Genes and organisms in the legacy of the modern synthesis

J. Arvid Ågren

Department of Evolutionary Biology, Uppsala University, Uppsala, Sweden

arvid.agren@ebc.uu.se

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Abstract

The gene's-eye view of evolution is an influential but contentious perspective on biology. It emerged in the aftermath of the Modern Synthesis and both proponents and detractors have stressed the link between the two. In particular, both the Modern Synthesis and the gene's-eye view have been criticized for overemphasizing the role genes at the expense of organisms in evolutionary explanations. In this chapter, I discuss the connection between the Modern Synthesis and the gene’s-eye view and evaluate the status of genes and organisms in contemporary biology. I show that while the gene’s-eye view traces its origin back to the Modern Synthesis, it can most accurately be said to represent a specific – adaptationist and gene-centric – version of it. To assess the role of genes and organisms, I examine the intimate relationship between the gene’s-eye view and another post-Synthesis development, the concept of inclusive fitness. I argue that the popularity and influence of inclusive fitness theory demonstrate that the individual organism remains safe at the heart of modern evolutionary biology.

Key words: the gene’s-eye view of evolution; adaptationism; inclusive fitness

Introduction

Following a public poll in 2017 to celebrate the 30th anniversary of the Royal Society book prizes, Richard Dawkins's *The Selfish Gene* (Dawkins 1976) was named the most influential science book of all time. (*The Origin of Species* came in third place.) Regardless of one's views on the poll's results – or the book's argument – the far reaching sway of *The Selfish Gene* means that anyone interested in the history and future of evolutionary theory has no choice but to grapple with its ideas. Chief among these, is the so-called gene's-eye view of evolution. This is the approach to biology originally introduced by George Williams in *Adaptation and Natural Selection* (Williams 1966), and elaborated and popularized by Dawkins, that it is genes, and not organisms as Darwin originally envisioned, that deserve the status as the unit of selection in evolution. Emerging in the decades succeeding the Modern Synthesis, the gene's-eye view of evolution has become an emblem of orthodoxy in biology. That symbolism has been especially prominent in the minds of those who criticize current evolutionary thought for being too focused on genes at the expense of organisms.

Depending on who you ask, and when, the Modern Synthesis has meant different things (Huxley 1942; Provine 1971; Mayr and Provine 1980; Gould 1983; Smocovitis 1996; Pigliucci and Müller 2010; Huneman and Walsh 2017; Dickins 2021). That is perhaps not too surprising, given that it involved contributions from fields ranging from palaeontology to plant ecology, physiology to fly genetics. One answer was provided in a 1951 letter from one Modern Synthesis architect to another. In it, Julian Huxley (author of *Evolution: The Modern Synthesis*; Huxley 1942) wrote to Ernst Mayr (editor with W.B. Provine of *The Evolutionary Synthesis*; Mayr and Provine 1980) to say that he considered the central claim of the synthesis to be that

> "Natural selection, acting on the heritable variation provided by the mutations and recombination of a Mendelian genetic constitution, is the main agency of biological evolution" (Huxley 1951, quoted in Huneman 2017)

From the very beginning, the gene's-eye view of evolution has emphasized its place in the Modern Synthesis. And in Huxley's letter emerges a picture of a framework committed to adaptationism and gene-centric explanations (Huneman 2014a; Huneman 2017), much like the gene's-eye view. Indeed, in *Adaptation and Natural Selection*, Williams argued that

> "genic selection should be assumed to imply the current conception of natural selection often termed neo-Darwinism" (Williams 1966, p. 96)

And when Dawkins in his autobiography reflected upon how he came to the concept, he noted that

> "I should point out that neither in my lectures of the 1960s nor in *The Selfish Gene* did I see as very novel the idea of the gene as the fundamental unit of natural selection. I thought of it – and clearly said so – as implicit in the orthodox neo-Darwinian theory of evolution" (Dawkins 2013, p. 268)

Leaving aside the issue of conflating neo-Darwinism and the Modern Synthesis (Svensson this volume), the sentiment that the gene's-eye view represents the essence of the Modern Synthesis has been shared by both supporters (e.g., Dickins 2021) and critics (e.g., Noble 2011) of the two. However, the connection is not straightforward. Take Mayr, one of the few active participants in the Modern Synthesis that lived long enough to comment on the value of the gene's-eye view, who suggested that

> "the funny thing is if in England, you ask a man in the street who the greatest living Darwinian is, he will say Richard Dawkins. And indeed, Dawkins has done a marvellous job of popularizing Darwinism. But Dawkins' basic theory of the gene being the object of evolution is totally non-Darwinian" (Mayr 1999)

Another long-living Modern Synthesis architect and gene's-eye view detractor, Sewall Wright, was equally critical in one of his last publications when he described the gene's-eye view as a "false statement, backed by great prestige" (Wright 1980).

