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Inclusive fitness and the major transitions in evolution

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Highlights:

- Inclusive fitness provides a framework and a tool for analysing social evolution.
- Recent work defines point of occurrence of, and conditions for, a major transition.
- Evolution of individuality remains a key aspect of major transitions.

Abstract:

Inclusive fitness theory is the leading framework for explaining the major transitions in evolution, whereby free-living subunits (e.g. cells, organisms) have cooperated to form new, higher-level units (e.g. organisms, eusocial societies). The theory has attracted considerable controversy. From a brief survey of the controversy's present status, I conclude that inclusive fitness theory continues to provide both a concept and a principled modelling tool of value for understanding social evolution, including major transitions. Turning to new developments in the study of major transitions, I describe work defining the point of occurrence of major

transitions and, from inclusive fitness theory, the required conditions. I also suggest that it remains important to understand the evolution of individuality that occurs beyond such thresholds.

Introduction

Evolutionary biology has successfully explained several fundamental characteristics of the living world, namely adaptation, common descent and biological diversity. Less appreciated is the fact that, via the concept of the major transitions in evolution [1], evolutionary biology has explained another of life's fundamental characteristics, namely the nested, hierarchical organisation of living things. This organisation is exemplified by genes grouping within cells to form genomes, cells grouping to form multicellular organisms, and many multicellular organisms grouping to form societies. It has been built up over evolutionary time as previously free-living entities (e.g. replicating molecules, cells, organisms) have united to form higher-level groups resembling individuals in their own right. Each event of this type constitutes a major transition in evolution [1-7].

The study of the major transitions has also identified the process that underpins each transition, namely social evolution or, more specifically, the evolution of cooperation. Hamilton's inclusive fitness theory [8-10] represents the leading theoretical framework for explaining social evolution. It is not the only framework used for this purpose, but it stands out for its highlighting the key role of relatedness, its ability to explain both cooperation and conflict within groups, its integrative nature and its richly diverse empirical successes [e.g. 4,10,11].

Here I review recent developments in inclusive fitness theory and in the theory's application to the major transitions. As is well known, inclusive fitness theory has been the subject of controversy in recent years, particularly following the extensive critique by Nowak et al. [12]. Hence, first, I consider the present status of this controversy, so as to justify why, in principle, using the theory is legitimate. Second, I consider recent insights, derived from the theory, that have improved our understanding of the major transitions, focusing on fraternal transitions (see Box 1 for definitions of this and other key terms), and point to possible resolutions of differing perspectives in the literature.

The inclusive fitness controversy: present status

A full discussion of the development and present status of the inclusive fitness controversy is not possible here. Relevant papers focusing on the theoretical issues include [13], [14] and [15] critiquing the theory, and [16], [17] and [18] defending it. However, it is possible to pick out a number of points around which the controversy has crystallised. Examining these shows that inclusive fitness theory continues to provide a principled basis for analysing social evolution and, by extension, the major transitions.

1. *Inclusive fitness theory and multilevel selection*: A confusing feature of the inclusive fitness controversy is that critiques of the theory [e.g. 12,14,19] have advocated replacing it with two theoretical frameworks – multilevel selection and evolutionary dynamics – that themselves differ widely. However, as regards multilevel selection, it appears that a consensus or near-consensus has been reached. It has long been recognised that inclusive fitness theory and multilevel selection theory share strong formal similarities, with each being derivable from the

same starting point, the Price equation [20,21]. At least, inclusive fitness and multilevel selection theory show formal equivalence for the case of intrademic group selection [3,22], which is the version applicable to many of the major transitions. Hence the consensus is that inclusive fitness theory and multilevel selection theory, for many relevant applications, represent separate, but essentially interchangeable, frameworks for addressing problems in social evolution [e.g. 22-27]. If so, then this aspect of the controversy has been resolved, with the choice of framework for a given application becoming a mainly pragmatic one [22].

