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Group selection, kin selection, altruism and cooperation: When inclusive fitness is right and when it can be wrong

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ABSTRACT

Group selection theory has a history of controversy. After a period of being in disrepute, models of group selection have regained some ground, but not without a renewed debate over their importance as a theoretical tool. In this paper I offer a simple framework for models of the evolution of altruism and cooperation that allows us to see how and to what extent both a classification with and one without group selection terminology are insightful ways of looking at the same models. Apart from this dualistic view, this paper contains a result that states that inclusive fitness correctly predicts the direction of selection for one class of models, represented by linear public goods games. Equally important is that this result has a flip side: there is a more general, but still very realistic class of models, including models with synergies, for which it is *not* possible to summarize their predictions on the basis of an evaluation of inclusive fitness.

1. Introduction

It is safe to say that there is no consensus concerning the value of group selection models for the explanation of the evolution of altruism and cooperation. A history of disagreement has made the question evolve from whether group selection is probable or even possible (Allee, 1951; Wynne-Edwards, 1962; Williams, 1966) to whether group selection models help us understand things one would not understand without them (Sober and Wilson, 1998; Wilson and Wilson, 2007; Traulsen and Nowak, 2006; Lehmann et al., 2007; Killingback et al., 2006; Grafen, 2007; West et al. 2007a, b, 2008). In order to show that different views need not be incompatible, I will begin with a simple but very general framework for models of the evolution of altruism and cooperation. This general framework allows us to see how and to what extent both an approach with and an approach without group selection terminology are insightful ways of looking at the same models. It also allows for a formal proof of a theorem that states that the sign of the inclusive fitness determines the direction of selection, if the model translates to a linear public goods game. The requirement of linearity turns out to a necessity; a simple example is given of a non-linear public goods game for which inclusive fitness points in the wrong direction. While a two-player situation still allows for (adjusted) formula's that do use relatedness, a slightly less simple example shows that with groups larger than two, relatedness can be the wrong population characteristic to look at. This implies that the prediction of the model cannot be given in a formula with costs, benefits and relatedness only.

There are at least three reasons why this formalism is useful. First of all it gives a formal framework for a dualistic view. This can help avoid unnecessary disagreements and helps bring out the value of both views. Second, although the first counterexample for Hamilton's rule failing is not new (see for similar counterexamples Wenseleers, 2006; Gardner et al., 2007, which in turn relate to work by Grafen, 1979; Day and Taylor, 1998), we should realize that the results in the literature concern 2-player games. When we think of group selection, we tend to think of groups of any size, not just size 2. Also when we for instance think of the transition from single-celled to multicellular life, we tend to think of multicellular life as organisms typically consisting of more than two cells. An extension from groups of 2 to groups of n—or from 2-player to n-player games—and a formal proof for when Hamilton's rule does and when it does not work therefore are quite useful here. Because this goes against the intuition provided in Hamilton (1975) for why inclusive fitness should work, this paper also provides an intuition for why it only does so for models that translate to linear public goods games, and not for models that translate to non-linear ones. The proof of the theorem also provides a general recipe for determining the direction of selection if Hamilton's rule fails due to non-linearity in the public goods game.

The third reason why this formalism is useful is at first perhaps a bit more difficult to see. In the literature, relatedness is regularly defined as a statistical property. In modelling, this would in

