

Review

The validity and value of inclusive fitness theory

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Social evolution is a central topic in evolutionary biology, with the evolution of eusociality (societies with altruistic, non-reproductive helpers) representing a long-standing evolutionary conundrum. Recent critiques have questioned the validity of the leading theory for explaining social evolution and eusociality, namely inclusive fitness (kin selection) theory. I review recent and past literature to argue that these critiques do not succeed. Inclusive fitness theory has added fundamental insights to natural selection theory. These are the realization that selection on a gene for social behaviour depends on its effects on co-bearers, the explanation of social behaviours as unlike as altruism and selfishness using the same underlying parameters, and the explanation of within-group conflict in terms of non-coinciding inclusive fitness optima. A proposed alternative theory for eusocial evolution assumes mistakenly that workers' interests are subordinate to the queen's, contains no new elements and fails to make novel predictions. The haplodiploidy hypothesis has yet to be rigorously tested and positive relatedness within diploid eusocial societies supports inclusive fitness theory. The theory has made unique, falsifiable predictions that have been confirmed, and its evidence base is extensive and robust. Hence, inclusive fitness theory deserves to keep its position as the leading theory for social evolution.

Keywords: altruism; eusociality; inclusive fitness; kin selection; relatedness; social evolution

1. INTRODUCTION

Why should cooperation exist in a world of Darwinian competition? Answering this question is one of the great tasks of evolutionary biology. In particular, evolutionary biologists have sought to explain the puzzling existence of eusocial societies. In these, typified by the colonies of eusocial Hymenoptera (ants, bees and wasps) or of termites, some members (workers) are partially or completely sterile and labour altruistically on behalf of their reproductive nest-mates (queens). The problem has been to explain how natural selection, a process based on reproductive success, can bring about societies founded on altruism.

The leading theory in the study of social evolution and eusociality is Hamilton's [1] inclusive fitness theory, also known as kin selection theory. The formal version of inclusive fitness theory is summarized by Hamilton's rule (box 1). Informally, the theory shows that, other things equal, individuals should behave towards others as if they valued their reproduction in proportion to how related they are. Hence the theory shows that altruism can evolve between relatives, because a gene for altruism, by directing aid at individuals likely to bear the same gene, adds extra copies of itself to the population despite the reduced offspring production of its bearer (box 1). Hamilton's rule can be easily modified to apply to non-cooperative forms of social behaviour (box 1). Accordingly, inclusive fitness theory has proved extraordinarily rich, having been used to explain social phenomena in everything from microbes to people (e.g.

[6,7]). Moreover, the theory transformed the study of behavioural ecology and evolutionary biology by leading to the gene's-eye or 'selfish gene' interpretation of natural selection [8]. Inclusive fitness theory therefore stands as one of the central pillars of modern evolutionary biology. However, like any theory with fundamental claims, it has attracted criticism. Early misunderstandings of the theory were addressed by a number of authors (e.g. [2,9,10]). Nonetheless, subsequently there have been renewed criticisms of the theory. These can conveniently be divided into three sets.

First, studies have presented models of social evolution that, it is argued, represent novel alternatives to inclusive fitness theory (e.g. [11–15]). However, other analyses have challenged the novelty of these models by showing that their results can be derived from inclusive fitness theory itself [3,4,16–20]. Second, a group of authors has criticized both the conceptual robustness of inclusive fitness theory and its empirical applications, especially in the eusocial insects [21–30]. In turn, several responses have argued that these critiques are without foundation and that inclusive fitness theory remains empirically illuminating [5,31–37]. Third, Nowak *et al.* [38] recently produced a comprehensive critique of inclusive fitness theory that questioned its mathematical basis as well as its explanatory value across all taxa. If the analysis of these authors is correct, then inclusive fitness theory has been a decades-long distraction in the field that is theoretically unsound, unnecessarily focused on genetic relatedness and poorly supported by the empirical evidence. If it is not correct, then the theory has been on the right lines all along and it is the critiques that are shaky. The critique by Nowak *et al.* [38] has met

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with both support [39–41] and rebuttal [42–50]. In a response, Nowak *et al.* [51] maintained their view that ‘Inclusive fitness theory is neither useful nor necessary to explain the evolution of eusociality or other phenomena’.

Box 1. Hamilton’s rule.

