Introduction

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Inclusive fitness: 50 years on

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1. Introduction

The cardinal problem of evolutionary biology is to explain adaptation, or the appearance of design in the living world [1,2]. Darwin [3] convincingly argued that the process of adaptation is driven by natural selection: those heritable variations—i.e. genes—that are associated with greater individual reproductive success are those that will tend to accumulate in natural populations. To the extent that the individual's genes are causally responsible for her improved fitness, natural selection leads to the individual appearing designed as if to maximize her fitness. Thus, Darwinism is a theory of both the process and the purpose of adaptation.

However, correlations between an individual's genes and her fitness need not reflect a direct, causal relationship. For example, genes for altruism can be associated with greater fitness, despite the direct cost that they inflict on their bearer, if relatives interact as social partners. This is because an individual who carries genes for altruism will tend to have more altruistic social partners. That altruism can be favoured by natural selection suggests that the purpose of adaptation is not, in general, to maximize the individual's personal fitness [4].

Although Darwin [3] recognized the potential for such indirect effects to drive the evolution of social behaviours, discussing the logic of kin selection theory in connection with the adaptations of sterile insect workers, it was William D. Hamilton (figure 1), more than a century later, who developed these insights into a full mathematical theory. By quantifying the relative strengths of direct selection, acting via the individual's own reproduction, and indirect selection, acting via the reproduction of the individual's relatives, Hamilton [4] revealed the ultimate criterion that natural selection uses to judge the fate of genes.

Hamilton's rule states that any trait—altruistic or otherwise—will be favoured by natural selection if and only if the sum of its direct and indirect fitness effects exceeds zero [4–7]. That is $-c + \sum_i b_i r_i > 0$, where $-c$ is the impact that the trait has on the individual's own reproductive success, b_i is its impact on the reproductive success of the individual's ith social partner and r_i is the genetic relatedness of the two individuals. This mathematical partition of fitness effects underpins the kin selection approach to evolutionary biology [8]. The general principle is that with regards to social behaviours, natural selection is mediated by any positive or negative consequences for recipients, according to their genetic relatedness to the actor. Consequently, individuals should show greater selfish restraint, and can even behave altruistically, when interacting with closer relatives [4].

Having clarified the process of social adaptation, Hamilton [4] revealed its true purpose: to maximize *inclusive fitness* (figure 2). That is, Darwinian individuals should strive to maximize the sum of the fitness effects that they have on all their relatives (including themselves), each increment or decrement being weighted by their genetic relatedness. This is the most fundamental revision that has been made to the logic of Darwinism and—aside from a possibly apocryphal quip attributed to J. B. S. Haldane, to the effect that he would give his life to save the lives of two brothers or eight cousins—it was wholly original to Hamilton.

Since its inception 50 years ago, inclusive fitness theory has grown to become one of the most successful approaches in evolutionary biology. In addition to igniting an explosive interest in altruistic behaviour, it also energized the investigation of many other social traits (table 1). In all its
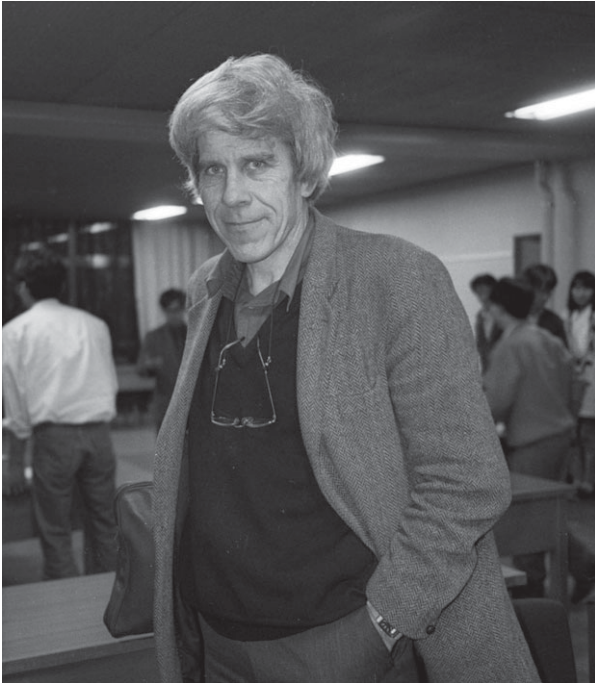
Figure 1. William D. Hamilton (1936–2000). Copyright: Tokyo Zoological Park Society.

Figure 2. Inclusive fitness comprises the effects that the actor has on her own reproductive success and the reproductive success of her relatives (solid arrows), but not the effects that her relatives have on her reproductive success or on their own reproductive success (dashed arrows). If an action incurs a direct fitness cost of c to the actor's own fitness, and provides an indirect fitness benefit of b to her social partner, then natural selection favours that action if $rb - c > 0$, where r is the genetic relatedness of the two individuals [4].

applications, the usefulness of inclusive fitness theory, and its encapsulation in Hamilton's rule, lies in how it provides a simple conceptual framework that can be applied with relative ease to a wide range of scenarios, successfully translating between the dynamical process of natural selection and the design objective of Darwinian adaptation, on paper, in the laboratory and in the field [9–11].