In general, the gene's-eye view has divided biologists, philosophers, and laypeople since its formation half a century ago. In *The Gene's-Eye View of Evolution* (Ågren 2021a), I traced its origin and development and considered its position in contemporary evolutionary theory. In this chapter, I am concerned with two specific issues:

1. The relationship between the Modern Synthesis and the gene's-eye view.
2. The criticism that the two have caused the field of evolutionary biology to lose sight of what ought to be its primary object of study, organisms.

To that end, I start by outlining the core argument of the gene's-eye view. I show how it stems from a particular version of the Modern Synthesis that is committed to the centrality of adaptations and the form of population genetics spear-headed by R.A. Fisher. Next, I discuss the relationship between the gene's-eye view and Hamilton's inclusive fitness theory, another major post-synthesis development. The concept of inclusive fitness was instrumental in the rise of the gene's-eye view, and most of the time the two are equivalent and complementary approaches. When they do diverge, it is over whether organisms should be abandoned in evolutionary explanations, which the gene's-eye view favours and inclusive fitness theory rejects. Examining the gene's-eye view's debt to Fisherian population genetics and Hamiltonian social evolution theory helps clarify the role of organisms and genes in the legacy of the Modern Synthesis.

The core argument of the gene's-eye view

Though the term itself would come later – most likely in Barash (1980) – the concept of the gene's-eye view came onto the scene in the 1960s and 1970s. Whereas *The Selfish Gene* (Dawkins 1976) has enjoyed enormous sales, in multiple languages, *Adaptation and Natural Selection* (Williams 1966) has had a more limited, academic, readership. Among professional evolutionary biologists, however, its influence might well exceed that of *The Selfish Gene* (Cronin 2005; Sober and Wilson 2011; Boomsma 2016).

In both *Adaptation and Natural Selection* and *The Selfish Gene*, the overarching argument is that evolutionary biologists should shift their explanatory focus away from the level of individuals and groups – the way Darwin had originally introduced the theory – to the level of genes. To see why such shift is necessary, it is important to appreciate that advocates of the gene's-eye view have a clear opinion not only what the most important question in evolutionary biology is, but also about how to answer it. According to the gene's-eye view, the problem of design (that is, the existence adaptations) is the most significant issue in biology. Understanding adaptations requires figuring out what they are good for (Williams 1997; Dawkins 1998), what Elizabeth Lloyd called the beneficiary question (Lloyd 2017): what is the thing that ultimately benefits from natural selection?

According to Williams and Dawkins, only genes possess the necessary qualities to answer the beneficiary question. Only they have the required evolutionary longevity; organisms (and groups) are too salient to work (Williams 1966, pp. 23–24; Dawkins 1976, p. 34). In *Adaptation and Natural Selection,* Williams illustrates this point using the life and death of Socrates:

> "Socrates consisted of the genes his parents gave him, the experiences they and his environment later provided, and a growth and development mediated by numerous meals. For all I know, he may have been very successful in the evolutionary sense of leaving numerous offspring. His phenotype, nevertheless, was utterly destroyed by the hemlock and has never since been duplicated. If the hemlock had not killed him, something else soon would have. So however natural selection may have been acting on Greek phenotypes in the fourth century B.C., it did not of itself produce any cumulative effect. The same argument also holds for genotypes. With Socrates' death,

> not only did his phenotype disappear, but also his genotype. (…) Socrates' genes may be with us yet, but not his genotype, because meiosis and recombination destroy genotypes as surely as death.” (Williams 1966, pp. 23-24)

As hinted at by Williams’s last sentence, the gene’s-eye view defines ‘genes’ in a rather special way, and this definition provides the key to why only genes can be the beneficiary of natural selection.