Inclusive fitness theory can be summarized by Hamilton’s rule, which states that a gene for any social behaviour is favoured by natural selection if the sum of rb and c exceeds zero, where c and b are the lifetime changes in the direct fitnesses (offspring numbers) brought about as a result of the behaviour being performed in, respectively, the performer (actor) and recipient of the behaviour and r is their genetic relatedness at the locus for the social behaviour. Relatedness has a strict definition as a regression coefficient, but more loosely means the probability of sharing a focal gene over and above the average probability, which is given by the population average gene frequency [2]. The usual cause of relatedness is kinship, but it is not the only possible one. Altruism is defined as the social behaviour in which the actor experiences a decrease in direct fitness (negative c , cost) and the recipient experiences an increase in direct fitness (positive b , benefit). Hence Hamilton’s rule finds that altruism can evolve provided $rb - c > 0$, i.e. provided that the number of copies of the gene for altruism added to the population by the altruistic act (proportional to rb) exceeds the number lost from it (proportional to c). Inclusive fitness theory, therefore, predicts that the evolution of altruism requires positive relatedness and is facilitated by high relatedness. Hamilton’s rule also generates conditions for other forms of social behaviour, namely cooperation (both c and b positive), selfishness (positive c and negative b) and spite (both c and b negative) [1,3–5].

In this review, I present a defence of inclusive fitness theory. Given the many existing responses to the first two sets of critiques, and the prominence and breadth of the article by Nowak *et al.* [38], I concentrate on meeting new points in that article. Nowak *et al.* [38] specifically criticized the mathematical basis and assumptions of inclusive fitness theory. These criticisms have already been met by existing responses, which have shown that inclusive fitness theory has a solid mathematical basis, that its assumptions are not restrictive, that limitations of the theory are shared by other approaches and that the alternative mathematical approaches proposed by Nowak *et al.* [38] do not substantially extend social evolutionary theory relative to existing theory (summarized in [48–50]). I therefore seek to address the new points of Nowak *et al.* [38] that have not yet received a full examination.

Note that some confusion in the debate over inclusive fitness theory has arisen because Nowak *et al.* [38] appear sometimes to use ‘inclusive fitness theory’ to mean the specific approach of modelling social evolution by calculating Hamilton’s inclusive fitness itself [1], an approach which has long been recognized as being subject to technical limitations [52–54]. The solution in the field has been to model social evolution by applying Hamilton’s rule [52,53] or by employing the so-called ‘direct fitness approach’ in which direct fitness incorporates social effects received by the actor [48,49,54–56]. These are still inclusive fitness approaches because they rely on

Hamilton’s core insight that selection of genes for social behaviour depends on social effects on genetic co-bearers (see below). Nowak *et al.* [38] criticized inclusive fitness theory in its general sense as well, for example, by querying the centrality of genetic relatedness in social evolution, by criticizing empirical studies claiming to support the theory and by arguing that the theory’s explanation of the origin of eusociality is inadequate. In this review, I use inclusive fitness theory in its general sense, that is, to mean the entire body of theory stemming from the Hamiltonian approach to social evolution. My conclusion is that inclusive fitness theory is robust to recent criticisms and so retains its validity and value.

2. THEORETICAL ASPECTS OF INCLUSIVE FITNESS THEORY

(a) *Fundamental insights of inclusive fitness theory*

Nowak *et al.* [38] argued that inclusive fitness theory provides no additional insights on top of those provided by modelling social evolution using population-genetic, game-theoretic approaches (their ‘standard natural selection theory’). On the contrary, inclusive fitness theory has added three fundamental biological insights that, prior to inclusive fitness theory’s development, natural selection theory had failed to recognize. The first is the insight that selection on a gene for a social behaviour depends on the behaviour’s effects on the fitness of genetic co-bearers [1,2]. To expand, inclusive fitness theory finds that selection on a gene for social behaviour is determined by the gene’s effects not only on the direct fitness of the bearer but also on the direct fitness of other individuals bearing the same gene (co-bearers, usually relatives) affected by the behaviour (box 1). This is the insight that allowed Hamilton [1] to solve the problem of altruism (see below) and that led to the gene’s-eye view of adaptive evolution [8]. Effectively, any model of social evolution that relies on this point draws on the insight provided by inclusive fitness theory.

