly, even with linear cost and benefit functions B and C , the spatial continuous Prisoner's Dilemma can exhibit evolutionary branching. Figure 2 illustrates scenarios in which the population splits into multiple phenotypic clusters with cooperative types making high investments and defecting types making very low investments. As there are no direct benefits resulting from an individual's own investment, and as there are no iterated interactions, kin selection is the only mechanism among those classified by Lehmann & Keller (2006) that could be responsible for the fact that more cooperative mutants can invade. However, the fact that kin selection favours cooperation is contradicted by the fact that less cooperative mutants can also invade; or put the other way around, as less cooperation is favoured selectively, Hamilton's rule should not be satisfied, which contradicts the fact that more cooperative mutants can invade. Thus, again, describing evolutionary branching in terms of the classification in Lehmann & Keller (2006) does not seem feasible.

The considerations illustrated by these two examples would not carry much weight if convergence to fitness minima were an unlikely evolutionary scenario. This is not the case in general, as many different types of evolutionary models yield this type of dynamics for at least part of parameter space (Doebeli & Dieckmann, 2000; Kisdi & Gyllenberg, 2005), and the examples described above show that evolutionary branching is also a robust outcome in models for the evolution of

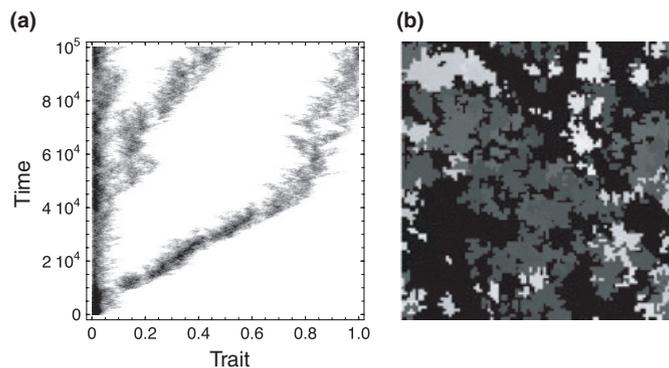


Fig. 2 Spatial Prisoner's Dilemma game with continuously varying investment levels and linear cost and benefit functions, $C(x) = cx$ and $B(y) = by$. The individuals are arranged on a square lattice and interact with their four nearest neighbours to the north, east, south and west. (a) Evolution of the phenotypic traits when starting with an initial population with low levels of cooperative investments. After 10^5 generations, three distinct phenotypic clusters co-exist corresponding to low, intermediate and high investors. (b) Depicts the lattice configuration at the end of the simulation run. The shades of grey indicate the investment levels ranging from black (low investments) to white (high investments). Parameters: $b = 1.11$, $c = 0.11$, population size 100×100 , Gaussian mutations with probability 0.01 and standard deviation 0.005. The results can be verified using the VirtualLabs (Hauert, 2005).

cooperation in which cooperation is given by a quantitative trait (Koella, 2000; C. Hauert & M. Doebeli, unpublished data). The general framework proposed by Lehmann & Keller (2006) may apply to evolutionary scenarios in which selection is directional. But if selection is frequency-dependent, evolutionary dynamics generically converge to points where the selection gradient vanishes, and hence where selection ceases to be directional. Such points may be evolutionary branching points and thus need not be the endpoint of the evolutionary process. This occurs if frequency dependence generates disruptive selection. As the framework of Lehmann & Keller (2006) does not explicitly include cases where selection is frequency-dependent, it is difficult to assess in general to what extent this framework extends to such scenarios. The examples provided here show that there are at least some circumstances where such an extension is impossible. There is no doubt that Hamilton's rule and its extensions, most notably the one derived by Queller (1985), are a very useful conceptual framework for understanding many aspects of the evolution of cooperation (see Fletcher and Doebeli, this volume). However, these rules can only be used when selection is directional, and even then they can typically be used only to predict evolution over the next time step. In the long run, evolution naturally tends to annihilate fitness gradients, and Hamilton's rule seems to be insufficient to capture evolutionary dynamics ensuing for vanishing fitness gradients, such as diversification in cooperative investment levels.

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