2. *Inclusive fitness and evolutionary dynamics*: Nowak and colleagues [12,14] argued that the evolution of cooperation should be modelled using an evolutionary dynamics approach. Supporters of inclusive fitness theory do not fault this approach *per se*, but point to several interrelated drawbacks with it. One is that the approach requires very specific assumptions to be made, as regards, for example, the exact genetic basis of traits and the values taken by demographic parameters. But in most cases these are unknown and would be prohibitively difficult to measure in natural systems [23,26]. Hence the approach risks providing mathematical exactness at the expense of empirical applicability [23,26]. A second drawback is that, with numerous assumptions to make and parameters to assign, a given model's assumptions or exploration of parameter space might be restrictive or incomplete, with the result that the conclusions are also incomplete. For evolutionary-dynamics models of the evolution of eusociality [12] and worker sterility [28], this has been shown to be the case, by, respectively, [29] and [30], recovering results matching those of inclusive fitness theory. A third drawback is that, given their bespoke nature, evolutionary dynamics models do not necessarily yield generalisable insights [11,18]. Hence, depending on the problem to be solved, evolutionary dynamics models might serve as a valuable complement to broader approaches such as inclusive fitness theory, but are not a universal substitute.

3. *Inclusive fitness theory as a general concept*: Queller [31], building on earlier work [e.g. 20,32], has shown that the Price equation stands at the head of a rich hierarchy of interrelated theorems in quantitative genetics, including Fisher's fundamental theorem and the breeder's equation. It also yields, as mentioned, expressions from inclusive fitness theory (Hamilton's rule) and multilevel selection theory [31]. Hence, inclusive fitness theory sits within a set of mutually supportive fundamental concepts and, by the same token, criticisms of the theory apply to the entire quantitative genetics approach [31,32]. At the same time, it is acknowledged that this approach again trades off mathematical exactness and dynamic sufficiency against generality and simplicity [31,32]. The version of Hamilton's rule derivable from the Price equation is termed Hamilton's rule, general version (HRG) [24,33]. The case for inclusive fitness as a general concept is that the value of HRG lies precisely in the powerful organisational and integrative framework it brings to social evolution [16,27].

4. *Inclusive fitness theory as a modelling tool*: Hamilton's rule also exists in a marginal or approximate version, HRA [24], which explores conditions, near the equilibrium of a social trait, of selection for mutants of small effect for alternative states [9,23]. One of the key criticisms of inclusive fitness theory as a modelling tool, and of inclusive fitness as a property of individuals, is that the theory's assumptions of actor's control and fitness additivity are not met under many conditions [13,14]. However, Birch [34] has shown that HRA addresses this criticism, because actor's control and fitness additivity are justifiable approximations when considering marginal effects. Moreover, marginal effects are integral to a gradualist view of the cumulative assembly of complex adaptations, including those produced by social evolution, and, in this context, only inclusive fitness provides a stable criterion for unidirectional phenotypic improvement [27,34]. In sum, HRA provides a principled tool for modelling social

evolution with inclusive fitness [34], and indeed has been extensively employed for this purpose [e.g. 30,35-37]. A related issue concerns whether evolutionary models should properly focus on equilibria or dynamics [22,23,26,30]. There is no general answer to this question, but demonstrable progress has been made in social evolution by focusing on equilibria, through deriving (from inclusive fitness theory) conditions for stable states and then testing experimentally or comparatively whether perturbations leads to differences in the expected direction [23].

The overall conclusion from these points is that inclusive fitness theory remains a robust theory in the study of social evolution, providing both a well-founded, unifying concept and a valid and productive modelling tool (Figure 1). Indeed, the theory has continued to generate new extensions [38], syntheses [7,39-41] and empirically supported tests [42-44].

New insights from inclusive fitness theory for understanding major transitions

With this background, this section considers recent insights into the major transitions derived from inclusive fitness theory. In [4], I suggested that major transitions can usefully be classified into three stages – social group formation, maintenance and transformation, at the end of which the evolution of individuality has occurred and the major transition is complete. Inclusive fitness theory has proved particularly apt for analysing major transitions because, both as a concept and as a modelling tool, it helps explain each stage [4]. Nonetheless, because social group transformation remains the least understood stage [4,7,27], recent work has focused on defining when, and under what precise conditions, a major transition can be said to

have occurred. I address only the fraternal major transitions, as their study is where most progress has been made.

