1   What is inclusive fitness theory, and what is it for?

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12   Abstract:

13   Inclusive fitness theory is a cornerstone of modern evolutionary biology, yet

14   critics contend it is not general but subject to serious limitations, and is ripe for

15   replacement, for example by multilevel selection theory. These critics also

16   question empirical predictions made using inclusive fitness theory, such as on

17   sex allocation, and the use of statistical concepts in understanding responses to

18   selection. Here I summarise recent resolutions of these criticisms, then discuss

19   what inclusive fitness theory actually is and why it is useful for evolutionary

20   biology. In doing so I focus on recent developments in evaluating causal

21   explanations for social evolution, and the role of inclusive fitness theory in

22   explaining group adaptations, including the major transitions to obligate

23   eusociality and eukaryotic multicellularity.

24

25   Highlights

26   • Criticisms of inclusive fitness theory have consistently been shown to be

27   incorrect

28   • Understanding causality is helpful for resolving between competing

29   viewpoints

30   • Inclusive fitness is essential for understanding group adaptations like

31   eusociality

32   • Recent controversies over inclusive fitness seem more sociological than

33   scientific

The competition between paradigms is not the sort of battle that can be resolved by proofs.

T. S. Kuhn

Introduction

Despite its status as a cornerstone of modern evolutionary biology, inclusive fitness theory, conceptualised and formalised by W. D. Hamilton over 50 years ago [1,2], is no stranger to misunderstanding and controversy. In the 21st century version of the controversy E. O Wilson, author of *Sociobiology* and erstwhile supporter of inclusive fitness theory [3], shifted to attacking the theory, in collaboration with a number of colleagues. The profile of Wilson and his collaborators, his former support for the theory, and the profile of the venues in which these attacks were published, moved this controversy from being confined to technical discussions amongst biologists, and into the limelight; in 2010 the front cover of *Nature* featured the highest profile attack to date by Wilson, in conjunction with the mathematical biologists Martin Nowak and Corina Tarnita [4]. These attacks drew extensive responses from the community of inclusive fitness theory theorists and empiricists (e.g. [5]), and in turn further critiques, in a cycle that shows little sign of being escaped. In this article, over 10 years after the first high profile attack on inclusive fitness theory by Wilson and Hölldobler [6], I attempt to provide a personal view on what the disagreements are about. Critiques of inclusive fitness theory have become increasingly mathematical in recent years, as have their defences. I suggest that there is nothing wrong with the mathematics of the critiques, but it is the conceptual interpretations of these mathematics that are flawed. Hence, if the ongoing controversy is to be 'put to bed' then the resolution will be conceptual, not mathematical, in agreement with the quote by Thomas Kuhn reproduced above ([7], p. 148).

What is inclusive fitness theory?

Inclusive fitness theory had its first formal presentation in two papers by W. D. Hamilton [1,2]. Hamilton's work had two aims, the first and most generally known being to propose a method of accounting for fitness effects that provided

67   a rigorous explanation for the evolution of social behaviour. This method divides

68   the inclusive fitness effect of a social trait individual into direct and indirect

69   fitness components. The direct fitness effects of a trait are the change in fitness

70   of the bearer that results from the trait's expression, often referred to as the

71   'cost' c of the behaviour, although this 'cost' can be negative; direct fitness is

72   'stripped' of fitness effects received from other bearers of the same trait. Indirect

73   fitness effects are changes in fitness by recipients of the social behaviour, usually

74   referred to as 'benefit' b which can again be negative, weighted by their genetic

75   relatedness r to the behaving individual. Baseline fitness due to other traits and

76   factors completes the description of the individual's total fitness, but since this

77   does not systematically vary according to whether the trait is borne or not it falls

