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Abstract

Proponents of the “Extended Evolutionary Synthesis” argue that the current state of evolutionary biology departs from what was established in Modern Synthesis to such a degree that a new synthesis is needed. They present a “laundry list” of complaints concerning the core focus and assumptions of the Modern Synthesis and argue that the perspective of evolutionary biology must be shifted and these core assumptions relaxed in order to incorporate a plethora of new evolutionary factors. However, we contend that this revolution is already well underway, in the form of the inclusive-fitness research programme. We provide an overview of the inclusive-fitness revolution, charting its origins, explaining its core concepts and outlook, and describing the ways in which it has developed into a fully fledged and extraordinarily productive programme of scientific research. We then consider the apparently neglected processes and perspectives from an inclusive-fitness viewpoint. We conclude that progress in evolutionary theory is facilitated by focusing research attention on areas where there is a relatively poor fit between theoretical predictions and empirical observations, rather than complexifying models in pursuit of extra realism for its own sake.

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20.1 Introduction

In the last few years, several researchers have suggested that evolutionary biology requires a rethink in the form of an “Extended Evolutionary Synthesis” (EES; Pigliucci and Müller 2010, Laland et al. 2015, Müller 2017). Proponents of the EES argue that the current state of evolutionary biology departs from what was established in the Modern Synthesis (Huxley 1942) to such a degree that a new synthesis is needed. They present what has been described as a “laundry list” (Welch 2017) of complaints concerning the core focus and assumptions of the Modern Synthesis and argue that the perspective of evolutionary biology must be shifted, and these core assumptions relaxed in order to incorporate a plethora of new evolutionary factors (Table 8.1). In short, they call for revolution.

Our contention is that this revolution is already well underway, in the form of the inclusive fitness research programme (Hamilton 1964; Frank 1998; Bourke 2011; Gardner and West 2014). The concept of inclusive fitness arose in the 1960s and therefore postdates the Modern Synthesis of the 1940s. In its nearly 60 years of productive interplay between theoretical and empirical science, the inclusive fitness research programme has already incorporated much of the laundry list of supposedly neglected evolutionary factors. It is therefore surprising that proponents of the EES have variously mischaracterised (Wilson 2010), sidelined (Pigliucci and Müller 2010) or outright ignored (Müller 2007; Pigliucci 2007; Laland et al. 2014; Müller 2017) inclusive fitness theory, or even sought to characterise it as part of the edifice of the Modern Synthesis itself (Laland et al. 2015).

In this chapter, we provide an overview of the inclusive fitness revolution, charting its origins, explaining its core concepts and outlook, and describing the ways in which it has developed into a fully-fledged and extraordinarily productive programme of scientific research. We then consider each of the items of the EES “laundry list” in turn, showing how these apparently neglected processes and perspectives have been readily addressed within the framework of inclusive fitness. In doing so, we reveal a sharp contrast between the scientifically driven inclusive fitness revolution, on the one hand, and the philosophically driven EES movement, on the other, suggesting that progress in evolutionary theory has been facilitated by focusing research attention on areas where there is a relatively poor fit between theoretical predictions and empirical observations, rather than on needlessly complexifying models in the pursuit of extra realism for its own sake.

20.2 The Inclusive Fitness Revolution

The problem of adaptation is an ancient one but was expressed particularly clearly and urgently by William Paley in his landmark book *Natural Theology* (Paley 1802), which had a profound influence on Charles Darwin's thinking. Paley framed the problem of adaptation in terms of how to explain the apparent design of biological organisms, which he defined in terms of “contrivance and relation of parts”—that is, concerning the way in which each part of the organism appears intricately devised to carry out some purpose, and the way in which all parts of the organism appear devised to carry out the same purpose (Gardner 2009). Paley particularly highlighted the human eye, and its component parts, as a clear example of exquisite design, and Darwin likewise gave the eye special attention in *The Origin of Species* (Darwin 1859) when explicating how his theory of natural selection provided an explanation for this contrivance and relation of parts.

Darwin's theory of natural selection is based on the empirical observation that individual organisms vary, including in ways that are heritable. Accordingly, those variations in organismal characters that are associated with greater survival and fecundity will tend—by virtue of their bearers enjoying greater lifetime reproductive success—to accumulate in natural populations. Consequently—Darwin argued—subsequent generations of biological organisms are expected to appear increasingly well designed to maximise their reproductive success, as each and every one of their heritable characters becomes increasingly contrived as if for this purpose. Darwinism thereby provides a scientific theory for the process and purpose of organismal design (Gardner 2009).

However, Darwin (1859, pp. 192, 236–242) realised that there were clear examples of exquisite biological design that could not readily be explained by the above principle. In particular, he discussed the adaptations of sterile worker insects that are neither borne by members of the reproductive castes nor passed onto the sterile workers' offspring—for these individuals have no offspring. At first sight, it appeared that there was no possibility for natural selection to have moulded these adaptations. But, by drawing an analogy with the artificial selection practices of animal breeders, Darwin offered a solution to this problem. In situations where a desirable trait—such as delicious meat—cannot be assessed until after the individual has been killed, animal breeders understood that they may nevertheless have an opportunity to perform artificial selection indirectly, by prioritising the close kin of the killed individual for breeding, as relatives are expected to share heritable tendencies in common. In relation to the social insects, Darwin suggested that natural selection could also work indirectly, through the survival and fecundity of the workers' fertile family members, such that if the worker traits improved the reproductive success of their kin, then these too could be moulded through the action of natural selection.