1. *Major transitions and conflict*: West et al. [7] emphasised that satisfying Hamilton's rule alone does not bring about a major transition. Instead, given the attenuation of conflict inherent in the evolution of individuality, the process is favoured when both Hamilton's rule is satisfied and between-helper conflict over delivering help is absent. In the transition to obligate multicellularity, these conditions arise through clonality (present at social group formation) [45,46], which, under inclusive fitness theory, removes all potential conflict between clone-mates [8]. In the transition to obligate eusociality, they arise via lifetime monogamy of the founding queen [41,45,47,48]. The reason is that then each helper is, on average, equally related to queen offspring (sibs, relatedness, r , = 0.5) (removing between-helper conflict) and related by an equal amount to its own offspring (r = 0.5) (satisfying Hamilton's rule given even the slightest economic benefit). (Note that these conditions are the same as those allowing a 'virtual dominant' – also hypothesised to be a key component of fraternal major transitions -- to arise in large, single-queen eusocial societies [4,49].) West et al. [7] and Boomsma and Gawne [41] further suggested that active repression of conflict has played a limited role in the fraternal major transitions. Given clonality or lifetime monogamy, there is little conflict to be repressed [7], and much within-group conflict is over reproductive resource allocation occurring after sexual maturity, and so is not disruptive of organismal or colony growth [41]. However, as discussed below (see 'Major transitions and the evolution of individuality'), conflict reduction retains an important role in the evolution of individuality.

2. *Major transitions: defining a threshold condition*: Boomsma and Gawne [41], building on [45,47,48], have argued that the major transition to obligate eusociality or superorganismality

occurs at the point that permanent reproductive and helper castes irreversibly evolve. Analogously, multicellular organisms undergo a major transition (to complex organismality) at the point that separate germline and somatic cell lineages irreversibly evolve. Moreover, both these thresholds require, as a necessary condition, lifetime commitment of founding partners (a strictly monogamous royal pair and female and male gametes, respectively). Such a condition, as described above ('Major transitions and conflict'), is maximally conducive to a major transition, because, with the relatedness terms cancelling out of Hamilton's rule (relatedness to recipient's offspring = relatedness to own offspring), even the slightest economic benefit reinforces workers' permanent commitment to their role [41,47].

Clarifying the point of occurrence of a major transition, and defining the theoretical underpinning of this threshold, are valuable insights. A note of qualification is that both obligate eusocial societies and complex multicellular organisms evolve from simpler ancestors. So what looks like a sharp threshold may represent a stepwise acquisition of the necessary traits over evolutionary time. Such a process may play out in unexpected ways, as exemplified by the recently characterised social system of an obligately eusocial beetle (*Austroplatypus incompertus*). This species has workers that permanently commit to their worker role (by tarsal loss) as adults [50], whereas all other cases of obligate eusociality (e.g. Hymenoptera and termites) involve worker determination early in development [41].

3. *Major transitions and the evolution of individuality*: Boomsma and Gawne's [41] scheme assigns a secondary role to the evolution of individuality, with the increase in complexity that arises in this process occurring downstream of the point of occurrence of the major transition itself. For the same reason, the scheme suggests that conflict reduction plays little part in the major transition. This contrasts with the view that the evolution of individuality, of which

conflict reduction is a key element, is an integral component of a major transition [4,51]. A resolution may perhaps be found by dissociating the point when a major transition occurs (Boomsma and Gawne's [41] threshold) from the evolution of individuality (Figure 2). Why this would be informative can be seen in two examples. First, volvocine algae occur in a series of types ranging from groups of undifferentiated cells to groups of dimorphic germline and somatic cells [52]. Yet all types, being clonal [4], meet the threshold condition of maximal coincidence of fitness interests. Second, bumblebees (*Bombus* spp.) and honeybees (*Apis* spp.) have both crossed Boomsma and Gawne's [41] major transitions threshold of obligate eusociality, as workers in both genera are permanently unmated. But, in *Bombus*, queen and workers each have 4 ovarioles per ovary [53,54] and up to 45% of workers lay eggs within the nest [55], whereas, in *Apis*, queen and workers have, respectively, 150-180 ovarioles and 2-12 ovarioles per ovary [56] and only 0.01% of workers lay eggs [57]. Hence, these two obligately eusocial systems differ considerably in their degrees of queen-worker reproductive dimorphism and worker productivity. If one seeks to explain such differences, specifically the increase in germline-soma differentiation or queen-worker reproductive dimorphism, evolution of individuality remains an essential concept [2,4,51]. In [4], following [58], I suggested that rising group size (cell number, organism number) is a primary driver of increases in complexity and individuality (the size-complexity hypothesis). Recent studies of eusocial insects [59,60] and conceptual extensions [27] have supported this view, but more work in this area, especially as regards the transition to multicellularity, is required.

