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Selfish genetic elements and the gene's-eye view of evolution

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Received on 1 February 2016; accepted on 19 August 2016

Abstract

During the last few decades, we have seen an explosion in the influx of details about the biology of selfish genetic elements. Ever since the early days of the field, the gene's-eye view of Richard Dawkins, George Williams, and others, has been instrumental to make sense of new empirical observations and to the generation of new hypotheses. However, the close association between selfish genetic elements and the gene's-eye view has not been without critics and several other conceptual frameworks have been suggested. In particular, proponents of multilevel selection models have used selfish genetic elements to criticize the gene's-eye view. In this paper, I first trace the intertwined histories of the study of selfish genetic elements and the gene's-eye view and then discuss how their association holds up when compared with other proposed frameworks. Next, using examples from transposable elements and the major transitions, I argue that different models highlight separate aspects of the evolution of selfish genetic elements and that the productive way forward is to maintain a plurality of perspectives. Finally, I discuss how the empirical study of selfish genetic elements has implications for other conceptual issues associated with the gene's-eye view, such as agential thinking, adaptationism, and the role of fitness maximizing models in evolution.

Key words: hierarchy, intragenomic conflict, levels of selection, major transitions, multilevel selection, Richard Dawkins.**Introduction**

Historically, the predominant view of genomes was one of a highly coordinated network, with all parts playing fair, working together to produce individual organisms. This view is challenged by the existence of stretches of DNA that can promote their own transmission at the expense of other genes in the genome, but have no or a negative effect on organismal fitness. These days, we usually refer to such stretches of DNA as selfish genetic elements, but over the years they have also been known by a variety of names including parasitic DNA, selfish DNA, ultra selfish genes, genomic outlaws, and self-promoting elements (reviewed in, e.g., Werren et al. 1988; Hurst et al. 1996; Burt and Trivers 2006; Werren 2011). Although foreshadowed by Weisman's "germinal selection" (Weismann 1903), proper discussions of selfish genetic elements began in earnest a couple of decades later. Haldane (1932) discussed several examples of conflict between different levels in the biological hierarchy,

including how pollen competition could lead to the spread of traits that were deleterious to the individual organism. In 1945, the Swedish botanist and cytogeneticist Gunnar Östergren's argument that supernumerary (i.e., non-vital) B chromosomes were best perceived as parasitic provided the first clear articulation of what we now refer to as selfish genetic elements (Östergren 1945). Östergren's work coincided with several other similar empirical observations, particularly in plants (Ågren and Wright 2015). For example, female meiotic drive was first reported in maize (Rhoades 1942), and Lewis (1941) presented evidence that cytoplasmic male sterility in plants was due to the conflict between the organellar and nuclear genes. However, such cases were typically considered to be genetic oddities with few implications for evolutionary theory (Burt and Trivers 2006; Werren 2011). It would take several decades until selfish genetic elements in general, and their evolutionary implications in particular, became widely appreciated.

A conceptual development that coincided with and contributed to the raised status of selfish genetic elements was the arrival of the gene's-eye view on evolution. Introduced in George Williams' (1966) *Adaptation and Natural Selection* and more forcefully in Richard Dawkins' (1976) *The Selfish Gene*, the gene's-eye view, or selfish gene theory, can be defined as the idea that the gene is the ultimate beneficiary of selection. Whereas organisms and their phenotypes are unique occurrences, each a product of the genome and its environment at a particular time, genes are the only units passed on intact and thus survive across generations. The gene is therefore the fundamental unit of selection.

Although the gene's-eye view was instrumental in the development of the study of selfish genetic elements, the framework has been criticized and various other models have been suggested. Given that the central role of selfish genetic element in evolutionary biology is increasingly being recognized (Lisch 2013; Rice 2013), it is important to explore how to make sense of new empirical observations. Reciprocally, studying selfish genetic elements under different frameworks will also aid in building a unified theory of conflict and cooperation (Keller 1999; Michod 1999; Queller and Strassmann 2009; Bourke 2011; Foster 2011; Ågren 2014; West et al. 2015). In this paper, I discuss this relationship between the empirical study of selfish genetic elements and the gene's-eye view as a conceptual model of evolution. I begin by outlining the historical origins of both the study of selfish genetic elements and the gene's-eye view. After discussing the extent to which their histories are intertwined, I examine how the association between the study of selfish genetic elements and the gene's-eye view holds up in face of alternative models of selfish genetic element evolution. In particular, I focus on the critique from proponents of multilevel selection models. Often these models are not mutually exclusive and my aim is not to argue in favor of one framework, nor to suggest how the various models can be morphed into one unifying framework. Instead, using on examples from transposable elements and the major transitions, I show how different perspectives highlight distinctive aspects of the biology of selfish genetic elements. Finally, in the last section of the paper, I discuss 3 other conceptual issues that have been associated with arguments about the gene's-eye view: agential thinking, adaptationism, and fitness maximizing models in evolution, and how selfish genetic elements can inform these debates.