Darwin's core logic of adaptation by natural selection was formalised by R. A. Fisher in *The Genetical Theory of Natural Selection* (Fisher 1930) as the “fundamental theorem” of natural selection. This reveals that the direct action of natural selection on the average of individual fitness is equal to the heritable variance in

fitness, which can never be negative, and hence the fundamental theorem provides a maximisation principle in which natural selection is always working to improve the individual's Darwinian fitness. Crucially, in setting out his assumptions, Fisher (1930, p. 27) explicitly excluded indirect effects whereby "an animal favours or impedes the survival or reproduction of its relatives", understanding that such kin effects need not result in the individual appearing to maximise its own Darwinian fitness, and perhaps feeling that there was no corresponding maximisation principle to be recovered under such circumstances (Gardner 2017). However, he did return to this indirect form of selection in his discussion of the evolution of anti-predator distastefulness in gregarious insect larvae (Fisher 1930, p. 158–159), suggesting that this is driven by a selective advantage enjoyed by siblings; this passage appears to represent the first quantitative use of the kin selection coefficient of relatedness (Best et al. 2018).

More than a century after Darwin had set out the basic logic, indirect selection finally received a formal, comprehensive, population genetics treatment through W. D. Hamilton's work on the evolution of altruistic behaviour (Hamilton 1963, 1964), and was given the name "kin selection" (Maynard Smith 1964). Hamilton showed how direct and indirect selection aggregate as a simple sum to give the overall action of natural selection, such that individual traits are expected to be moulded under their combined action, and he clarified that the impact that an individual's traits have on the fitness of her relatives translate into the action of indirect selection in proportion to their degree of relatedness. These insights are encapsulated in "Hamilton's rule" (Hamilton 1963, 1964, 1970; Charnov 1977), which in its simplest form states that the condition for a trait to be favoured by natural selection is that the sum of the fitness impact upon self ($-c$) and the product of the fitness impact upon a social partner (b) and the relatedness to this social partner (r), exceeds zero (i.e. $-c + br > 0$). As Hamilton's focus was mainly upon altruism, the impact of an individual upon her own fitness is often described in terms of "cost" and her impact on her social partner's fitness is often termed a "benefit", but more generally Hamilton's rule applies just as readily to mutually beneficial, selfish, or even spiteful behaviours (Hamilton 1964, 1970; West et al. 2007).

Kin selection can be conceptualised in two different ways (Fig. 20.1). The "personal fitness" (or "neighbour-modulated fitness") approach fastens attention upon a focal recipient and describes how her personal fitness is modulated by her own traits and also those borne by her social partners (Hamilton 1964; Frank 1998). Under this view, the cost term ($-c$) describes the impact that the individual has upon her own reproductive success and the benefit term (b) describes the impact the individual's social partner has upon her reproductive success. The idea here is that natural selection favours those heritable traits that are associated with higher fitness, and this association can be positive even if the trait directly reduces the individual's fitness (described by $-c$) so long as carriers of the heritable trait tend to have social partners who also bear the trait (described by r), and these social partners provide a sufficiently large benefit to her (described by b). Accordingly, under the personal fitness view of kin selection, the coefficient of relatedness functions as a statistical constraint that exists between the heritable traits of social partners, and which acts as

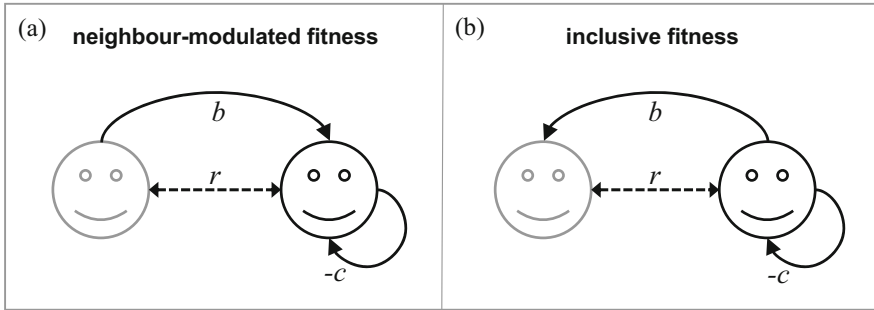


Fig. 20.1 Alternative formulations of kin selection. **(a)** The personal fitness approach fastens the attention on a focal recipient (black), her impact ($-c$) upon her own fitness, and the impact (b) of her social partner (grey) upon her own fitness, with the coefficient of relatedness (r) representing a statistical constraint that exists between the heritable traits of social partners. **(b)** The inclusive fitness approach fastens the attention on a focal actor (black), her impact ($-c$) upon her own fitness, and her impact (b) upon the fitness of her social partner (grey), with the coefficient of relatedness (r) representing a measure of the value that the actor places upon her social partner

a confounding effect such that the correlation between trait and fitness that drives natural selection does not reflect straightforward causation.

Alternatively, the “inclusive fitness” approach to kin selection fastens attention upon a focal actor and describes how her trait modulates her own fitness and the fitness of her social partners (Hamilton 1964; Frank 1998). Under this view, the cost term ($-c$) describes the impact that the individual has upon her own reproductive success, the benefit term (b) describes the impact the individual has on her social partner’s reproductive success, and relatedness (r) enters into the calculus not as a constraint but as a measure of the value that the actor places upon her social partner. This reframing of kin selection recovers a direct causal pathway between trait and fitness, by changing the definition of fitness itself. The individual’s inclusive fitness is defined as her personal fitness, minus all the effects of her social partners, and plus all the effects she has on her social partners, with each of the latter effects being weighted by her genetic relatedness to these recipients.

In developing the concept of inclusive fitness, Hamilton recovered a maximisation principle for natural selection that applies irrespective of whether kin selection is present or absent. Natural selection can be framed both from personal fitness and inclusive fitness perspectives: the overall action of natural selection with respect to any heritable trait can be viewed either in terms of that trait’s correlation with personal fitness or with inclusive fitness—both approaches give exactly the same result. But personal fitness does not yield a maximisation principle, simply because the individual does not have full control over her own reproductive success, such that if she were viewed as striving to maximise her personal fitness then her only means of doing so would be by maximising her direct fitness, and this would not account for the confounding effects of kin interactions. In contrast, the individual does—by definition—have full control over her inclusive fitness, and hence can be validly viewed as striving to maximise this quantity (Grafen 2006; West and Gardner

2013). That is, Hamilton not only revolutionised the way we think about the process of adaptation—by formalising the logic of indirect selection and placing it on the same footing as direct selection—but also revolutionised the way we think about the purpose of adaptation—by revealing that organisms are not expected to appear designed to maximise their personal fitness but rather they are expected to appear designed to maximise their inclusive fitness.