78   out of the subsequent analysis. Then asking when a social trait experiences

79   positive selection yields Hamilton's rule

80
$$rb - c > 0.$$

81   Hamilton's derivation of this result [1] was exact, but under certain simplifying

82   assumptions. At the same time however, inspired by R. A. Fisher, Hamilton

83   claimed to have identified inclusive fitness as the quantity that organisms under

84   natural selection should act as if to maximise. Hamilton's reasoning here was less

85   formal, and recently inclusive fitness theorists have both advocated and debated

86   the validity of his maximisation claim (*e.g.* [8–12]). Furthermore, it is important

87   to note that correct reasoning about inclusive fitness and behaviours requires

88   consideration of the behavioural options available [13]; for example, a female

89   honeybee may have higher inclusive fitness as a queen, but when forced into a

90   worker role through epigenetics resulting from not being fed a diet of royal jelly

91   during development [14], the only behavioural options available are to raise

92   sisters, produce males, and police the male reproduction of sisters [15].

93   Perhaps because of some initial opacity in Hamilton's proposal, perhaps

94   because of simplifying assumptions made but subsequently relaxed, and perhaps

95   simply because of the volume of the literature that it inspired, Hamilton's

96   inclusive fitness method of analysing selection on social traits attracted criticism,

97   the intensity of which has increased in the last ten years as described above.

98   Since the criticisms I address are all to do with the Hamilton's rule version of

99   inclusive fitness theory, rather than the inclusive fitness maximisation

100   arguments, I shall refer to 'inclusive fitness theory' in the Hamilton's rule sense

101   in what follows.

102

103   ***Critiques of inclusive fitness theory, and their responses***

104   Various summaries of the recurrent or recent misunderstandings of

105   inclusive fitness theory exist (see for example [16–19]). Here I briefly break

106   down the development of some of the main arguments against inclusive fitness

107   theory over the last 10 years, and summarise their responses. Having provided a

108   brief introduction to inclusive fitness theory above, I assume a passing

109   familiarity with the basic concepts of multilevel (or 'trait group') selection

110   theory, in which social behaviours are favoured when between-group selection

111   outweighs within-group selection.

112   The first criticism, originally publicised by Wilson and Hölldobler [6], is

113   that inclusive fitness theory models of the evolution of social behaviour in

114   colonies are less general than models of competition between colonies.

115   Commentators at the time [20] noted that this 'new' form of model appeared to

116   be inclusive fitness theory in disguise; the critique that inclusive fitness theory is

117   less general than multilevel selection theory has been repeated subsequently

118   (e.g. [4]), despite the long-standing result that inclusive fitness and multilevel

119   selection analyses are different partitionings of fitness and therefore always

120   agree on the direction of selection (see [16] for a summary), and despite the

121   longstanding existence of methods for generalising Hamilton's rule beyond the

122   simple additive social interactions he originally considered [21].

123   In support of the arguments that inclusive fitness theory could not explain

124   the evolution of reproductive division of labour in colonies, Nowak, Tarnita and

125   Wilson presented a mathematical model in which they claimed the evolution of

126   costly helping was not correlated with within-colony relatedness, as predicted

127   by Hamilton's rule [4]. However a subsequent more thorough analysis of the

128   model found that under systematic variation of relatedness Hamilton's rule

129   predicted correctly when helping would and would not be favoured [22].

130   A concurrent criticism of inclusive fitness theory, although it was not fully

131   appreciated at the time [23], is that inclusive fitness is no more than a

132   conceptually difficult reorganisation of classical Darwinian / Fisherian fitness

133   [4]. A version of this viewpoint has recently been echoed by inclusive fitness

134   theorists, who focus on a 'gene's eye view' of individual fitness averaged across

135   time, individuals and states to claim that inclusive fitness is not an extension of

136   classical Darwinian fitness [24], and that considering it as such is not

137   conceptually useful. Hamilton clearly conceived of inclusive fitness theory as an

138   extension to classical fitness [25], and as I have written elsewhere it seems

139   reasonable to characterise the classical understanding of fitness as indeed being

140   the fitness an individual would express 'stripped' of all its components due to the

141   behaviour of others, as first outlined by Hamilton [1]; simply put, Darwin and the

142   modern synthesists implicitly excluded the social from their formulation of

143   fitness, with Fisher even going so far as to consider it 'unimportant' ([23], pp. 56-

144   57)). Regardless of conceptual utility, investigating the history and likely original

145   definitions of concepts is important in correctly ascribing priority, and useful in

146   considering how misunderstandings can arise.

