

An apology for inclusive fitness

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In the last half-century, social evolution emerged as a flourishing field that has profound impacts across biology and social sciences. Yet the field at times seems overburdened with conceptual turmoil, as evidenced by recent broadsides exchanged over the generality of inclusive fitness and Hamilton's rule (Nowak et al., 2010; Abbot et al., 2011; Rousset and Lion, 2011). Perhaps due to this turbulent state of the field, there have been fewer attempts than one might expect for a book-length treatment of inclusive fitness theory that provides a self-contained introduction. Steve Frank's classic *Foundations of Social Evolution* (Frank, 1998) is the only example I can think of, and it is now approaching its 20th anniversary (though it has aged well). There are also at least a couple of good texts aiming to provide accessible guides to the mathematical toolbox used in social evolution (McElreath and Boyd, 2008; Kokko, 2007), but these books are mainly focused on mathematical tools, rather than the theory itself. Then there is François Rousset's *Genetic Structure and Selection in Subdivided Populations*, which is a great resource for population genetic modeling in viscous populations, but it is focused on that particular type of approach, and perhaps is somewhat dense to be a true introduction.

Against this background, Marshall sets out to provide a short, self-contained, and accessible introduction to inclusive fitness theory in the context of the contemporary debate about its status. And he largely succeeds: Chapters 2 through 7 of the book introduce the basic concepts and results in a clear and logical sequence that anyone with a basic background in evolutionary biology and elementary mathematics should be able to follow. There are many ways to derive Hamilton's rule or construct inclusive fitness; Marshall opts for (to me) the clearest way, using quantitative genetics and the Price equation. Chapters 2 and 3 are succinct introductions to the basic tools that stay with us for the rest of the book: the replicator dynamics, the additive¹ and non-additive donation games, and most importantly the Price

¹additive interactions are games where the fitness of an individual can be expressed as a sum of

equation. In Chapter 4, we finally meet Hamilton's rule itself, derived using the Price equation (for additive interactions). The subsequent three chapters then take up various wrinkles that appear when one goes beyond the symmetric, additive, unconditional behavior model. I especially found useful the discussion of the different versions of Hamilton's rule at genotype and phenotype levels (Chapter 7), because it reminds us that there is more than one valid way to express selection due to fitness consequences of different phenotypes, all while staying within the inclusive fitness framework. Although it comes in the "philosophical" part of the book as Marshall puts it in the introduction, Chapter 9 really is also concerned with the basics of the theory, concisely dealing with issues of class structure, reproductive value, and the definition of fitness in structured populations (which requires accounting for local competition with kin, etc.).

All of this is presented clearly and it would have made a great introduction to social evolution, but for two caveats. The first caveat is that most mathematical derivations, even pretty simple and central ones, are relegated to footnotes, typeset very small, at the end of the book. This is probably done to save space and avoid scaring away the less mathematically inclined readers, but it is very inconvenient for a reader who wants to really understand where the results come from. For example, given the centrality of Price equation to the book, I would have expected to find its derivation in the main text.

The other concern is about the intent of the book, which is more or less openly partisan. Marshall not only wants to teach inclusive fitness theory, but also to "celebrate the generality" of the theory or "address misunderstandings" of others who disagree with the said generality. Indeed, at times he seems more interested in settling scores with critics than giving a neutral presentation of the theory first. For example, he breaks off the first-ever derivation of Hamilton's rule in the book to specifically refute a recent paper (Allen et al., 2013) about causation and correlation. Likewise, Chapter 4 ends with a section titled "Perceived limitations of inclusive fitness theory," which not surprisingly contains a rebuttal to the alleged limitations. But the rebuttal feels premature, because much of the debate is over what happens in non-additive interactions, which are not discussed until the next chapter. There are passages like this throughout the book that I found distracting even if I agree with some the specific points raised. I suspect these passages will be popular with readers who already are convinced by Marshall's positions, but to my mind the apologetic (in the original meaning of the word) tone of the book reduces its effectiveness as an introduction to the topic.