Hamilton's work on kin selection was initially formalised by means of a simple population genetics model that made various simplifying assumptions about gene action, including additivity and weak selection. However, he subsequently made use of George Price's (1970) eponymous theorem to provide a much more general derivation (Hamilton 1970), and this approach has subsequently given rise to what is often termed the "regression" approach to Hamilton's rule, which is understood to apply as generally as the theory of natural selection itself (Orlove and Wood 1978; Queller 1992; Frank 1998; Gardner et al. 2011). Accordingly, in its general form, the theory of kin selection allows for heritable variants of large phenotypic effect, with concomitant strong and/or frequency-dependent selection, although in particular applications simplifying assumptions are often employed for the sake of analytical tractability. Price's theorem is celebrated for its substrate neutrality, such that it applies to genetical and non-genetical evolutionary change alike (Frank 1995; Price 1995). But less appreciated is that Hamilton's rule, too, can thereby be framed in general terms that transcend genetics. For example, the above account of Hamilton's work on kin selection has been framed without explicit reference to genes, and indeed Price's theorem allows for the logic of kin selection to be formalised under the assumption of blending inheritance, yielding exactly the same form of Hamilton's rule and with individuals placing the same value upon the reproductive success of their relatives (Gardner 2011).

A crucial step in the historical development of inclusive fitness was the way in which the re-derivation of Hamilton's rule from Price's theorem clarified the relationship between kin selection and group selection. During the first half of the twentieth century, evolutionary geneticists understood that natural selection was in principle a multi-level process, with Sewall Wright (1931) placing much emphasis on inter-demic selection as a facilitator of adaptation under his "shifting balance" view of evolution. Partly on account of Wright's work, much of the study of social evolution during the middle years of the century was in thrall to the idea that natural selection drives the evolution of adaptations that function to maximise the overall fitness of the population or species, with many apparently altruistic behaviours being explained away on the basis of confused and confusing "for the good of the species" thinking (Wynne-Edwards 1962; Lorenz 1963). Inclusive fitness theory provided an alternative explanatory framework for such behaviours and in a way that truly reflected how natural selection operates. Yet, Price (1972) showed that his theorem also provides a rigorous account of how selection operating at the between-group level can contribute to the overall action of natural selection, albeit alongside selection operating at the within-group level, which will often be stronger and sometimes acting in the opposite direction. That Price's equation underpins the theories of both kin selection and group selection has allowed the conceptual links

between the two theories to be clarified, and 50 years later most social evolution researchers understand that the two theories are not in opposition and simply provide alternative ways of describing the very same process of natural selection (Hamilton 1975; Leigh 2010; Frank 2013; Gardner 2020).

Just as the original motivation for the theory of inclusive fitness was strongly empirical, and stemmed from an apparent mismatch between the predictions of classical Darwinism versus the observations of puzzling organismal adaptation, so too have the many successful applications of inclusive fitness theory been driven by a tight interplay of theoretical and empirical considerations. A striking example is the study of sex allocation, wherein the classic prediction that natural selection favours an even investment of parental resources into offspring of both sexes—on account of individuals of the rarer sex tending to leave more descendants than individuals of the more common sex (Fisher 1930)—is flagrantly disregarded by many chronically inbreeding arthropods that exhibit highly female-biased sex ratios, and this mismatch stimulated the theory of “local mate competition” (Hamilton 1967), concerning the inclusive fitness consequences of sex allocation when mating groups are made up of close relatives. This close interaction of theoretical and empirical research has continued unabated, with the result that the theory of sex allocation enjoys excellent empirical support, and those areas within which the fit between theory and data is less strong quickly receive research attention such that the underlying biology rapidly becomes illuminated (West 2009).

The concept of inclusive fitness was developed to recover a fitness measure that the individual organism could be viewed as striving to maximise, yet it may also be usefully applied to the level of single genes to illuminate their evolutionary interests (Gardner and Welch 2011). For the most part, fair meiosis aligns the inclusive fitness interests of genes inhabiting the same body, such that the whole organism can be viewed as a unified inclusive fitness maximiser (Leigh 1977). However, genes residing in the same body may in some circumstances have divergent inclusive fitness interests, resulting in intragenomic conflict (Burt and Trivers 2006; Gardner and Úbeda 2017). One way in which this may happen is if different genes follow different rules of inheritance—such as nuclear genes that are inherited biparentally versus cytoplasmic genes that are inherited uniparentally—which may, for example, lead to disagreements over sex allocation on account of these genes disagreeing as to the valuation of sons versus daughters (Werren et al. 1988). Alternatively, even if inheritance is fair and Mendelian, genes may come into conflict with each other owing to their bearer engaging in social interactions that modulate their inclusive fitness in different ways. For example, if an individual engages in social interaction with her maternal half-siblings, then whereas her maternal-origin genes would maximise their inclusive fitness by inclining her to behave relatively altruistically her paternal-origin genes would maximise their inclusive fitness by inclining her to behave relatively selfishly, on account of the former being more related than the latter to these social partners (Haig 2002). The resulting parent-of-origin conflict is predicted to result in the self-imposed silencing of one of the genes, i.e., “genomic imprinting”, a phenomenon that is difficult to account for in terms of individual-level advantage (Haig 2002).