147   Other critiques concerned the empirical predictions from inclusive fitness

148   theory, starting with the 'haplodiploidy hypothesis' that the genetics of the

149   Hymenoptera facilitate the evolution of costly helping by daughters [4], and then

150   moving on to sex ratio theory [26] The former critique was in fact not a new

151   observation, as evidence and theory against the haplodiploidy hypothesis had

152   already been accumulating, as well as pointing to a replacement theory

153   (discussed in 'Causality, group adaptations, and major transitions' below) [5];

154   the extension of the attack to sex ratio theory [26] has since been expertly

155   addressed by Andrew Bourke [27].

156

157   ***Separating concepts and tools***

158   As mentioned in the preceding section, in response to claims that

159   inclusive fitness has limited applicability, theorists began advocating a

160   generalisation of Hamilton's rule first proposed by David Queller [21], which

161   applies the Price equation to derive a version of Hamilton's rule in which fitness

162   costs and benefits, and relatedness, are all defined in terms of (partial)

163   regression coefficients (e.g. [16,17,23]).

164   In response to this generalisation, critics of inclusive fitness theory have

165   also taken aim at this methodology, claiming that it risks confusing correlation

166   with causation [28], as well as making a more general point that applying

167   statistical models to decompose the selective pressure in exact game theoretic or

168   population genetic models is pointless [29] (writing in response to [30]).

169   The link between the partial regression formulation of costs and benefits,

170   and Hamilton's original presentation in terms of average fitness effects, has

171   recently been derived afresh by Francois Rousset [31] (but see [32] in section

172   'Causality, group adaptations, and major transitions'), also criticising the

173   deliberate misapplication of causal interpretations to correlational models [28]

174   and the general critique of the statistical approach to analysing social evolution

175   models (e.g. [29]). Since this approach is fundamentally-rooted in the field of

176   quantitative genetics [21,33], presumably the critics of the statistical approach to

177   studying responses to selection also take issue with this well-established and

178   very productive field. Others have also noted that finding shortcomings in the

179   mathematical tools used to analyse models in inclusive fitness terms does not

180   equate to finding shortcomings in the underlying biological concepts that these

181   tools attempt to describe [16,17,23].

182

183   ***Causality, group adaptations, and major transitions***

184   The preceding sections appear to give a gloomy, and well-known, picture

185   of misunderstandings of inclusive fitness theory, and their associated

186   correctives. However in parallel with these attacks, and possibly in part because

187   of them, inclusive fitness theory has over the last few years begun moving in

188   increasingly fruitful and important directions. Here I highlight developments in

189   three closely related areas; evaluating causality, determining sufficient

190   conditions for the evolution of group adaptations, and studying the link between

191   inclusive fitness theory and major transitions in organismality, particularly from

192   single cellular life to complex multicellularity, and from subsociality to obligate

193   eusociality, or superorganismality.

194   Assessing causality is of fundamental interest to evolutionary biologists,

195   dating back to the ultimate / proximate distinctions of Tinbergen [34] and Mayr

196   [35]. Hamilton was motivated to develop inclusive fitness theory because of the

197   apparent gap in the power of neo-Darwinism to explain why self-sacrificing

198   behaviour should evolve. In the simplest cases, separating direct (own) from

199   indirect (others') fitness effects makes clear what conditions are necessary for a

200   social behaviour to evolve, and enables it to be classified as either altruism, spite,

201   mutual benefit, or selfishness [1]. These questions are those that evolutionary

202   biologists seek to answer on a daily basis when asking 'why did this trait evolve?'

