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Hamilton's rule

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Moshe Hoffman^{2,5,6}, Burton Simon⁷, and Carl Veller^{2,8}.

This paper reviews and addresses a variety of issues relating to inclusive fitness. The main question is: are there limits to the generality of inclusive fitness, and if so, what are the perimeters of the domain within which inclusive fitness works? This question is addressed using two well known tools from evolutionary theory: the replicator dynamics, and adaptive dynamics. Both are combined with population structure. How generally Hamilton's rule applies depends on how costs and benefits are defined. We therefore consider costs and benefits following from Karlin & Matessi's (1983) "counterfactual method", and costs and benefits as defined by the "regression method" (Gardner et al., 2011). With the latter definition of costs and benefits, Hamilton's rule always indicates the direction of selection correctly, and with the former it does not. How these two definitions can meaningfully be interpreted is also discussed. We also consider cases where the qualitative claim that relatedness fosters cooperation holds, even if Hamilton's rule as a quantitative prediction does not.

We furthermore find out what the relation is between Hamilton's rule and Fisher's Fundamental Theorem of Natural Selection. We also consider cancellation effects – which is the most important deepening of our understanding of when altruism is selected for. Finally we also explore the remarkable (im)possibilities for empirical testing with either definition of costs and benefits in Hamilton's rule.

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