The kinship theory of genomic imprinting does not only illuminate patterns of gene-level adaptation but also patterns of organism-level maladaptation. In particular, the effective haploidy of imprinted loci renders the individual especially vulnerable to mutations that would otherwise be recessive under diploidy, and the tension that exists between genes in conflict means that when mutational or epimutational perturbations occur the phenotypic effects can be drastic. Accordingly, genomic imprinting is associated with an array of debilitating human disorders—particularly concerning fertility, pregnancy, and infancy, wherein conflicts over resource allocation are expected to be rife—with the associated clinical pathologies having patterns that are predictable in light of the inclusive fitness interests of maternal-origin versus paternal-origin genes (Wilkins and Úbeda 2011). For example: Prader–Willi syndrome is associated with a deletion of a gene cluster in chromosome q15 being inherited from the individual’s father, and involves a clinical phenotype in children that makes sense in terms of reducing the amount of resource to be extracted from the mother, such as lack of appetite; whereas Angelman syndrome results from the very same deletion being inherited from the individual’s mother, and involves a clinical phenotype in children that makes sense in terms of increasing the amount of resources to be extracted from the mother, such as frequent waking at night to feed (Haig and Wharton 2003; Haig 2014).

Conversely, shifting up a level of biological organisation from the individual organism, inclusive fitness also illuminates the major transitions in individuality (Maynard Smith and Szathmáry 1995; Bourke 2011). These transitions can be viewed as occurring when what was previously a group of separate individuals evolves to such a high degree of coordination and complexity—i.e. exhibiting the contrivance and relation of parts that provides the hallmark of design—that they are more usefully regarded as higher-level individuals in their own right. Examples include repeated evolutionary transitions from unicellular to multicellular life and from solitary individuals to eusocial colonies. Mirroring the principle that it is divergent inclusive fitness interests of genes that foment intragenomic conflicts which undermine the adaptive integrity of the organism, major transitions in individuality are best understood in terms of the inclusive fitness interests of social partners coming into such close alignment that conflicts between them are, at least in many respects, extinguished (Gardner and Grafen 2009). Accordingly, complex multicellular life has only arisen in lineages where a single-cell bottleneck ensures clonal relatedness between constituent cells (Fisher et al. 2013), and eusociality has only arisen in lineages where colonies are headed by a single, singly mated female, which ensures that the inclusive fitness value of rearing a sibling is equal to that of rearing one’s own offspring (Hughes et al. 2008; Boomsma 2009). Thus, the theory of inclusive fitness explains the broadest scale evolutionary patterns through the history of life.

20.3 The Laundry List in the Light of Inclusive Fitness

Returning to the “laundry list” of neglected evolutionary processes that have been highlighted by proponents of the EES as necessitating a revolution in evolutionary biology, we now provide an assessment of these claims from an inclusive fitness perspective. The details of the list vary between tellings, as different researchers naturally have different emphases and different complaints to raise as to the ways in which they perceive that evolutionary biology has been pursued. Accordingly, we focus on the list given by Kevin Lala (formerly Laland) and colleagues in *The extended evolutionary synthesis: its structure, assumptions and predictions* (Laland et al. 2015), as the authorship of this paper includes many of the core contributors to the EES movement and thereby promises to provide a definitive account (Table 20.1).

A core complaint made by proponents of the EES is that conventional evolutionary biology focuses attention upon an arrow of causation that flows from environment to organism and does not give due attention to causal pathways running in the reverse direction, such that the possibility for “reciprocal causation”—whereby organisms both shape and are shaped by their environments—is neglected (Laland

Table 20.1 Extended evolutionary synthesis core assumptions and views from inclusive fitness theory

Extended evolutionary synthesis core assumptions (Laland et al. 2015)	The view from inclusive fitness theory
“Reciprocal causation (organisms shape, and are shaped by, selective and developmental environments)”	A core motivation for the theory of inclusive fitness is that organisms shape, and are shaped by, their selective and developmental environments—i.e., social interaction.
“Organism-centred perspective”	A core motivation for the concept of inclusive fitness is to provide an organism-centred perspective on social adaptation.
“Variable rates of change”	Inclusive fitness theory allows for mutational steps of arbitrarily large effect, and its whole-organism outlook reaffirms that the “gradualism” versus “saltationism” controversy concerns the process of adaptation rather than the process of evolution.
“Inclusive inheritance”	The logic of inclusive fitness holds even under non-genetic systems of inheritance, such as blending, and it explains the evolution of epigenetic effects.
“Non-random phenotypic variation”	Inclusive fitness theory predicts patterns of mutational and epimutational maladaptation, including by showing how these align with fitness interests of conflicting agents.
“Macro-evolution”	Inclusive fitness theory explains major transitions in individuality, which represent the most fundamental events in the unfolding of the history of life.

et al. 2015, Müller 2017; Table 20.1). This comes as a surprise to those working within the inclusive fitness research programme, as the basic motivation for this topic of study is to understand the consequences of an evolving population being part of its own selective environment.

A simple but striking illustration is provided by the evolution of dispersal. In seeking to understand why an individual would go to the effort to relocate from one place to another, often at considerable cost, a traditional approach has been to imagine that the prospects for the individuals are—at least on average—better at their destination than at their point of origin. However, the kin-selection analysis of Hamilton and May (1977) showed that even in stable, saturated environments, whereby the reproductive prospects for an individual at home are no better nor worse than anywhere else in the population, a substantial proportion of individuals are nevertheless expected to disperse because, were they to instead remain in their natal patch and succeed in achieving reproductive success, this would come at the expense of their kin who are competing for the same reproductive resources. Indeed, in their simple model involving a single, asexually reproducing breeder in each patch, Hamilton and May showed that even if dispersal is associated with almost-certain death nearly one-half of all individuals are expected to disperse, despite this reducing their reproductive opportunities to essentially zero, in order to improve the prospects of their surviving family members. More generally, for sublethal costs of dispersal, Hamilton and May's analysis captures the reciprocal causality of kin competition modulating selection for altruistic dispersal and altruistic dispersal modulating the intensity of kin competition, such that as the overall rate of dispersal increases then resource competitors become less related to each other, which reduces the kin-selected benefit of dispersal, and hence the overall rate of dispersal always stabilises at an intermediate level at which these forces exactly balance out (Frank 1986, 2013).