203   Mathematical biologists considering exact models of evolution may be apt to

204   forget this [29]; without the decomposition that inclusive fitness provides the

205   only adaptive explanation to the biologists' question that a mathematical model

206   may provide is the tautological and insight-free 'because it was favoured by

207   selection'. Inclusive fitness theory is particularly useful for empirical

208   evolutionary biology because it facilitates construction of hypotheses about what

209   might be expected to evolve, naturally taking account of conflicts between

210   groups, within groups, and even within individuals and genomes; given that

211   inclusive fitness theory summarises complexity with simple parameters with

212   well-defined biological meanings, these hypotheses lend themselves well to

213   empirical validation (e.g. [5,36]).

214   As discussed in 'Separating concepts and tools', the increasingly popular

215   partial regression approach to deriving Hamilton's rule has been derived from

216   Hamilton's initial verbal consideration of average fitness effects [31]. Yet Samir

217   Okasha and Johannes Martens have noted that in non-additive social

218   interactions, the partial regression definitions of the costs and benefits of

219   Hamilton's rule do not equal the expected fitness changes from 'mutating' the

220   genotype of a random member of the population [32]. The solution they follow,

221   also briefly suggested in [23], is to apply Fisher's 'average effect of a gene

222   substitution'; Okasha and Martens find that, under a very particular

223   interpretation of Fisher's argument, it does indeed provide a causal explanation

224   for the costs and benefits of Hamilton's rule [32].

225   While the evolution of social behaviour within groups due to inclusive

226   fitness benefits, or equivalently due to between-group competition outweighing

227   within-group competition, is well understood, the evolutionary process by which

228   group-level adaptations arise has been far less so [37]. As noted in 'Critiques of

229   inclusive fitness theory, and their responses', models based on inclusive fitness

230   and based on group competition necessarily predict the same direction of

231   evolutionary change. Yet as Okasha notes the two frameworks, despite giving

232 equal evolutionary change predictions, can differ in the causal explanations they

233 provide [38,39]. By constructing causal graphs of different social scenarios in

234 which group-level fitness emerges from individual-level fitnesses, and vice-

235 versa, Okasha found instances in which each framework provided incorrect

236 causal explanations. Since the evolution of group-level adaptations requires a

237 transition from group-fitnesses-determined-by-individual-fitnesses to

238 individual-fitnesses-determined-by-group-fitnesses [40,41], such causal analyses

239 will be very important in understanding how these adaptations can arise, and be

240 correctly identified as such. Juusi Lehtonen subsequently showed how multi-

241 level selection models can be recast using inclusive fitness theory quantities,

242 making clearer the deep conceptual relationships between the two approaches,

243 and illustrating this with reference to causal graph models of sperm competition

244 [42].

245   As alluded to above, identification of group adaptations has a long and

246 contentious history [37,43,44]. Jonathan Pruitt and Charles Goodknight recently

247 claimed to have collected evidence that adaptive changes in aggressiveness

248 phenotype ratio in colonies of social spiders, in response to varying colony size

249 and environmental conditions, arise due to group-level selection and constitute

250 group-level adaptations [45]. Various authors have pointed out the need to

251 account for the potential for individual-level selection within groups conflicting

252 with selection between groups [46–48]. Recently Jay Biernaskie and Kevin

253 Foster presented ecologically-motivated models incorporating within-group

254 competition; these models give improved fits to Pruitt and Goodnight's data,

255 concluding that the 'group-level' adaptive trait identified by those authors is

256 actually explained by individual-level within-group selection [49].