The second insight is that very different social behaviours can be explained by adjusting the signs and magnitudes of the same basic parameters [1,4]. This insight arises via inclusive fitness theory’s explanation of the four basic social behaviours (cooperation, altruism, selfishness and spite) as occurring conditional on the signs of the effects of the social behaviour on the direct fitnesses of the social actor and recipient, and on actor–recipient relatedness (box 1). For example, changing these parameters takes us from the prediction that (other things equal) increasing relatedness within social groups promotes altruistic behaviour to the prediction that selfishness is curtailed by relatedness but can occur at any level of cost to non-relatives [1,5,57]. Hence, inclusive fitness theory has elucidated at a profound level the common basis to the different forms of social behaviour.

The third insight of inclusive fitness theory is the demonstration that conflict between members of a society is potentially present if they are unequally related to group offspring, since differential relatedness leads to unequal inclusive fitness optima [1,58]. From this has sprung an understanding of an immense range of kin-selected conflicts, including conflicts within families and eusocial societies (e.g. [59–61]) and intragenomic conflicts that follow the same underlying logic [5,62]. The corollary

of this insight is that societies are stable to the extent that the inclusive fitness optima of their members coincide. This in turn provides the rationale for the entire ‘major transitions’ view of evolution, whereby the origin of novel types of group in the history of life (e.g. genomes within cells, multicellular organisms and eusocial societies) can be explained as the result of their previously independent constituent units achieving a coincidence of inclusive fitness optima through grouping [5,63]. From this standpoint, a multicellular organism is a eusocial society of cells in which the members of the society happen to be physically stuck together; the more fundamental glue, however, is the clonal relatedness that (barring mutations) gives each somatic cell within the organism a common interest in promoting the production of gametes [5,64].

In sum, inclusive fitness theory is rich in insights, which is why it has guided research on social evolution so fruitfully since its inception. Moreover, the theory’s insights are highly unifying, because, as further detailed below (see §3b), they allow a broad range of social behaviours, across many social contexts and taxa, to be understood in the same terms. By contrast, the critiques of inclusive fitness theory offer no insights of corresponding magnitude or range. Nowak *et al.* [38] proposed that researchers should construct bespoke population-genetic models for each particular social context under study. Such models may indeed prove informative in the context to which they are applied. However, because the exact genetic basis of different social behaviours is likely to vary (and is generally unknown), the sole use of such models would come at a cost to the ability of researchers to discern common selective processes acting across many social contexts, which inclusive fitness theory provides. Even the main model (‘mutation-selection analysis’ in part A of supplementary information) of social evolution of Nowak *et al.* [38] appears to be of limited generality [49], since it assumed asexual reproduction (most eusocial species reproduce sexually) and offered no general predictions. Finally, Nowak *et al.* [38] argued that their perspective assumes a ‘gene-centred approach’ that ‘makes inclusive fitness theory unnecessary’. This is puzzling, because entirely lacking from their perspective is the idea, which underpins each of inclusive fitness theory’s insights, of the gene as a self-promoting strategist whose evolutionary interests are conditional on the kin class in which it resides (e.g. [8,62]).

(b) *The problem of altruism*

The problem of altruism is the problem of how reproductive self-sacrifice arises in nature. Simply put, how does natural selection lead to something like a sterile worker ant? As earlier discussed, inclusive fitness theory solved the problem by finding that a gene for altruism can spread if bearers aid relatives and Hamilton’s rule is satisfied (box 1).

In their model of the evolution of eusociality, Nowak *et al.* [38] deduced that the problem of altruism is illusory. They wrote that ‘There is no paradoxical altruism that needs to be explained’ because they assumed that potential workers (daughters of a colony-founding female or queen) are ‘not independent agents’ but rather can be seen ‘as “robots” that are built by the queen’ or the ‘extrasomatic projection of [the queen’s] personal genome’. If this claim were correct, then only the queen’s interests

would need to be addressed and one could conclude that worker altruism is more apparent than real. But it is incorrect, for two reasons. One is that, as has repeatedly been argued in response to previous ‘parental manipulation’ theories of the origin of eusociality [65], the inclusive fitness interests of workers and the mother queen do not coincide, because the two parties are differentially related to group offspring (e.g. [60,66,67]). The second is that worker behaviours such as eating of the queen’s eggs [68], egg-laying in response to perceived declines in queen fecundity [69], sex-ratio manipulation by destruction of the queen’s offspring [70] and lethal aggression towards the queen [71] all demonstrate that workers can act in their own interests and against those of the queen. In the light of this proven lack of worker passivity, workers’ reproductive self-sacrifice is paradoxical at first sight and this is the genuine problem of altruism that inclusive fitness theory has solved.