Beyond simple models of single organismal traits, the theory of inclusive fitness also illuminates complex, multi-trait, long-term, open-ended evolution. For example, the sperm-storage capabilities of the ancestors of the social hymenoptera permitted an iteroparous lifecycle to be compatible with a strictly monogamous mating system, such that an individual's relatedness to her maternal siblings is exactly equal to that of her own offspring, and hence her inclusive fitness is maximised by giving up her own reproductive success in order to improve the reproductive success of her mother provided there are any efficiency benefits of such cooperative breeding (Hamilton 1964; Boomsma 2007, 2009, 2013). The ensuing evolution of a non-reproductive helper caste with concomitant division of labour and efficiencies of scale have given rise to elaborate insect societies, in which the selection pressures exerted upon individuals and their traits are qualitatively different from those experienced by their non-social ancestors, and which have been associated with the further elaboration of phenotypes, including the evolution of multiple non-reproductive castes and the conquest of previously inaccessible ecological spaces (Boomsma and Gawne 2018).

A further core complaint made by proponents of the EES is that conventional evolutionary biology is focused on genes and has lost sight of the organism, including as an active participant in its own evolutionary fate (Laland et al. 2015,

Müller 2017; Table 20.1). Again, this claim is surprising to those working within the inclusive fitness research programme because, as discussed above, the recovery of a whole-organism adaptive rationale in the context of social interactions among relatives was precisely what motivated the development of the concept of inclusive fitness in the first place. Hamilton (1964) initially framed his analysis of the action of kin selection in terms of the individual's personal (or "neighbour-modulated") fitness, whereby indirect fitness effects are described from a recipient-centred perspective, but he went on to reframe the theory in terms of inclusive fitness, in which attention is fastened on a focal actor who wields full control over the maximand that captures her evolutionary interests. Inclusive fitness is firmly rooted into the whole-organism perspective of Paley (1802) and Darwin (1859), who both sought to explain the same contrivance and relation of parts manifested by organisms, though in rather different ways. Indeed, we find it surprising that proponents of the EES would seek to champion the whole-organism view whilst simultaneously arguing against the "pre-eminence" of natural selection (Laland et al. 2015), given that it is from the logic of natural selection that the concept of whole-organism fitness is derived and hence it is difficult to see how, in a hypothetical scenario in which natural selection is overpowered by non-Darwinian forces, biological organisms manifesting a unity of purpose could arise at all.

Insofar as the concept of inclusive fitness has also been applied at the intra-individual level, to understand the interests of single genes, the motivation for this has also largely stemmed from a whole-organism perspective, whereby the gene's-eye view has been taken in order to illuminate instances of organismal maladaptation (Burt and Trivers 2006; Gardner and Úbeda 2017). Inclusive-fitness interests are not perfectly aligned within genomes, and even genes obeying the rules of autosomal, mendelian inheritance can come into conflict with each other, as illustrated by the kinship theory of genomic imprinting whereby an individual's maternal-origin and paternal-origin genes disagree as to how their carrier should behave towards her matrilineal versus patrilineal relatives, resulting in parent-of-origin specific gene expression and a concomitant range of debilitating human disorders (Haig 2002; Wilkins and Úbeda 2011). Yet the detection of such intragenomic conflicts also provides evidence that organisms are, on the whole, close to their inclusive-fitness optima, because it is only when the genes' carrier is close to her optimum that they are actually favoured to pull her phenotype in different directions (West and Gardner 2013).

Proponents of the EES also highlight the importance of "variable rates of change", which they contrast with the assumption of "gradualism"—defining this in terms of the phenotype evolving via multiple, small steps—that they say characterises current evolutionary biology thinking (Table 20.1). This, too, is surprising to those working within the inclusive fitness research programme. The inclusive-fitness framing of natural selection, and its encapsulation in the form of Hamilton's rule, emerges directly from Price's (1970) theorem (Hamilton 1970, Queller 1992, Frank 1998, Gardner et al. 2011; Box 20.1) and thereby enjoys a vast scope of application. There is no requirement that mutations must always be of small effect, or that mutations of larger effect cannot be favoured by natural selection

(Gardner et al. 2011). Of course, particular analyses often do make use of simplifying model assumptions and streamlined methodologies for the purpose of tractability, simplicity and transparency, and on this basis the assumption of small allelic effects is sometimes employed in order to bring the powerful tools of differential calculus to bear on a particular problem (Taylor and Frank 1996; Gardner et al. 2011). Insofar as these simplifications enable the derivation of clear and testable predictions, then they are scientifically valid, and it is good practice to combine these approaches with methodologies that enable the relaxation of such assumptions albeit at the price of reduced transparency—such as individual-based simulations—in order to check that the results are robust and not artefacts of the simplifying assumptions (e.g., Rodrigues and Gardner 2012).

Box 20.1 Price's Equation, Kin Selection, Inclusive Fitness and Multi-Level Selection

Price's (1970, 1972) equation provides a general description of evolutionary change. The following exposition is based on that of Gardner (2020). Price's equation states that the change in the population average value of any trait of interest z is given by:

$$\Delta E(z) = \text{cov}(w, z) + E(w\Delta z) \quad (20.1)$$

where w is relative fitness, Δz describes the difference between a parent's and their offspring's trait values, and cov denotes a covariance and E an expectation—with both of these descriptive statistics taken over all individuals in the population.

