# Inclusive Fitness Theory as a Scientific Revolution: A Commentary on Futuyma

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**Abstract**

Futuyma reviews what he suggests are the main controversies to have gripped the field of evolutionary biology since the time of the Modern Synthesis. He argues that although some of these developments have led to significant and lasting insights (and he names the neutral theory as having been the most important in this respect), none have amounted to an actual revolution in the sense of the "overturning of a former verity". Futuyma then considers the call for an Extended Evolutionary Synthesis, and he argues that this is, in effect, already underway, though only as part of the normal evolution of our field, which proceeds by building upon—rather than rejecting—that which has come before. We fully agree with Futuyma's assessment of the Extended Evolutionary Synthesis. However, we disagree with his suggestion that there have been no revolutions within evolutionary biology since the time of the Modern Synthesis. We contend that the explosive and far-reaching growth of inclusive-fitness theory represents a major revolution in evolutionary understanding. Indeed, the inclusive-fitness revolution has involved the only revision to the core logic of Darwinism since the 1850s—let alone the 1950s. And its ramifications certainly far surpass those of the neutral theory.

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Adaptationism · Appearance of design · Darwinism · Natural selection · Research programs · Scientific revolutions

In his chapter, Futuyma reviews what he suggests are the main controversies to have gripped the field of evolutionary biology since the time of the Modern Synthesis. He argues that although some of these developments have led to significant and lasting insights (and he names the neutral theory as having been the most important in this respect), none have amounted to an actual revolution in the sense of the "overturning of a former verity". Futuyma then considers the call for an Extended Evolutionary Synthesis, and he argues that this is, in effect, already underway, though only as part of the normal evolution of our field, which proceeds by building upon—rather than rejecting—that which has come before.

We fully agree with Futuyma's assessment of the Extended Evolutionary Synthesis. In our own chapter, we similarly detailed how the "laundry list" (Welch 2017) of supposedly neglected factors highlighted by proponents of the Extended Evolutionary Synthesis (Laland et al. 2015) have readily been integrated into evolutionary biology, with a particular focus on the inclusive fitness research programme. We have shown that these factors have not merely been accommodated by the theory of inclusive fitness, but indeed that some (such as the whole-organism view of adaptation and the role of organisms in modifying their own selective environment) have provided the very motivation for the concept of inclusive fitness and others (such as epigenetics and macro-evolutionary patterns) have themselves been illuminated and explained by application of inclusive fitness logic.

We do, however, disagree with Futuyma's suggestion that there have been no revolutions within evolutionary biology since the time of the Modern Synthesis. We contend that the explosive and far-reaching growth of inclusive fitness theory represents a major revolution in evolutionary understanding. Indeed, the inclusive fitness revolution has involved the only revision to the core logic of Darwinism since the 1850s—let alone the 1950s. And its ramifications certainly far surpass those of the neutral theory.

At its core, Darwinism is a theory of design. The logic of natural selection not only explains the process by which adaptive design emerges through purely mechanical means—and thereby destroys the "Argument from Design" for the existence of a supernatural creator—but it also reveals what this design is for (Gardner 2009). Those heritable variations that are associated with higher reproductive success have a tendency to accumulate in natural populations and accordingly—Darwin (1859) argued—each organism will appear designed to maximize its own reproductive success, i.e., Darwinian fitness.

However, Darwin's argument confuses correlation with causation (Gardner and West 2014). A heritable variation that causes a decrease in its bearer's reproductive success whilst also increasing the reproductive success of its bearer's relatives can, on account of the tendency for relatives to share heritable tendencies in common,

enjoy an overall positive correlation with reproductive success, and hence be favoured by natural selection. Accordingly, the organism will not generally appear designed to maximize its own reproductive success. Instead, it will appear designed to maximize the total reproductive success of all of its relatives, each being weighted according to their degree of relatedness, i.e., inclusive fitness (Hamilton 1964).

It is difficult to think of a stronger example of the "overturning of a former verity" within evolutionary biology than the discovery of inclusive fitness. And the implications of this fundamental revision to the core logic of Darwinism are immense. Of perhaps most immediate consequence are the ramifications for the adaptationist programme—the scientific value of which Futuyma has underlined in his chapter—as optimality modelling can only deliver accurate predictions of organismal phenotypes insofar as we have correctly understood the criterion according to which they are optimized. Outwith evolutionary biology, the concept of inclusive fitness has found useful application right across the life sciences and beyond.