(c) *Alternative theory of eusocial evolution*

Nowak *et al.* [38] presented an ‘alternative theory of eusocial evolution’ (as alluded to in §2b), backed up by a ‘mathematical model for the origin of eusociality’. However, these do not represent true alternative theories, either alone or in combination, because they do not make any points or predictions that have not been made within inclusive fitness theory.

Take first the alternative theory of eusocial evolution [38]. This suggested that there have been five critical steps in the evolution of insect eusociality: (i) individuals group around some common resource, typified by a defensible nest close to sources of food; (ii) various pre-adaptations such as progressive provisioning (parental feeding of developing larvae) then ‘spring-load’ the group for becoming eusocial should this be favoured by selection; (iii) ‘eusocial alleles’ arise that provide the genetic basis for eusocial evolution, a process that could involve nothing more complex than a single mutation that silences offspring dispersal; if environmental factors favour the origin of eusociality, selection acts on these genes and eusociality originates; (iv) emergent traits of the colony, arising from the interactions of its members, become subject to selection, with the roles of queens and workers being flexible expressions of the same genotypes; and (v) between-colony selection, as one component of a system of multi-level selection, drives elaborations of the life cycle and caste structure of the eusocial society.

These steps constitute a reasonable scenario for the origin and elaboration of insect eusociality, but neither the sequence of steps nor the individual elements differ substantially from those that have been proposed to occur within the inclusive fitness framework (e.g. [67,72–74]). As regards the sequence of steps, almost all models of eusocial evolution assume a population of solitary individuals as a starting point, with non-dispersal then being favoured for some set of ecological reasons, and with other processes, including between-colony competition, then bringing about an increase in social complexity in established eusocial lineages (e.g. [73,75]). As regards the individual elements, in inclusive fitness theory, both the nest and the mode of provisioning have long been recognized as furnishing important pre-adaptations for social life. The nest facilitates the maintenance of relatedness and increases

the benefits to would-be altruists of not dispersing (e.g. [65,76,77]). Progressive provisioning provides an opportunity for complex social interactions between parent and offspring [72,78]. In addition, a mutation at a single locus leading to non-dispersal of offspring is a standard assumption in models of the origin of eusociality within inclusive fitness theory [66]. Conditional expression of helping is exactly what inclusive fitness theory leads one to expect [67,77]. Benefits of division of labour stemming from the presence of multiple group members have previously been recognized as integral to the success of incipient eusocial societies (e.g. [79]). Finally, the between-colony selection that acts upon group-beneficial, emergent traits can be viewed with equal validity either as a component of multi-level selection, as Nowak *et al.* [38] suggested, or as selection on the benefit term (b) in Hamilton's rule [67].

Take now the supporting mathematical model for the origin of eusociality proposed (in part C of the supplementary information) by Nowak *et al.* [38]. This is a model for the origin of eusociality by non-dispersal of young, first assuming asexual reproduction and then assuming sexual reproduction in a haplodiploid population (i.e. one in which males are haploid and are produced from unfertilized eggs, as in the Hymenoptera). The model concludes that eusociality is favoured if the presence of workers boosts the queen's fecundity and survivorship. This is not a new prediction [42,43,49]. It is true that the model specifies that a greater than sevenfold increase in the queen's birth rate is required for the origin of eusociality. But this quantitative finding arises from the numerical values assumed for the model's parameters in various runs. It is not shown to be a necessary feature of eusocial evolution. The main prediction is not new because Hamilton's rule also finds that eusociality in mother–daughter associations originates when workers rear offspring of the queen additional to those she would have had alone ($b > c$) [80]. This can occur only through workers increasing the queen's fecundity or survivorship. Indeed, quantitative estimates of the terms in Hamilton's rule in facultatively eusocial bees and wasps have already documented the fulfilment of Hamilton's rule in precisely this way (e.g. [5,79,81]).

The alternative theory of eusocial evolution of Nowak *et al.* [38] also exhibits two important weaknesses. To begin with, by allowing groups to form in multiple ways in step (i) (e.g. subsocially through parent–offspring associations but also by any other means, including 'randomly by mutual local attraction'), their scenario ignores two critical points that are inconsistent with it but consistent with inclusive fitness theory [42,43,46]. First, the evidence is that, in almost all eusocial lineages, eusociality has originated in social groups that were ancestrally subsocial and therefore characterized by high within-group relatedness [35,73]. Second, the evidence is that the origin of obligate or complex eusociality, defined as involving adult workers irreversibly committed to a worker phenotype, is associated with ancestral lifetime parental monogamy and hence, again, with predictably high within-group relatedness [35,80,82].