257   Arguably the most significant of group adaptations are those in which a

258 new level of evolutionary individual emerges; in understanding these scenarios,

259 dubbed major evolutionary transitions [50], inclusive fitness theory is

260 increasingly proving its worth. While the inclusive fitness theory community has

261 accumulated evidence and theory to undermine the 'haplodiploidy hypothesis'

262 (see 'Critiques of inclusive fitness theory, and their responses'), inclusive fitness

263 theory has been crucial in providing a new framework, the 'monogamy

264 hypothesis' [51] that has explanatory power for transitions to (and from)

265 reproductive helping by offspring, in social insects [52] and in cooperatively

266 breeding birds [53], for example; this approach has also been adapted to

267 consider the evolution of multicellularity [54]. Wilson's collaborator Martin

268 Nowak, and colleagues, have recently presented a population genetical model

269 claimed to show that monogamy is not necessary for the evolution of

270 reproductive division of labour under haplodiploidy, which they take to be a

271 refutation of the monogamy hypothesis [55]; while it is beyond the scope of this

272 Opinion to address this model in any detail, others question whether the result

273 may be little more than a mathematical curiosity [56], and given that previous

274 detailed models claiming to show no role for relatedness in the evolution of

275 eusociality [4] have subsequently been re-analysed to show its central

276 importance [22], as described above, the model of [55] will merits analysis from

277 an inclusive fitness perspective. In fact, Nick Davies and Andy Gardner do

278 precisely this, and do indeed show that the disconnect between monogamy and

279 the evolution of reproductive division of labour is indeed a mathematical artefact

280 of the assumptions made in the model [57]. There is also the issue of whether

281 this result, if it were correct, really addresses the monogamy hypothesis, as

282 discussed below.

283 Recently, focussing on social insects, Jacobus Boomsma and Richard

284 Gawne have reviewed the literature on the 'superorganism concept' from its

285 earliest statements at the turn of the 20th century through to its present day

286 presentation and usage. Boomsma and Gawne [58] note that the historical

287 conception of superorganismality, as requiring an irreversible group-level

288 adaptation in the form of a distinct non-reproductive caste, dates back to

289 Wheeler, Huxley and Fisher, but that this strict criterion was subsequently

290 diluted by weaker and biologically-ungrounded definitions of eusociality, and in

291 particular by the rise to prominence of E. O Wilson's definition of the

292 superorganism. By linking with the monogamy hypothesis Boomsma and Gawne

293 highlight the importance of inclusive fitness theory and irreversible

294 commitments to caste formation, in the form of germ/soma segregation, in

295 explaining the major transitions to complex eusociality and multicellularity, and

296 the genuine group-level adaptations they exhibit. It is worth briefly noting that in

297 criticising the monogamy hypothesis, Nowak and colleagues [55] use the less

298 specific definition of eusociality as reproductive division of labour, rather than

299 irreversible commitment to a sterile caste. Sterility of workers can be reversed

300 over evolutionary time in their model, and indeed the original transition to

301 workers foregoing mating, and hence by necessity foregoing production of

302 daughters, is not even considered; thus their model is not well-motivated as a

303 critique of the monogamy hypothesis, which seeks to explain eusociality *sensu*

304 *stricto* [58].

305

306 ***Conclusions***

307 Most of the critiques of inclusive fitness theory mentioned above ('Critiques of

308 inclusive fitness theory, and their responses') would be uncontroversial, and

309 potentially useful, if presented as investigations into the subtleties of inclusive

310 fitness theory, rather than debunkings of it; as discussed above, they may well

311 claim to have inspired further research into the subtleties and application of

312 inclusive fitness theory. Of course iconoclasm provokes attention, and fame is

313 usually attached to the protagonists in 'revolutionary science' than the

314 practitioners of 'normal mode' science [7], so we may never be free of attempts

315 to dethrone Hamilton, or the modern synthesists, or even Darwin. However the

316 theory of evolution through natural selection, and its expositions and

317 refinements, have withstood sustained assault for over 150 years, and there is

318 now little reason to expect fatal flaws to be discovered in the future. One thing