The covariance term on the right-hand side of Eq. (20.1) represents the part of evolutionary change that is due to selection, i.e. arising from statistical associations between trait and fitness, and the expectation term on the right-hand side of Eq. (20.1) represents the part of evolutionary change that is due to transmission, i.e. arising from imperfect heredity of trait values between parent and offspring. Accordingly, Price's equation isolates and formally defines the separate selection— $\Delta_S E(z) = \text{cov}(w, z)$ —and transmission— $\Delta_T E(z) = E(w\Delta z)$ —components of evolutionary change.

The action of selection can be expressed in terms of least-squares linear regression, as $\Delta_S E(z) = \beta(w, z)\text{var}(z)$, where $\beta(w, z) = \text{cov}(w, z)/\text{var}(z)$ is the least-squares linear regression of fitness against trait value and $\text{var}(z)$ measures the variance in trait value. This highlights that for selection to act in relation to any trait there must be variation in that trait and there must be a nonzero slope to the least-squares linear regression line fitted through the fitness and trait values. So long as there is variation present in the trait (i.e. $\text{var}(z) > 0$) then the condition for selection to favour an increase in the trait is that its marginal fitness is positive (i.e. $\beta(w, z) > 0$).

(continued)

Box 20.1 (continued)

Kin selection emerges directly from Price's equation simply by adding the trait values z' of social partners as an additional predictor of fitness. Marginal fitness is then given by $\beta(w, z) = \beta(w, z|z') + \beta(w, z'|z)\beta(z', z)$, where: $\beta(w, z|z') = -c$ is the effect of the focal individual's trait on her own fitness, holding the social partner's trait constant; $\beta(w, z'|z) = b$ is the effect of the social partner's trait on the focal individual's fitness, holding the focal individual's trait constant; and $\beta(z', z) = r$ is the coefficient of relatedness, describing the statistical association between the traits of social partners. The condition for selection to favour an increase in average trait value is therefore given by $\beta(w, g) > 0$, or

$$-c + br > 0 \quad (20.2)$$

i.e., Hamilton's rule of kin selection (Hamilton 1964, 1970; Queller 1992). Note that this derivation of Hamilton's rule has focused on the individual's personal fitness and considered how it is modulated by the traits of her social partners (including herself), and therefore represents the "personal fitness" approach to kin selection. The alternative "inclusive fitness" approach to kin selection is obtained by rewriting marginal fitness as $\beta(w, z|z') + \beta(w', z|z')\beta(z', z)$, where w' is the relative fitness of the actor's social partner. The marginal fitness $\beta(w, z|z') + \beta(w', z|z')\beta(z', z)$ thereby describes the inclusive fitness effect of the trait.

An alternative approach to social evolution is the "multi-level selection" approach, which emerges by partitioning Price's equation in a different way:

$$\Delta_S E(z) = \text{cov}_{i \in I} (E_{j \in J_i}(w_j), E_{j \in J_i}(z_j)) + E_{i \in I} (\text{cov}_{j \in J_i}(w_j, z_j)) \quad (20.3)$$

where every group in the population has been assigned a unique index $i \in I$ and where every individual in group- i has been assigned a unique index $j \in J_i$. The first term on the right-hand side of Eq. (20.3) represents the covariance of group-average fitness and group-average trait value across all social groups in the population and thereby describes the action of between-group selection, and the second term on the right-hand side of Eq. (20.3) represents the average within-group covariance of individual fitness and individual trait value and thereby describes the action of within-group selection.

It is important to clarify that such considerations of phenotypic change proceeding at variable rates, in fits and starts and in jumps of small and large size, are in fact tangential to the real issues underpinning the "gradualism" versus "saltationism" controversy. This debate concerns not phenotypic evolution as such, but rather the origin of adaptation—i.e., the appearance of design, as manifest in contrivance and relation of parts. The "saltationism" stance is that the *de novo* appearance of design can occur in a single step, e.g., the human eye arising fully formed as the result of a

single mutation, whereas the “gradualism” view is that such adaptations arise in multiple steps. The saltationism stance can be rejected purely on grounds of probability: although in principle a single mutation could result in the *de novo* appearance of an organ as complex as the human eye, this is highly improbable, and the cumulative action of natural selection, working over multiple generations, retaining those variants that lead to improvement and disposing of those that do not, represents a much more efficient route to biological design. Inclusive fitness theory, which has emerged from the wider study of whole-organism complex adaptation, reaffirms that Darwinism—rather than saltationism—explains the design of organisms (Gardner 2013).

The proponents of the EES also object to the conventional focus on genetic inheritance, which they claim is too narrow (Laland et al. 2015; Table 20.1). They counter with the need for a broader understanding of inheritance, deemed “inclusive inheritance”, that shifts the focus from genes to other forms of non-genetic inheritance, which may take place at other levels of biological organisation. This statement, again, is surprising when viewed from an inclusive fitness perspective. First, the fundamental logic of inclusive fitness theory assumes neither genetic nor particulate inheritance. As described above, Price’s equation provides a general statement about the action of selection, irrespective of the form of inheritance. Further, it shows that inclusive fitness gives an exact description of the action of natural selection even under the assumption of blending inheritance (Gardner 2011). Second, far from ignoring them, inclusive fitness theory actually predicts and explains patterns of epigenetic effects. A notable example of this explanatory power of inclusive fitness theory is the kinship theory of genomic imprinting (Haig 2000, 2002), which predicts the evolution of epigenetic parent-of-origin effects modulating the phenotypes of offspring.