The other weakness is that one of the model's conclusions is poorly supported. Nowak *et al.* [38,51] argued that their finding that a large increase in the queen's birth rate is required for the origin of eusociality helps explain why it is hard for eusociality to evolve. Setting aside the

point (above) that the quantitative conclusions of the model in Nowak *et al.* [38] stem from its numerical assumptions, I suggest that in fact the origin of eusociality is not a particularly rare event. Summing the number of eusocial origins across taxa conventionally defined as eusocial returns at least 24 independent origins of eusociality [5,83], or over double that number if one includes cooperatively breeding vertebrates [5]. The number of origins of complex eusociality from simple eusociality is smaller [5]. But the argument of Nowak *et al.* [38] that eusociality is rare and hence that the conditions required for it to originate are particularly stringent is weakly founded. The conditions required for the origin of eusociality are at least six times less stringent than those required for the origin of powered flight, which is a highly successful trait and yet has arisen independently only four times [84].

In sum, Nowak *et al.* [38] make a case for considering the effect of the population-dynamic context in which eusocial evolution occurs. But their alternative theory and its associated model add no fundamentally new elements on top of those identified within the inclusive fitness framework and, relative to this framework, exhibit substantial shortcomings.

3. EMPIRICAL ASPECTS OF INCLUSIVE FITNESS THEORY

(a) *Status of the haplodiploidy hypothesis*

The haplodiploidy hypothesis is the idea that the relatedness asymmetries caused by haplodiploid sex determination facilitate the origin of eusociality in haplodiploid species [1,85]. Nowak *et al.* [38] argued that the hypothesis has failed because eusociality has increasingly been found to occur in diploid species, which shows that 'The association between haplodiploidy and eusociality fell below statistical significance'. They concluded that this serves to weaken inclusive fitness theory. However, the haplodiploidy hypothesis has not failed in the sense that it has been tested and falsified (the source of the 'statistical significance' to which Nowak *et al.* [38] allude is therefore unclear). Instead, a rigorous test has not been conducted. Such a test would require a phylogenetically corrected comparative analysis of the association of eusociality and systems of sex determination, which in turn would require a robust and detailed (e.g. family-level) phylogeny encompassing the entire pool of diploid and haplodiploid clades in which eusociality has and has not originated. No such phylogeny exists, and empirical analyses of the haplodiploidy hypothesis have therefore used approximate methods (e.g. [34]). Furthermore, even if such a phylogeny were constructed, the problem would remain that, with the exception of the haplodiploid eusocial thrips, all haplodiploid eusocial lineages lie within the aculeate Hymenoptera, which would mean that other aculeate features might confound effects of haplodiploidy [9,67]. Hence, the haplodiploidy hypothesis remains in limbo—hard to test, untested, arguably unhelpful, but not falsified.

More fundamentally, as has long been recognized [9,85] and repeatedly stressed (e.g. [67,77]), the haplodiploidy hypothesis is not an essential component of inclusive fitness theory, since Hamilton's rule for altruism can hold without the relatedness asymmetries caused by haplodiploidy being present. Highlighting the status of the haplodiploidy hypothesis to criticize inclusive fitness theory therefore

Table 1. Social phenomena that provide evidence for inclusive fitness theory.

social phenomenon	evidence	selected comparative analyses/review references
distribution of social behaviours as a function of relatedness	altruism (including eusociality and cooperative breeding) is associated with interactions among relatives whereas selfishness and cooperation (defined in box 1) are associated with interactions among non-relatives	[5,35,87]
conditionality of social behaviours	reproductive division of labour is conditional (same genotype can lead to reproductive or helper phenotypes)	[67,77]
effect of localized competition on evolution of social behaviour	localized competition dampens the evolution of altruism as predicted by inclusive fitness theory	[4]
kin discrimination	kin discrimination occurs almost universally between groups and (in some social taxa) within groups	[88–90]
conflict within families and societies	distribution and nature of conflict within families and societies are as predicted by inclusive fitness theory	[61,91–94]
intragenomic conflict	phenomena of intragenomic conflict are as predicted by inclusive fitness theory	[5,62,95]
sex allocation	sex investment ratios in eusocial Hymenoptera and other taxa are as predicted by inclusive fitness theory	[67,91,96–98]
major transitions	phenomena of the major evolutionary transitions (e.g. evolution of multicellularity) are as predicted by inclusive fitness theory	[5,63,82,99,100]

misses the target. It also overlooks the fact that all diploid eusocial societies identified since the haplodiploidy hypothesis was proposed have turned out to be either clonal or family groups and so, as predicted by inclusive fitness theory (box 1), to exhibit positive relatedness. This is true of ambrosia beetle, social aphids, polyembryonic wasps, social shrimps and mole-rats [5]. It is even true of a newly discovered eusocial flatworm [86]. In short, the diploid eusocial societies, far from weakening inclusive fitness theory, serve to strengthen it.