319 that may mark out the recent controversy as a sociological phenomenon are the

320 shifting arguments of the critics of inclusive fitness theory (see 'Critiques of

321 inclusive fitness theory, and their responses'), which are more typical of the

322 defence of a particular world-view than a genuine search for scientific

323 understanding. These may also be symptomatic of differences in the viewpoints

324 of Wilson and his various collaborators. Furthermore, David Queller has shown

325 how understanding the historical development of inclusive fitness theory and its

326 application may help to understand recurrent criticisms [59]. To echo Darwin's

327 words, however, "I look with confidence to the future, to young and rising

328 naturalists, who will be able to view both sides of this question with

329 impartiality." ([60], quoted in [7], p. 151)

330

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449   56.   Queller DC: **The theory of inclusive fitness**. *Q. Rev. Biol.* 2016, **91**:343–
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454   **points of no return: how the major evolutionary transitions were lost**
455   **in translation**. *Biol. Rev.* [date unknown], [no volume].
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458   60.   Darwin C: *On the Origin of Species by Means of Natural Selection; Or, the*
459   *Preservation of Favored Races in the Struggle for Life*. John Wiley; 1889.
460
461   *Reference Annotations*

462   • Liao, Rong and Queller (2015) - ** In this modelling paper the authors

463   present a fuller examination of the model of the evolution of 'eusociality'

464   presented by Nowak, Tarnita and Wilson. They find that while the model

465   is correct, an overly restrictive set of assumptions led to Nowak et al.'s

466   claims that it was inconsistent with inclusive fitness theory. Relaxing

467   these assumptions Liao et al. find that the model actually confirms

468   predictions from inclusive fitness theory.

469   • Marshall (2015) - * This monograph attempts to provide an accessible

470   introduction to how inclusive fitness theory works, and how to interpret

471   the controversies surrounding it; a particular focus on causality, for

472   example explaining competing classifications of the same social

473   behaviour, is held.

474   • Bourke (2015) - ** In this review Bourke addresses recent criticisms of

475   sex-ratio predictions derived from inclusive fitness theory, by Wilson and

476   Nowak. With reference to classical sex ratio theory and empirical data

477   Bourke shows how Wilson and Nowak's thesis fails to explain

478   experimental observations that match standard predictions of inclusive

479   fitness theory.

480   • Okasha (2015) - ** In this modelling paper Okasha uses causal graphs to

481   examine conditions under which inclusive fitness and multilevel selection

482   partitions are more or less 'causally apt' as descriptions of evolutionary

483   change, despite the fact that both approaches predict the same gene

484   frequency change under selection. Examples are presented in which each

485   partition provides the more appropriate causal representation.

486   • Davies and Gardner (2016) - * This article reviews the mathematical

487   assumptions in the model of the evolution of worker sterility by Olejarz et

488   al. (2015), showing that main results of that model arise from assuming

489   genes of large effect. When these assumptions are relaxed the model

490   shows monogamy promotes raising of siblings in social insect colonies, as

491   predicted by inclusive fitness theory.

492   • Boomsma and Gawne (2016) - ** In this review the authors forensically

493   investigate the history and conceptual content of the superorganism

494   concept, from its origin in the early 20th century to its present day form.

495   With reference to inclusive fitness theory and the major transitions to

496   obligate eusociality and multicellularity, the authors show that the

497   original presentation of superorganismality was biologically sound and

498   useful, but subsequent presentations of the idea have diluted its biological

499   meaning.

500   • Lehtonen (2016) - * In this article Lehtonen shows how inclusive fitness

501   quantities (the r, b and c of Hamilton's rule, equation in main text) can

502   appear explicitly in multi-level selection analyses. Lehtonen illustrates the

503   utility of recognising the 'kin selection' components of multilevel selection

504   with reference to causal graph models, and the popular 'evolutionary

505   stable strategy' approach to building inclusive fitness models.