The nature of phenotypic variation has also been under intense scrutiny within the EES literature (Table 20.1). Proponents of the EES programme have rejected what they describe as the classic view of evolutionary biology that there is “no relationship between the direction in which mutations occur—and hence the supply of phenotypic variants—and the direction that would lead to enhanced fitness” (Laland et al. 2015), and instead propose that developmental bias means that mutations are more likely to occur in some directions than in others. This overlooks the extent to which inclusive fitness theory not only accommodates but also explains and predicts patterns of mutational bias, precisely by considering the fitness consequences of different phenotypes. As discussed above, the kinship theory of genomic imprinting predicts parent-of-origin specific gene expression as an evolutionary consequence of differences in the inclusive fitness interests of maternal-origin versus paternal-origin genes residing in the same genome with respect to certain social phenotypes (Haig 2002; Gardner and Úbeda 2017). Accordingly, inclusive fitness considerations imply that mutational effects will be particularly strong with respect to these social phenotypes. Moreover, as the direction of genomic imprinting—e.g., maternal expression and paternal silencing, or vice versa—is predicted to depend upon the direction of the intragenomic conflict between maternal-origin versus paternal-origin genes, so too are the phenotypic effects of different classes of genetic and epigenetic

mutations predicted to depend on the inclusive fitness interests of these conflicting genes (Haig and Wharton 2003; Haig 2014). Although originally developed to explain the adaptive “wildtype” design of organisms, the theory of inclusive fitness also provides a predictive framework for understanding patterns in relation to mutant phenotypes (Gardner and Úbeda 2017).

Finally, proponents of the EES have identified macroevolution as a topic for which they feel classic evolutionary theory provides an inadequate account, such that a revolution in understanding is required in order to explain phylogenetic patterns (Table 20.1). In particular, they suggest that the accumulated action of the canonical microevolutionary processes of natural selection, mutation, random drift and gene flow operating within evolving lineages cannot explain patterns at this higher level (Laland et al. 2015). Once again, such claims are puzzling from an inclusive-fitness perspective, as understanding of the major transitions in evolution—representing the broadest-scale patterning that exists across all the domains of life—features the principles of the theory of inclusive fitness at its core (Maynard Smith and Szathmáry 1995; Bourke 2011). As discussed above, major transitions in individuality from prokaryotic to eukaryotic cell, from unicell to multicellular organism, and from solitary individual to eusocial colony occur when the inclusive-fitness interests of previously free-living individuals are reconciled and aligned to such a degree that the social group is elevated to a new level of individuality in its own right (Gardner and Grafen 2009). This body of theory explains why, for example, obligate eusociality has only ever evolved in the context of strict female monogamy, and hence why it has been restricted to those rare lineages in which strict female monogamy is facilitated by pre-existing features such as sperm storage (Boomsma 2013), with decisive implications for macroevolutionary patterns concerning ecological success, the evolution of complexity and rates of speciation.

20.4 Conclusions

Proponents of the EES programme have highlighted a number of complaints concerning various aspects of the evolutionary process that they feel have been neglected by evolutionary biology to such an extent that the entire foundations of the discipline are in need of a rethink. Here we have considered their complaints from the vantage point of inclusive-fitness theory, showing that some of these apparently neglected factors (i.e. reciprocal causation and the role of the organism) were key motivators for the development of the concept of inclusive fitness and that the others (i.e. variable rates of change, inclusive inheritance, non-random phenotypic variation and macroevolution) are all accommodated—and, indeed, illuminated—by the theory of inclusive fitness. We are not suggesting that there is no need for further work on these issues, but we are surprised that the proponents of the EES have overlooked the accomplishments of the inclusive fitness programme, and that they have failed to acknowledge the successes of inclusive fitness theory in relation to addressing the shortfalls of the Modern Synthesis. More generally, consideration of the origin and subsequent developments of the inclusive fitness programme has

yielded insights into what makes for a successful revolution within evolutionary biology. In contrast to the EES approach, which has been to quibble with model assumptions and demand that researchers should incorporate more complexity for the sake of “realism”, the theory of inclusive fitness has instead focused on identifying mismatches between theoretical predictions and empirical observations, as these mismatches draw our attention to the areas where our understanding is less complete and enable us to work productively towards putting that right.

References

- Best R, Ruxton GD, Gardner A (2018) Intragroup and intragenomic conflict over chemical defense against predators. *Ecol Evol* 8:3322–3329
- Boomsma JJ (2007) Kin selection versus sexual selection: why the ends do not meet. *Curr Biol* 17: R673–R683
- Boomsma JJ (2009) Lifetime monogamy and the evolution of eusociality. *Philos Trans R Soc B* 364:3191–3207
- Boomsma JJ (2013) Beyond promiscuity: mate-choice commitments in social breeding. *Philos Trans R Soc B* 368:20120050
- Boomsma JJ, Gawne R (2018) Superorganismality and caste differentiation as points of no return: how the major evolutionary transitions were lost in translation. *Biol Rev* 93:28–54
- Bourke AFG (2011) *Principles of social evolution*. Oxford University Press, Oxford
- Burt A, Trivers R (2006) *Genes in conflict: the biology of selfish genetic elements*. Harvard University Press, Cambridge, MA
- Charnov EL (1977) An elementary treatment of the genetical theory of kin-selection. *J Theor Biol* 66:541–550
- Darwin CR (1859) *On the origin of species*. John Murray press, London, UK
- Fisher RA (1930) *The Genetical theory of natural selection*. Clarendon Press, Oxford
- Fisher RM, Cornwallis CK, West SA (2013) Group formation, relatedness, and the evolution of multicellularity. *Curr Biol* 23:1120–1125
- Frank SA (1986) Dispersal polymorphisms in subdivided populations. *J Theor Biol* 122:303–309
- Frank SA (1995) George Price’s contributions to evolutionary genetics. *J Theor Biol* 175:373–388
- Frank SA (1998) *Foundations of social evolution*. Princeton University Press, Princeton, NJ
- Frank SA (2013) Natural selection. VII. History and interpretation of kin selection theory. *J Evol Biol* 26:1151–1184
- Gardner A (2009) Adaptation as organism design. *Biol Lett* 5:861–864
- Gardner A (2011) Kin selection under blending inheritance. *J Theor Biol* 284:125–129
- Gardner A (2013) Darwinism, not mutationism, explains the design of organisms. *Prog Biophys Mol Biol* 111:97–98
- Gardner A (2017) The purpose of adaptation. *Interface Focus* 7:20170005
- Gardner A (2020) Price’s equation made clear. *Philos Trans R Soc B* 375:20190361
- Gardner A, Grafen A (2009) Capturing the superorganism: a formal theory of group adaptation. *J Evol Biol* 22:659–671
- Gardner A, Úbeda F (2017) The meaning of intragenomic conflict. *Nat. Ecol. Evol* 1:1807–1815
- Gardner A, Welch JJ (2011) A formal theory of the selfish gene. *J Evol Biol* 24:1801–1813
- Gardner A, West SA (2014) Inclusive fitness: 50 years on. *Philos Trans R Soc B* 369:20130356
- Gardner A, West SA, Wild G (2011) The genetical theory of kin selection. *J Evol Biol* 24:1020–1043
- Grafen A (2006) Optimization of inclusive fitness. *J Theor Biol* 238:541–563
- Haig D (2000) The kinship theory of genomic imprinting. *Annu Rev Ecol Syst* 31:9–32
- Haig D (2002) *Genomic imprinting and kinship*. Rutgers University Press, New Brunswick, N.J