The term ‘gene’ has undergone many changes over the years (Griffiths and Stotz 2013; Kampourakis 2017). If some biologists have advanced an empirically informed concept, revised and refined in light of new advances, the gene’s-eye view has relied on a more old-fashioned notion, agnostic about the precise material basis (Lu and Bourrat 2018). For example, molecular biologists have typically meant something like a sequence of DNA that encodes a product with a specific function. In contrast, Williams and Dawkins used a gene definition whereby a gene simply is any chromosome part that is not broken up by recombination and crossing-over during sex. As long as the same structure is transmitted intact long enough, the sequence can in principle be arbitrarily long. As Dawkins, building on Williams (1966, p. 24), put it: a gene is

> “any portion of chromosomal material that potentially lasts for enough generations to serve as a unit of natural selection” (Dawkins 1976, p. 28).

Following this definition to its logical conclusion, it means that, for example, the whole mitochondrial genome counts as one gene. Ultimately, both Williams and Dawkins favoured a notion whereby genes should be thought of not in terms of molecules, but in terms of the information encoded in those molecules (Williams 1985; Williams 1992; Williams 1996; Dawkins 1986, p. 111).

With this gene definition in place, the central tenet of the gene’s-eye view then emerges. Evolution by natural selection requires two entities: replicators and vehicles (Hull

1980;1981; Dawkins 1982). As Dawkins put it in one of the most quoted parts *The Selfish Gene*:

> "What was to be the fate of the ancient replicators? They did not die out, for they are past masters of the survival arts. But do not look for them floating loose in the sea; they gave up that cavalier freedom long ago. Now they swarm in huge colonies, safe inside gigantic lumbering robots, sealed off from the outside world, communicating with it by tortuous indirect routes, manipulating it by remote control. They are in you and in me; they created us, body and mind; and their preservation is the ultimate rationale for our existence. They have come a long way, those replicators. Now they go by the name of genes, and we are their survival machines." (Dawkins 1976, p. 20).

Replicators are whatever entities whose information is copied and passed on from generation to generation. In practice, this usually means genes, though the concept can in principle apply to any entity that satisfies the key properties of longevity, fecundity, and copy-fidelity (Dawkins 1978). These are the very properties that give replicators their unique role in evolutionary explanations. Because only replicators meet all criteria and form lineages of information across generations, they are the only entities that are the beneficiary of natural selection.

Vehicles (survival machines in Dawkins' nomenclature above) are where replicators are bundled together and housed in. They are the entities that interact with the surrounding environment, a responsibility usually taken on by individual organisms. Crucially, vehicles live and die, whereas replicators are immortal. The gene's-eye view is therefore also known as selfish-gene thinking, as vehicles provide the battle ground for selfish replicators competing for transmission to the next generation. Most of the time, the fitness interests of replicators and vehicles align – the higher the fitness of the organism the higher the chance of transmission for a specific allele – but sometimes they diverge, such as in the case of genetic conflicts (Ågren 2016a). In general, the replicator-vehicle distinction is a way to articulate the principles of evolution by natural selection in the abstract. There are others, the most serious rivals being those inspired by Richard Lewontin's recipe approach (Lewontin 1970; see, for example, Godfrey Smith 2009 for a Lewontin inspired critique of the gene's-eye view).

In sum, the gene's-eye view takes adaptation as its central problem and argues that the way to approach the problem is to recognize the unique properties of genes (replicators) relative to organisms (vehicles). To locate this view of life in the legacy of the Modern Synthesis, I now turn to examine its historical origins.

The genesis of the gene's-eye view

I have argued that the intellectual core of the gene's-eye view is built on three areas (Ågren 2021a), which I will summarize here.

The first is the above-mentioned focus on adaptations. Accompanying this focus is an argument that the cardinal problem in evolutionary biology is to provide an account for the appearance of design among living organisms. This tradition in biology has been called 'neo-Paleyan', in reference to the clergyman and Christian apologist William Paley, the author of *Natural Theology or, Evidences of the Existence and Attributes of the Deity, Collected from the Appearances of Nature* (Paley 1802). *Natural Theology* was Paley's last book, but the one that left a significant impression on biology. In particular, he popularized a version of the 'argument from design' for the existence of God. Paley opens the book with an account of the so-called watchmaker analogy – just as the intricate design of a pocket watch implies the work of a watchmaker, so do the remarkable adaptations of animals (Paley was not too impressed by plants; Paley 1802, Chapter 20) imply the presence of a creator. Paley's writings had a strong influence several generations of especially English biologists (Kohn 2004; McGrath 2011; Lewens 2019). While people like Darwin were convinced by the actual arguments, others have used Paley more for rhetorical purposes (e.g. Maynard Smith 1969, p.82; Gardner 2009). Dawkins devoted a whole book to the topic where he compared natural selection to a blind watchmaker (Dawkins 1986) and noted that