In addition to its traditional focus upon individual organisms, inclusive fitness theory has been applied equally successfully to explain social interactions between genes, illuminating the evolution of selfish genetic elements and genomic imprinting [12,13]. Indeed, by translating between—and characterizing conflicts of interest within—different levels of biological organization, inclusive fitness theory provides a framework for understanding major transitions in individuality (table 2; [14]).

Clearly, inclusive fitness is not a single hypothesis, but rather represents an entire programme of research. Scientific hypotheses are judged according to how amenable they are for empirical testing and how well they resist attempts at empirical falsification. By contrast, scientific research programmes are judged according to how well they facilitate the formulation and testing of hypotheses—that is, stimulating the interplay between theory and empiricism that drives progress in scientific understanding. For example, inclusive fitness theory has yielded a number of hypotheses concerning the factors driving the evolution of insect eusociality, including the 'haplodiploidy hypothesis' [4,18] and the 'monogamy hypothesis' [19–21]. The former hypothesis has not withstood detailed theoretical and empirical scrutiny, whereas the latter goes from strength to strength [19–25]. This is exactly what we expect of a productive research programme.

In order to better assess the health of inclusive fitness theory on its 50th anniversary, here we showcase research showing the research programme in action, from the extremely pure, mathematical realm, through basic empirical science, to bold applications in a variety of disciplines.
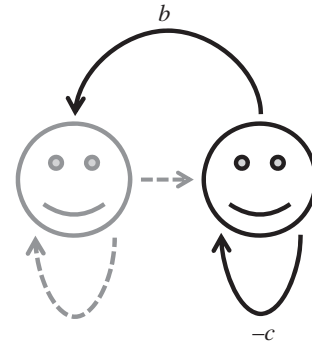
The first three papers of this theme issue explore the connections between inclusive fitness and the classical foundations of evolutionary theory, with Laurent Lehmann and François Rousset focusing upon population genetics, Allen Moore and co-workers focusing upon quantitative genetics, and David Queller revisiting the central mathematical result of Darwinian theory—Fisher's fundamental theorem of natural selection—from a social evolutionary perspective. These contributions are followed by an exploration of alternative mathematical approaches to inclusive fitness, with Peter Taylor and Wes Maciejewski considering social evolution in structured populations from a graph-theoretic angle and Hisashi Ohtsuki developing connections with game theory.

Moving on to specific biological questions, Geoff Wild and Cody Koykka explore the evolution of cooperative breeding from a theoretical perspective, whereas Andrew Bourke and Ben Hatchwell and co-workers take the stock of the empirical successes of inclusive fitness theory on this front, illustrating comparative and focused field approaches, respectively. Descending to the level of the gene, Ben Normark and Laura Ross investigate the role for inclusive fitness conflicts to drive the evolution of genetic systems.

This basic research is then followed by more applied uses of inclusive fitness theory. Helen Leggett and co-workers explore the insights that inclusive fitness theory yields for infectious disease, and Bernard Crespi and co-workers broaden out this exploration to consider non-infectious disease and 'Hamiltonian medicine', in general. We close the theme issue with Toby Kiers and Ford Denison's exploration of applications of inclusive fitness theory to agriculture, and Thom Scott-Phillips and co-workers on its application to understanding human culture.

These contributions confirm that inclusive fitness theory is in excellent shape. It still dominates the study of social interactions in behavioural ecology, and continues to break new ground in other disciplines. This is a testament not only to the generality and flexibility of the theory, but also to the efforts of its practitioners, including both theoreticians who maintain a firm grasp on the natural world and empiricists who keep a close eye on the latest theoretical developments. Hamilton was one of those rare individuals

Table 1. Some example areas where inclusive fitness theory has facilitated insights and understanding. Inclusive fitness theory is not the only way to model evolution, but it has proved to be an immensely productive and useful approach for studying social behaviours [9 – 17].

research areas
adoption, alarm calls, altruism, cannibalism, conflict resolution, cooperation, dispersal, division of labour, eusociality, kin discrimination, genomic imprinting, multicellularity, mutualism, parasite virulence, parent – offspring conflict, policing, selfish genetic elements, sex allocation, sibling conflict, spite, suicide and symbiosis.

who effortlessly combined theory with forays into the field, but most of the rest of us who specialize one way or the other need to communicate and collaborate to achieve the requisite interplay of theory and empiricism. Science is

Table 2. The major transitions in individuality, according to Bourke [14].

major transition in individuality	details
prokaryotic cell	separate replicators (genes) → cell enclosing genome
eukaryotic cell	separate unicells → symbiotic unicell
sexual reproduction	asexual unicells → sexual unicell
multicellularity	unicells → multicellular organism
eusociality	multicellular organisms → eusocial society
interspecific mutualism	separate species → interspecific mutualism

a social enterprise, so it may be unsurprising that inclusive fitness theory epitomizes the successful scientific research programme. The next 50 years promise to be very exciting.

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