The wide reach of inclusive fitness theory is illustrated by considering the twenty-five Web of Science research areas for which Hamilton (1964) is most cited (Fig. 33.1). The number of citations of Hamilton (1964) for each of these research areas exceeds—often greatly—those accumulated by Kimura's (1968) work on the neutral theory, with the sole exception of the category "Biochemistry Molecular Biology". And the influence of Hamilton (1964) is evident across a wider span of

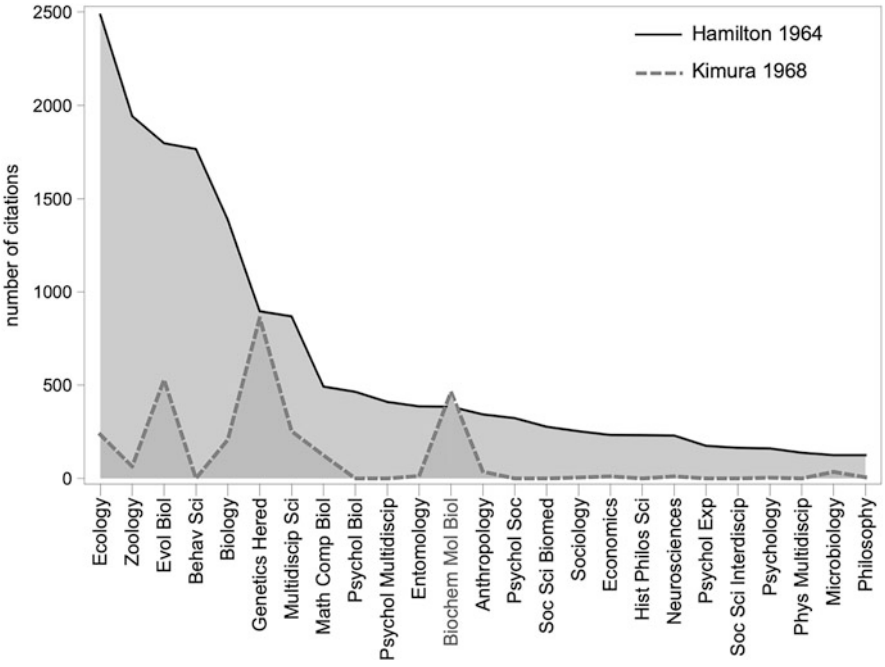


**Fig. 33.1** Citations of Hamilton (1964) and Kimura (1968) for the top-25 Web of Science research areas citing Hamilton (1964), as of the time of writing

categories than is the influence of Kimura (1968)—for example, Hamilton (1964) is cited ten times or more in ninety-six different research categories (i10 = 96), whereas Kimura (1968) is cited ten times or more in only forty-two different categories (i10 = 42), as of the time of writing.

Whilst we disagree with Futuyma's assessment of the major advances in evolutionary understanding since the Modern Synthesis—in particular, feeling that he has overlooked the inclusive fitness revolution—we are in close agreement with his proposition that successful advances, such as the neutral theory and inclusive fitness theory, have been driven by consideration of new (or at least relatively neglected) sources of data, whereby empirical observations are made that cannot readily be explained by pre-existing evolutionary theory. In the case of the neutral theory, the new sources of data were molecular and revealed the existence of nucleotide sequence and amino acid variation to a degree that was difficult to account for in terms of selective advantage. In the case of inclusive fitness theory, the observations came from the study of altruistic behaviours which—although lightly touched upon by Fisher (1930), Haldane (1932) and Wright (1945)—had been largely excluded from the Modern Synthesis and which, clearly not being compatible with individual advantage, led many—such as Lorenz (1963)—to frame them in woolly "for the good of the species" terms. This contrasts sharply with the major motivation for the Extended Evolutionary Synthesis, which seeks to complexify evolutionary models apparently for realism's own sake rather than because pre-existing models cannot adequately explain empirical observations.

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