> "I suppose people like me might be labelled neo-Paleyists, or perhaps 'transformed Paleyists'. We concur with Paley that adaptive complexity demands a very special kind of explanation: either a Designer, as Paley taught, or something such as natural selection that does the job of a designer." (Dawkins 1998, p. 16)

Also Williams paid tribute to Paley. To him, there was a strong link between the gene's-eye view and adaptationism (Williams 1985). Paley makes an appearance in *Adaptation and Natural Selection* and even more so in *Natural Selection: Domains, Levels and Challenges* (Williams 1992) where Williams included excerpts from Paley in the book's appendix. Thus, whereas the neo-Paleyan adaptationist tradition appears to have been especially strong in British biology (Lewens 2019), the American Williams highlights that putting too much emphasis on that aspect of history is too simplistic.

The second core area of the gene's-eye view is a Fisherian version of population genetics. R.A. Fisher, J.B.S. Haldane, and Sewall Wright, the triumvirate who showed how evolution can be mathematically described as changes in allele frequencies over time, played a central part in the general synthetic project (Provine 1971). Although the three had several spirited disagreements, including over the relative importance of selection, drift, epistasis, and dominance (Provine 1971, Chapter 5), but their work helped put genes at the heart of the synthesis. This move was criticized by fellow architects, especially by Mayr who felt their mathematical models contributed little beyond the obvious (see the exchange between him and Haldane; Mayr 1959 and Haldane 1964).

Similarly, Wright also had reservations about too much focus on individual genes, rather than organisms. The gene's-eye view grew out of Fisher's worldview (Sarkar 1994;

Okasha 2008; Edwards 2014) and several lingering differences in opinion over the gene's-eye view can be traced back to disagreements between Fisher and Wright (Ågren 2021b). In particular, Wright emphasized that he, in contrast with Fisher, was modelling "organismic, rather than genic selection" (Wright 1980) and that "selection relates to the organism as a whole and its environment and not to genes as such" (Wright 1931). Furthermore, Fisher had a commitment to adaptationism, which Wrigh Lacked. Fisher's views were manifested both through his scepticism of genetic drift, as well as his collaboration with the empiricist E.B. Ford (Turner 1985), whose hyper-adaptationist outlook left a long-lasting footprint on Dawkins's Department of Zoology at Oxford (Dawkins 2015a, pp. 342-345).

More technically, Fisher's importance for the gene's-eye view is revealed by examining his 1918 paper 'The correlation between relatives on the supposition of Mendelian inheritance' (Fisher 1918). It was here that Fisher first introduced the concept of variance and with that an expanded version of the environment foundational for the gene's-eye view. He gets to this point through his method to distinguish between genetic and environmental effects. Fisher's move may upon first reading not seem like much, but it has the consequence that from the perspective of an allele, the rest of the genome, as well as the whole segregating gene pool, are now part of the environment in the same way as the surrounding pH, rainfall, or temperature. "Genotypes have dual significance as genetic environments in which a gene temporarily resides and as sets of instructions for producing phenotypes", as Williams (1985) put it. This way of thinking about the environment only makes sense under a gene's-eye view.

The final area contributing to the origin of the gene's-eye view was the rejection of group selection. Group selection has a tumultuous past that has been reviewed numerous times (Cronin 1991; Sober and Wilson 1998; Borrello 2010; Wilson 2015). In its most basic form, it is the idea that selection acts not just on individuals but also on groups. The concept has featured most prominently in explanations for social behaviours that are harmful to the individual performing it, but that increase the fitness of other individuals. In the lead up to writing their own books, both Williams and Dawkins were frustrated with the popularity of certain kind of group selection, a form 'for the good of the species'-arguments popular at the time. Williams was once so exasperated with the state of things that he told his wife, Doris Williams (also a distinguished biologist), that if such arguments were considered sound, he would rather quit biology altogether than stay in a field with such poor standards. It was also the frustration with naïve group selection that led Dawkins to be so taken by the many advances in social evolution that centred on individual level selection, including Maynard Smith's game theory models (Maynard Smith and Price 1973), Trivers's idea of reciprocal altruism (Trivers 1971), and, especially, Hamilton's concept of inclusive fitness (Hamilton 1963; Hamilton 1964). As will become clear, however, Hamilton's insistence of keeping the individual as the central unit of explanation would cause some frustration for Dawkins and other proponents of the of gene's-eye view.