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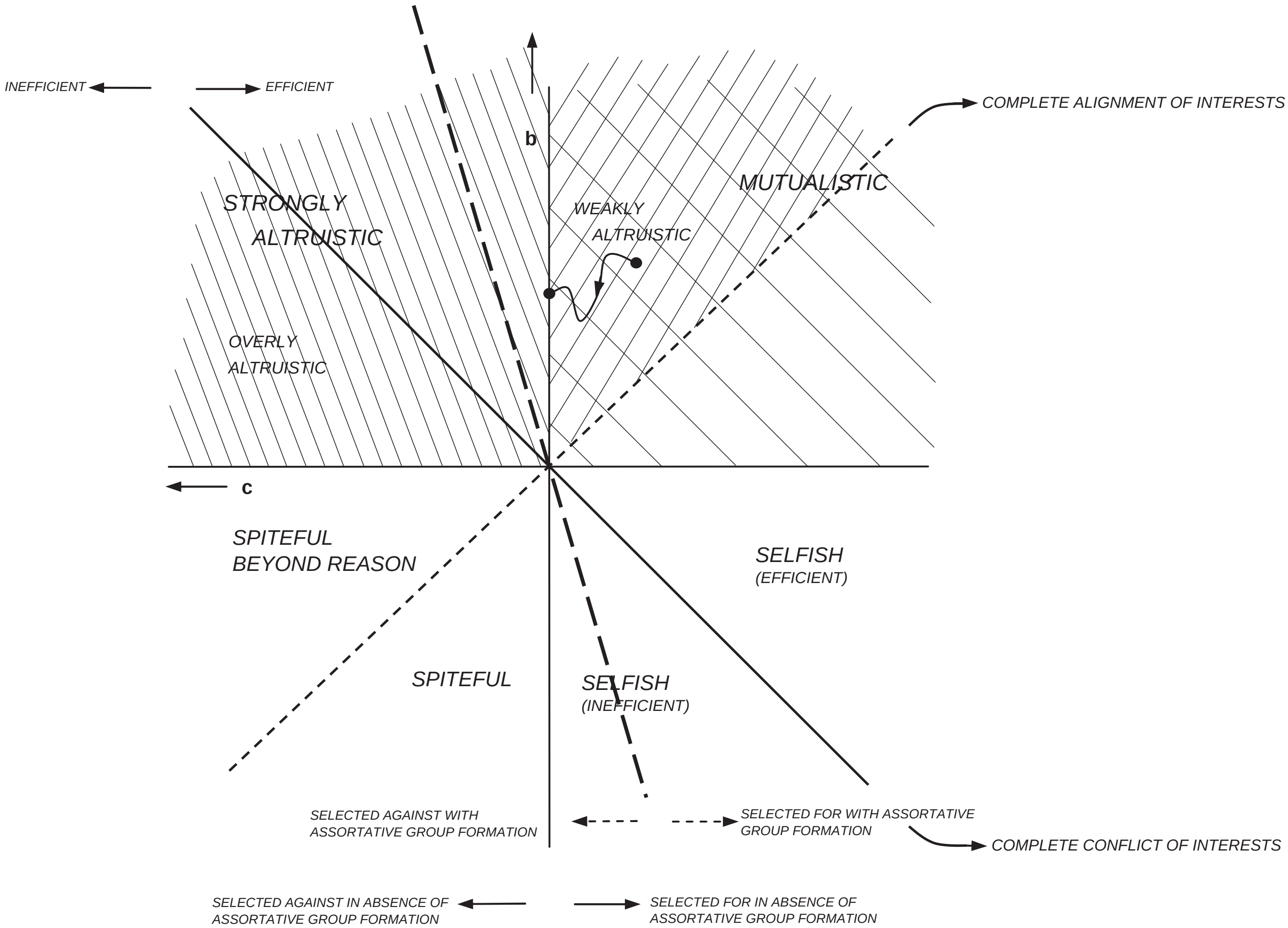

Fig. 1. Fitness effects are represented by net costs **c** to the acting individual on the horizontal axis and aggregate benefits to the other group members **b** on the vertical axis. Please note that net costs to the acting individual are positive to the left and negative to the right, so that the first quadrant consists of traits that have a positive fitness effect both on the acting individual itself and on the other group members.

principle be inappropriate; in a theoretical model, relatedness should be a probabilistic property, while statistics is only involved in testing of models or estimation of parameters using actual data. In the formal setup here, relatedness is a proper difference in conditional probabilities that is to follow from model assumptions. It fortunately does match with what we think relatedness should be in most models, and therefore one could see it as a formal justification for those cases. The formal setup on the other hand also helps understand why in some models with groups larger than 2 relatedness is the wrong population characteristic to look at. It thereby helps us formalize and sharpen our interpretation of relatedness.

2. Public goods games

Public goods games can be seen as the mother of all cooperation models.[1] Therefore it is useful to first properly define and picture how different situations in which selection takes place translate to different public goods games. In a selection process concerning a trait that has an effect on the carrier itself as well as on other members of the group it is in, we can write these effects as payoffs in a game. If the effects of different group members having the trait simply add up, then this results in a linear public goods game, in which the payoffs, or (expected) numbers of offspring, can be described as follows. In a group that consists of n individuals, i of which have the trait, payoffs for bearers (T) and for non-bearers (N) of the trait are, respectively,

$$\begin{cases} \pi(T,i,f) = 1 + b(f)\cdot i - c(f) \\ \pi(N,i,f) = 1 + b(f)\cdot i \end{cases} \tag{1}$$

Here, $f \in [0,1]$ represents the frequency of the trait in the entire population. This description matches models in for instance Hamilton (1975), Nunney (1985) and Wilson and Dugatkin (1997) and is only a little more general in that it allows for $b(f)$ and $c(f)$ to depend on the frequency of the trait in the entire population. One could also make them depend on other overall population characteristics without changing the analysis. The restriction that (1) imposes on the payoff function π can also be seen as a natural generalization of "equal gains from switching" as used in Traulsen et al. (2008), Wild and Traulsen (2007) and defined in Nowak and Sigmund (1990); see also Section 5 for a discussion.

Fig. 1 graphically describes behaviours for this class of models. This figure is perhaps not that easy to read at first, but I firmly believe it is very much worth the effort, as it embraces a wide variety of models.

[1] In an e-mail discussion group on the topic of multilevel selection theory, Michael Doebeli described public goods games as the mother of all cooperation models. I thought that was a nice description, so I borrowed it here.