Conclusions

Recent work has clarified a threshold condition, based on inclusive fitness theory, for the occurrence of fraternal major transitions (Figure 2). A corollary is that it might be useful to

make a distinction between the point when a social group crosses the threshold of a major transition and the evolution of individuality that ensues, the end point of which is increased social complexity and maximal individuality. The fundamental principle is that individuality, based on interdependent constituent subunits, increases to the extent that subunits share a coincidence of inclusive fitness interests. Future work could profitably seek to test these ideas further, both empirically and conceptually, and to apply them to the egalitarian transitions.

Conflict of interest statement

None declared.

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Box 1: Key terms in the study of social evolution and the major transitions

- Actor's control: The assumption in inclusive fitness theory that the magnitude of benefits to recipients depends on the actor's but not the recipient's genotype [e.g. 34].
- Additivity: The assumption in inclusive fitness theory that the fitness effects of separate instances of help or harm to recipients can be summed to give the actor's overall inclusive fitness [e.g. 34].
- Altruism: Social behaviour that leads to decreased expected lifetime offspring output (direct fitness) of actors and increased expected lifetime offspring output of recipients [8].
- Breeder's equation: A theorem in quantitative genetics relating the response to selection to the selection differential and heritability, derivable from the Price equation [31].
- Dynamic sufficiency: Describing the case when an evolutionary model can be reiterated over generations, so allowing the dynamics of change over time to be studied [e.g. 32].
- Egalitarian major transition: Major transition in which the partners are non-relatives [4,61].
- Eusociality: Describes an animal society showing reproductive division of labour (reproductive and helper phenotypes), cooperative brood care and overlap of generations [62]. Boomsma and Gawne [41] discuss the history of this term and, following Boomsma [45,47], argue that it should be restricted to cases in which there are morphologically distinct adult castes (reproductive and worker) that are fixed for life early in individual development (obligate eusociality).
- Evolution of individuality: The product of a major transition, with an individual (e.g. organism, obligate eusocial society) being defined as a stable, physically discrete entity composed of interdependent parts acting in a coordinated manner to achieve common reproductive goals, and typified by attenuated within-individual conflict [e.g. 4].

- Evolutionary dynamics: Population genetics-based modelling approach that tracks the fate over generations of a mutation for a focal trait, so as to provide a full description of its dynamics [e.g. 14,63].
- Fisher's fundamental theorem: A theorem in quantitative genetics relating the rate of fitness change to the variance in fitness; due to R.A. Fisher and derivable from the Price equation [31].
- Fraternal major transition: Major transition in which the partners are relatives [4, 61].
- Group selection: See under Multilevel selection.
- Hamilton's rule: See under Inclusive fitness theory.
- Inclusive fitness theory: Hamilton's [8] theory of social evolution, partitioning fitness into a direct, non-social component (direct fitness, i.e. offspring output) and, via help or harm to other individuals sharing causative genes for a social action, an indirect, social component (indirect fitness). It is encapsulated in Hamilton's rule, whereby a social action undergoes selection when the net sum of these components (cost, and benefit weighted by relatedness) is positive. When genetic co-bearers are relatives, it involves kin selection. For example, under the theory, kin-selected altruism occurs when the cost of decreased offspring output of the actor is exceeded by indirect fitness gained via the enhanced offspring output of recipient kin [e.g. 10,16].
- Major transition in evolution: For purposes of the present review, one of the events in the history of life in which previously independent entities (e.g. genes, cells, organisms) united to form a new higher-level collective resembling an individual in its own right (e.g. genome, multicellular organism, obligate eusocial society) [1-7].
- Multilevel selection: A theory of social evolution that partitions fitness into between- and within-group components; the modern version of group selection theory [3,64]. In intrademic group selection (MSL1 in [3]), mating is population-wide and individuals

reassort into new groups each generation, as, for example, in most eusocial insects (obligate or otherwise).

- Price equation: An expression derived by Price [65] that provides a formal expression for the occurrence of natural selection (partitioning evolutionary change into components representing, respectively, differential selection and differential transmission) [e.g. 32,66].
- Superorganism: Following Wheeler [67], defined by Boomsma and Gawne [41] as arising when societies undergo the major transition to obligate eusociality in which there are morphologically distinct adult castes (reproductive and worker) that are fixed for life early in individual development.
- Virtual dominant: The group member, in a social group (of cells or organisms) in which no single member monopolises physical power, to whose offspring the other group members have greatest mean relatedness. The virtual dominant therefore has a stable reproductive monopoly despite its lack of physical power. Large group size in animal societies creates conditions for virtual dominance by precluding physical dominance [4,49].