The emergence of the gene's-eye view takes place after the completion of the Modern Synthesis. While claiming to represent the Modern Synthesis as a whole, even to offer a "truer and clearer expression" of it (Dawkins 1982 p. 239), it can more accurately be traced back to the Fisherian version of the theory. As Michael Wade concluded in his review of Dawkins's attempt to summarize the state of evolutionary theory in *The Selfish Gene*: "[if] evolution in natural populations followed the paradigm developed by R. A. Fisher, he might have succeeded" (Wade 1977). Quite.

Has evolutionary biology forgotten about organisms?

The influence of the gene's-eye view has contributed to a worry that contemporary biologists pay too little attention to organisms (this worry has been expressed in, for example, West-

Eberhard 2003; Bateson 2005; Walsh 2006; Walsh 2015; and evaluated by Huneman 2010 and Huneman 2014b). Furthermore, the concern is a key part in the call to update the conceptual framework of the Modern Synthesis, resulting in a so-called Extended Evolutionary Synthesis (Pigliucci and Müller 2010; Laland et al. 2014; Laland et al. 2015). In a recent paper, a chief proponent of the Extended Evolutionary Synthesis described the key dividing line between the Modern and the Extended Synthesis as being that the former was genotype-centric and the latter phenotype-centric (Uller and Helanterä 2017).

However, the tensions over genic and organismic approaches to evolution is not just a matter of Modern vs. Extended Synthesis, but very much existed within the Modern Synthesis itself. This tension was manifested in the differences in modelling preferences between Fisher and Wright as well as in the Mayr-Haldane exchange. In both debates, the interlocutors probably agreed on more than they disagreed and all four were instrumental in their own ways in the construction of the Modern Synthesis. Another example of where the gene-organism tension arises among erstwhile close allies is the relationship between the gene's-eye view and inclusive fitness.

Inclusive fitness represents one of the most significant post-synthesis developments in evolutionary theory (Rodrigues and Gardner this volume). Importantly, it is also a phenotype-centric approach, focusing on the individual organism as a fitness maximizing agent. The models of inclusive fitness are a way to account for how an individual may causally affect her genetic contribution to the next generation through either her own reproduction (direct fitness) or through that of her relatives (indirect fitness). A key distinction between inclusive fitness and other related approaches (such as neighbour modulated fitness) is that inclusive fitness is under the full control of the individual organism. It is this unique control that formally justifies treating inclusive fitness as the goal that organisms should appear designed to try to maximize (Hamilton 1964; Grafen 2006; West and Gardner 2013; Grafen 2014a).

Hamilton's insight can also be captured from a gene's-eye view. In his very first paper, Hamilton provides an early and eloquent expressions of this approach

> "Despite the principle of 'survival of the fittest' the ultimate criterion that determines whether [a gene for altruism] will spread is not whether the behavior is to the benefit of the behaver but whether it is of benefit to the gene [itself]." (Hamilton 1963)

Inclusive fitness and the gene's-eye view emerged around the same time and played mutually supportive roles. Hamilton himself used both approaches in his work, with the best example of the gene's-eye view in action is his 1967 paper on extra-ordinary sex ratios (Hamilton 1967). In Hamilton (1972) he explains altruism in social insects from both a gene's-eye view perspective and an organism-centric inclusive fitness perspective. Hamilton plays a dominant role in *The Selfish Gene* and Williams was quick to recognize the importance of his ideas in *Adaptation and Natural Selection*. Both Williams and Dawkins viewed their gene-centric models as providing a more lucid account of Hamilton's insight. Dawkins described inclusive fitness as "that property of an individual organism which will appear to be maximized when what is really being maximized is gene survival" (Dawkins 1978) and notes that Hamilton approved of this definition (Dawkins 2015a, p. 318).