(b) Evidence for inclusive fitness theory

In their critique of inclusive fitness theory, Nowak *et al.* [38] described the contribution of the theory to the empirical understanding of social evolution as ‘meagre’, suggested that research within the inclusive fitness framework has become an ‘abstract enterprise’, and characterized the evidence for the theory as weak. None of these points is the case: a wealth of studies, of a large variety of specific social phenomena in many taxa, have been directly stimulated by the theory and confirm the theory’s predictions (table 1). Nowak *et al.* [38] also stipulated that to test the theory ‘one has to perform an inclusive fitness type calculation for the scenario that is being considered and then measure each quantity that appears in the inclusive fitness formula’. In fact, researchers have successfully tested the theory without measuring all factors [5]. For example, predicted effects of relatedness on social traits have been successfully tested either comparatively, with the assumption that unmeasured factors do not covary with the trait of interest, or experimentally, so that unmeasured factors are randomized across treatments through the experimental design [5]. Transitions from solitary to social living have also been tested in a phylogenetic context, with the finding that, as predicted, high within-group relatedness is associated with the origin of eusociality and cooperative breeding [35,87,101]. None of

these approaches is unique to inclusive fitness theory; they are standard methods of testing theory in evolutionary biology as a whole.

Contrary to Nowak *et al.* [38], many of inclusive fitness theory’s successful predictions are unique to the theory. For example, the theory uniquely predicted patterns of sex investment ratios and the distribution of male parentage between queens and workers in eusocial Hymenoptera [60,77,91,92,96]. It also uniquely predicted the finding in cooperatively breeding birds that helpers provide aid with higher frequency or to a greater extent when they are more closely related to the group aided [102–104]. More broadly, the theory uniquely predicts the absence of altruism (involving lifetime costs to direct fitness) between non-relatives, and indeed no such cases have been found except in systems clearly derived from ancestral societies of relatives [105].

Finally, inclusive fitness theory is unique in the range of social phenomena that it has successfully elucidated, including phenomena as superficially dissimilar as the origin of multicellularity and the origin of eusociality, or intragenomic conflicts and conflicts within eusocial societies (table 1). Overall, no other theory comes close to matching inclusive fitness theory’s record of successful explanation and prediction across such a range of phenomena within the field of social evolution [42,44,46]. The challenge to any approach purporting to replace inclusive fitness theory is to explain the same phenomena without using the insights or concepts of the theory.

4. CONCLUSION

Recent critiques of inclusive fitness theory have proved ineffective on multiple fronts. They do not demonstrate fatal or unrecognized difficulties with inclusive fitness theory. They do not provide a distinct replacement theory

or offer a similarly unifying approach. They do not explain previously unexplained data or show that explanations from inclusive fitness theory are invalid. And they do not make new and unique predictions [5]. The latest and most comprehensive critique of inclusive fitness theory [38], though broad-ranging in the scope of its criticism, suffers from the same faults. Certainly, relatedness does not explain all variation in social traits [106]. In addition, the long-standing message from inclusive fitness theory is that particular combinations of non-genetic (e.g. ecological) and genetic factors are required for the origin of eusociality (e.g. [5,76,77,85]). Nonetheless, relatedness retains a unique status in the analysis of eusocial evolution because no amount of ecological benefit can bring about altruism if relatedness is zero [1,5]. Additional theoretical explorations of the connections between, and limitations of, inclusive fitness theory and other modelling approaches should prove informative [49]. It is here, and in further empirical investigations of social phenomena, that the common ground between the critics and supporters of inclusive fitness theory is likely to be found [5]. But known limitations of the theory should not be allowed to obscure its penetrating insights, its elucidation of the role of relatedness in social evolution or its many empirical successes. Inclusive fitness theory retains its validity and value and hence deserves to keep its position as the leading theory for social evolution.

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