Figure legends

Figure 1 Proposed relationships between fundamental theory (concepts) and modelling tools in the study of social evolution. The Price equation is a fundamental theorem describing the action of natural selection. Adding social interactions leads to inclusive fitness theory (Hamilton's rule, general version, HRG) and multilevel selection theory, which are (in this context) considered mathematically if not causally equivalent [e.g. 22]. These theories can be analysed with various modelling tools, which serve a different purpose as specific implementations of the theories they stem from [16,18,21]. The tools include inclusive fitness models (Hamilton's rule, approximate version, HRA), intrademic group selection models, evolutionary dynamics models, game theory models and others, with the choice between these being pragmatic and context-specific. From [16], [21], [24], [22], [18], [27], [34] and [31].

Figure 2 Stages of a major evolutionary transition from [4], modified to include the threshold at which a fraternal major transition occurs (in multicellular organisms, irreversibly separate germline and somatic cell lineages evolve, and in obligate eusocial societies, irreversibly permanent reproductive and helper castes evolve) as identified by [41] and [48] (see also [45] and [47]). As in [4], there may be overlap in processes involved in social group maintenance and social group transformation.

Figure 1

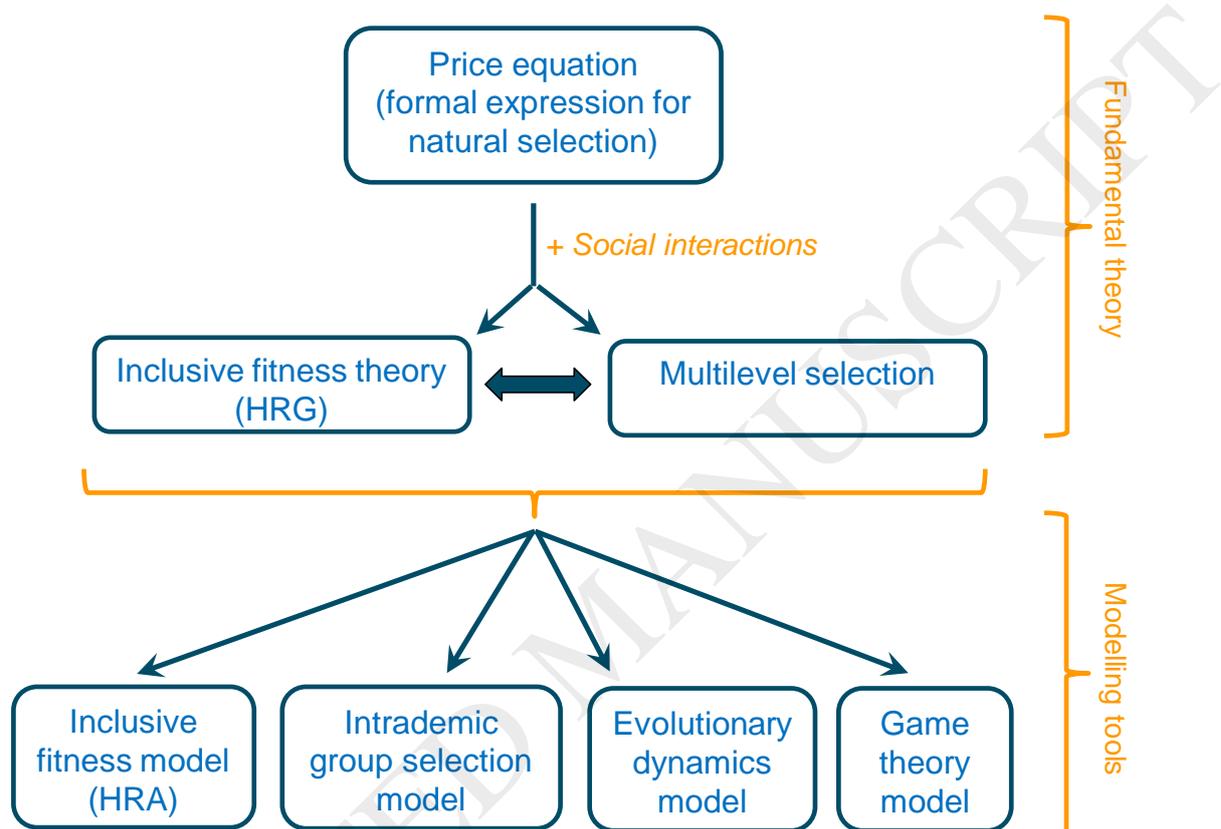


Figure 2