The consensus view that the gene's-eye view and inclusive fitness are equivalent is well articulated in the influential textbook on animal behaviour by Krebs and Davies

> "the field biologist sees *individuals* dying, surviving and reproducing; but the evolutionary consequence is that the frequencies of *genes* change. Therefore the field biologists tend to think in terms of individual selection whilst the theorists thinks in terms of selfish genes." (Krebs and Davies 1993, p. 375; original emphasis)

Yet, there have also been frustrations. Dawkins once described inclusive fitness as a "brilliant last-ditch rescue attempt to save the individual organism as the level at which we think about natural selection" (Dawkins 1982, p. 187). More recently, Dawkins re-iterated the complaint:

> "I think it was unfortunate that Hamilton, having realized this very important insight, chose to stick with the individual organism as the entity of action. He therefore coined the phrase "inclusive fitness", as the mathematical function which an individual organism will maximize if what it's really doing is maximizing its gene survival. It's a rather complicated thing to calculate. It's difficult to calculate in practice and this has led to a certain amount of, not hostility, but a certain amount of skepticism about inclusive fitness as a measure, skepticism which I share. But for me the remedy of that skepticism is to say, well, forget about the organism and concentrate on the gene itself." (Dawkins 2015b)

Similarly, Maynard Smith described inclusive fitness as an "absolute swine to calculate", noting that he much preferred the gene centric approaches of Hamilton's 1963 paper (Maynard Smith 1997; see also Maynard Smith 2002). To Dawkins and Maynard Smith, it seems, Hamilton was a revolutionary thinker who never completed his own revolution.

Contemporary inclusive fitness theorists clearly see value in the gene's-eye view. At times, however, they have afforded it a more limited role, such as in the study of genetic conflicts (West and Gardner 2013; Levin and Grafen 2019). How to handle the biology of genetic conflicts is an area where the gene's-eye view and inclusive fitness may come into tension. In *The Extended Phenotype*, Dawkins noted that

> "there is a sense in which a "vehicle" is worthy of the name in inverse proportion to the number of outlaw replicators that it contains" (Dawkins 1982a, p. 134).

In other words, the presence of genetic conflicts may erode the necessary unity of purpose required for the individual organism to act as the sole fitness maximising agent (Gardner and Grafen 2009; Okasha 2018, p. 29). It is not that the mathematical tools of inclusive fitness theory cannot be used to study genetic conflicts. They very much can, as conflicts can be modelled as a situation where the inclusive fitness of genes – here defined as a scrap of nucleic acid – diverge (Gardner and Welch 2011; Gardner and Úbeda 2017). Instead, the importance of genetic conflicts are downplayed in the name of understanding organismal phenotypes (West and Gardner 2013; Grafen 2014b). From the perspective of the gene's-eye view, this phenotypic gambit is awkward. A major strength of the gene's-eye view is that it forces us to reckon with why organisms are unified wholes to begin with – to re-discover the organism (Dawkins 1982, Chapter 14). Under the gene's-eye view, the best way to conceptualize organisms is not as cohesive fitness maximizers, but as 'adaptive compromises' (Haig 2006; Haig 2014) of multiple agents whose fitness interest mostly align but far from always.

Today, most biologists are happy to ignore genetic conflicts in their work on phenotypic evolution. Genetic conflicts have often been viewed as the best evidence of the utility of the gene's-eye view, but still represent a minor part of the field of evolutionary biology. Take, for example, the largest evolution meeting in history, the 2018 Second Joint Congress on Evolutionary Biology in Montpellier, France. The meeting brought together some 2700 attendees from almost 60 countries, presenting 800 talks and around 1200 posters across 78 thematic symposia. Only six symposia had fewer submissions than the one dedicated to genetic conflicts. My impression is that most of my colleagues in evolutionary biology do not think of genes first and as organisms as adaptive compromises, as Dawkins (1982), Haig (2014), Maynard Smith (1985), and I (Ågren 2014; Ågren 2016b) tend to do. The dominance and success of inclusive fitness theory show that evolutionary biology has not forgotten about organisms.

Conclusion

The gene's-eye view has been at the centre of evolutionary debates for the past half-century. While claiming to represent the whole of the Modern Synthesis, it can more accurately be traced back to a certain version of the synthetic project. It views adaptation as the most important problem of our field and uses a Fisherian approach to population genetics to conceptualize the answer. Critics of adaptationism (such as Wright) or of gene-centric explanations (like Mayr) are as much part of the Modern Synthesis as Fisher.

The gene's-eye view rose to prominence thanks to and alongside inclusive fitness theory. The two frameworks are equivalent in most situations, but do differ in their emphasis on genes and organisms. While the gene's-eye view would prefer to talk about genes rather than organisms, the success of inclusive fitness means that there is a strong post-synthesis movement, and consensus, to keep organisms at the centre of evolutionary explanations.

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