- Haig D (2014) Troubled sleep: night waking, breastfeeding and parent–offspring conflict. *Evol. Med. Public Health* 2014:32–39
- Haig D, Wharton R (2003) Prader-Willi syndrome and the evolution of human childhood. *Am J Hum Biol* 15:320–329
- Hamilton WD (1963) Evolution of altruistic behavior. *Am Nat* 97:354–356
- Hamilton WD (1964) The genetical evolution of social behaviour. I & II. *J Theor Biol* 7:1–52
- Hamilton WD (1967) Extraordinary sex ratios. *Science* 156:477–488
- Hamilton WD (1970) Selfish and spiteful behaviour in an evolutionary model. *Nature* 228:1218–1220
- Hamilton WD (1975) Innate social aptitudes of man: an approach from evolutionary genetics. In: Bischof N, Fox R (eds) *Biosocial anthropology*. Malaby Press, London, pp 133–153
- Hamilton WD, May RM (1977) Dispersal in stable habitats. *Nature* 269:578–581
- Hughes WOH, Oldroyd BP, Beekman M, Ratnieks FLW (2008) Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science* 320:1213–1216
- Huxley J (1942) *Evolution: the modern synthesis*. George Allen & Unwin Ltd, London
- Laland K, Uller T, Feldman M, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J, Wray GA, Hoekstra HE, Futuyma DJ, Lenski RE, Mackay TFC, Schluter D, Strassmann JE (2014) Does evolutionary theory need a rethink? *Nature* 514:161–164
- Laland KN, Uller T, Feldman MW, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J (2015) The extended evolutionary synthesis: its structure, assumptions and predictions. *Proc R Soc B* 282:20151019
- Leigh EG (1977) How does selection reconcile individual advantage with the good of the group? *Proc Natl Acad Sci* 74:4542
- Leigh EG (2010) The group selection controversy. *J Evol Biol* 23:6–19
- Lorenz K (1963) *Das sogenannte Böse: zur Naturgeschichte der Aggression*. G Borotha-Schoeler verlag, Wien
- Maynard Smith J (1964) Group selection and kin selection. *Nature* 201:1145–1147
- Maynard Smith J, Szathmáry E (1995) *The major transitions in evolution*. W.H Freeman Spektrum, Oxford
- Müller GB (2007) Evo–devo: extending the evolutionary synthesis. *Nat Rev Genet* 8:943–949
- Müller GB (2017) Why an extended evolutionary synthesis is necessary. *Interface Focus* 7:20170015
- Orlove MJ, Wood CL (1978) Coefficients of relationship and coefficients of relatedness in kin selection: a covariance form for the RHO formula. *J Theor Biol* 73:679–686
- Paley W (1802) *Natural theology*. Wilks & Taylor, London
- Pigliucci M (2007) Do we need an extended evolutionary synthesis? *Evolution* 61:2743–2749
- Pigliucci M, Müller GB (2010) *Evolution: the extended synthesis*. MIT Press, Cambridge
- Price GR (1970) Selection and covariance. *Nature* 227:520–521
- Price GR (1972) Extension of covariance selection mathematics. *Ann Hum Genet* 35:485–490
- Price GR (1995) The nature of selection. *J Theor Biol* 175:389–396
- Queller DC (1992) Quantitative genetics, inclusive fitness, and group selection. *Am Nat* 139:540–558
- Rodrigues AMM, Gardner A (2012) Evolution of helping and harming in heterogeneous populations. *Evolution* 66:2065–2079
- Taylor PD, Frank SA (1996) How to make a kin selection model. *J Theor Biol* 180:27–37
- Welch JJ (2017) What’s wrong with evolutionary biology? *Biol Philos.* 32:263–279
- Werren JH, Nur U, Wu C-I (1988) Selfish genetic elements. *Trends Ecol Evol* 3:297–302
- West S (2009) *Sex allocation*. Princeton University Press, Princeton, NJ
- West SA, Gardner A (2013) Adaptation and inclusive fitness. *Curr Biol* 23:R577–R584
- West SA, Griffin AS, Gardner A (2007) Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J Evol Biol* 20:415–432

- Wilkins JF, Úbeda F (2011) Diseases associated with genomic imprinting. In: Cheng X, Blumenthal RM (eds) Progress in molecular biology and translational science. Academic Press, New York, pp 401–445
- Wilson DS (2010) Multilevel selection and major transitions. In: Evolution: the extended synthesis. MIT Press, Cambridge, MA, pp 81–93
- Wright S (1931) Evolution in Mendelian populations. *Genetics* 16:97
- Wynne-Edwards VC (1962) Animal dispersion in relation to social behaviour. Oliver and Boyd, London

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