Perhaps not coincidentally, I found the discussion of the philosophical issues (mainly, Chapter 8) about inclusive fitness to be the weakest part of the book. For example, in section 8.2 Marshall argues that inclusive fitness should be favored amongst other mathematically equivalent approaches to representing social evolu-

the effects of own genotype and those of others; non-additive interactions cannot be expressed as such sums.

tion because it captures causality better than the alternatives. Marshall's argument relies on how to interpret heritability coefficients, i.e., the regression coefficients of individual genotypes on the phenotype of that individual and those of its social partners. Both neighbor-modulated and inclusive fitness formulations involve regressions of genotypes of one set of individuals on the phenotypes of another. Marshall asserts that the inclusive fitness version (where the regression runs from a focal individual to the social partner) makes "more biological sense", but gives no principled reasons for why. In contrast, I would argue that neighbor-modulated formulation is the most direct representation of the actual selective process. In this formulation, one simply keeps track of average fitness experienced by individuals as a result of their interactions with others and the actual physical transmission of genotypes through the focal individual.

Later in Chapter 8, Marshall takes up the question of whether individuals behave as if to maximize their inclusive fitness, which is a perennial debate predating Hamilton, going back to Fisher and Wright. Marshall gives an accurate account of existing results, but at the end of this section, I was left unclear what his answer to the question is. It is well known in population genetics that except for additive fitness, there is no guarantee in general that selection will reach the maximum of any fitness function. Accordingly, Marshall stops short of claiming that inclusive fitness is unconditionally maximized. He also points out that the most sustained effort to provide formal underpinnings for fitness maximization, Grafen's "Formal Darwinism Project" (Grafen, 2002, 2009), did not advance beyond additive interactions so far. Yet, Marshall still suggests that a general maximization principle could be obtained if only Grafen's results were somehow extended. At this point I would say this is a false hope given both classic and recent results (e.g. Lehmann et al., 2015).

The book closes with a discussion of the empirical evidence for inclusive fitness, where Marshall concisely reviews a select set of empirical issues, including the "monogamy hypothesis" for the evolution of eusociality that replaced the old "haplodiploidy hypothesis." Marshall concludes, not surprisingly, that the empirical evidence supports inclusive fitness. It is undeniable that inclusive fitness has been an enormous driving force of empirical research and discovery. Inclusive fitness theory certainly deserves credit for these discoveries, but I find claims of exclusive support for inclusive fitness hard to agree with, given that (as Marshall also emphasizes in various places in the book) it is equivalent to other theoretical frameworks such as multi-level selection.

To sum up, I think *Social Evolution and Inclusive Fitness Theory* is a good book to pick up if you want to get a self-contained introduction to modern social evolution theory and do not mind frequently flipping back and forth between the footnotes and the text. You will get a good idea of what all the fuss is about. But you also need a few grains of salt to take with some of the passages that defend (or celebrate) the generality of inclusive fitness and its philosophical status. These passages are not

without interest but I doubt that they will “convert” many people. Regardless, I do not imagine that this book will be the last word on that subject.

References

- Abbot, P., J. Abe, J. Alcock, S. Alizon, J. A. Alpedrinha, M. Andersson, J.-B. Andre, M. van Baalen, F. Balloux, S. Balshine, et al. 2011. Inclusive fitness theory and eusociality. *Nature* 471:E1–E4.
- Allen, B., M. A. Nowak, and E. O. Wilson. 2013. Limitations of inclusive fitness. *Proceedings of the National Academy of Sciences* 110:20135–20139.
- Frank, S. 1998. *Foundations of Social Evolution*. Princeton Univ Press, Princeton.
- Grafen, A. 2002. A first formal link between the price equation and an optimization program. *Journal of Theoretical Biology* 217:75–91.
- . 2009. Formalizing Darwinism and inclusive fitness theory. *Phil. Trans. R. Soc. B* 364:3135–41. doi:10.1098/rstb.2009.0056.
- Kokko, H. 2007. *Modelling for field biologists and other interesting people*. Cambridge University Press.
- Lehmann, L., I. Alger, and J. Weibull. 2015. Does evolution lead to maximizing behavior? *Evolution* doi:10.1111/evo.12701.
- Marshall, J. A. R. 2015. *Social Evolution and Inclusive Fitness Theory: An Introduction*. Princeton University Press.
- McElreath, R., and R. Boyd. 2008. *Mathematical models of social evolution: A guide for the perplexed*. University of Chicago Press.
- Nowak, M. A., C. E. Tarnita, and E. O. Wilson. 2010. The evolution of eusociality. *Nature* 466:1057–1062. doi:10.1038/nature09205.
- Rousset, F. 2004. *Genetic Structure and Selection in Subdivided Populations*. Princeton University Press, Princeton.
- Rousset, F., and S. Lion. 2011. Much ado about nothing: Nowak et al.’s charge against inclusive fitness theory. *Journal of evolutionary biology* 24:1386–1392.