Early connections between the gene'-eye view and selfish genetic elements

Selfish genetic elements played no role in the early developments of the gene's-eye view. Instead, Williams and Dawkins weaved together 2 strands of evolutionary theory. First, several assumptions can be traced back all the way to early days of population genetics and in particular to Fisher (1918, 1930). Although, Fisher never used the term "gene's-eye" or "gene-centered", the approach was nevertheless explicit in his writings (Okasha 2008a; Edwards 2014). Second, evolutionary biology was seeing a growing appreciation of conflict more generally in social evolution. Parker (1979) pioneered the study of sexual conflict and Trivers (1974) outlined the idea of parent-offspring conflict, which later inspired the kinship theory of genomic imprinting (Haig 2002). Finally, game theory models of conflict resolution were introduced to evolutionary biology, first by Lewontin (1961) and later to a broader audience by Maynard Smith and Price (1973). Most importantly, Hamilton's inclusive fitness models provided a formal alternative to the prevailing group selection thinking of the time (Hamilton 1963, 1964).

In addition to the general conceptual shift to gene level thinking in evolutionary biology, Werren (2011) identified 2 other parallel historical developments as central to the origin of the study of selfish genetic elements. First, empirical work on genome structure reported that large chunks of eukaryotic genomes were made up of genetic material, such as repetitive DNA, with seemingly no connection to organismal function or fitness (e.g., Britten and Kohne 1968; Britten 1969). This helped shift the focus away from individual organisms and to the gene level. Moreover, while it was clear that genome size varied dramatically across species (we now know eukaryotes vary more than 60,000-fold; Elliot and Gregory 2015), there was no correlation between the amount of DNA of a species (C-value) and its perceived complexity. For example, the genome of single-celled amoeba is about 100 times the size of that of humans. This lack of correlation was termed the "C-value paradox" (Thomas 1971) and later the "C-value enigma" (Gregory 2001). These observations were central to 2 papers published back-to-back in *Nature* in 1980, both of which cited Dawkins' writing as a key inspiration for their argument. Doolittle and Sapienza (1980) and Orgel and Crick (1980) independently argued that large parts of eukaryotic genomes can best be described as selfish DNA, with negative or neutral effects on organismal fitness. These papers resulted in a series of exchanges in the same journal (Cavalier-Smith 1980; Dover 1980; Dover and Doolittle 1980; Jain 1980; Orgel et al. 1980) representing the first high profile discussion of the implications of selfish genetic elements.

Second, empirical work in molecular genetics continued to provide new examples of selfish genetic elements. When Werren et al. (1988) published the first comprehensive review of all kinds of selfish genetic elements discovered at the time, their discussion covered examples ranging from meiotic drive and supernumerary B chromosomes to killer plasmids, selfish mitochondria, and transposable elements. We now know that selfish genetic elements are prominent features of the genomes of virtually all organisms (Hurst and Werren 2001; Burt and Trivers 2006; Werren 2011). In light of the growing evidence of the central role played by selfish genetic elements in all aspects of genome evolution, Rice (2013) recently argued that "nothing in genetics makes sense except in the light of genomic conflicts".

In retrospect it is perhaps easy to see how the gene's-eye view and selfish genetic elements came to be closely associated. Just consider the similarity in language in 2 key papers in each field, Hamilton's little read 1963 note in the *American Naturalist* where he first introduced the concept of inclusive fitness and Östergren's (1945) paper on B chromosomes mentioned above:

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

In many cases these chromosomes have no useful function at all to the species carrying them, but that they often lead an exclusively parasitic existence . . . [B chromosomes] need not be useful for the plants. They need only be useful to themselves. (Östergren 1945)

A crucial conceptual insight in both papers is that in order to explain the phenomenon under study, the origin of altruism and the spread of B-chromosomes, respectively, the investigator is better off viewing the world from the perspective of the gene, rather than the individual organism. As such, this is the main strength of the gene's-eye view. The evolutionary logic of selfish genetic elements is difficult to follow from an organismal perspective, but straightforward

from a gene's-eye view. Hamilton too was quick to make the connection between inclusive fitness and selfish genetic elements. In his 1967 paper on extraordinary sex ratios, he shows how asymmetries in transmission between autosomes and sex chromosomes will lead to conflict over the ideal sex ratio (Hamilton 1967).

Replicator and vehicles

Upon publication, *The Selfish Gene* (Dawkins 1976) received both enthusiastic praise (e.g., Hamilton 1977) and fierce criticism (e.g., Lewontin 1977). A common theme among critics was that the gene cannot be the unit of selection because selection cannot act on them directly, only via their effects on individual organisms (Gould 1977). The distinction between replicator and vehicles (Dawkins 1982a, 1982b; also known as interactors, Hull 1980) was introduced partly to address this issue. Under this model of evolution, natural selection requires 2 different units playing different roles in the evolutionary process (Godfrey-Smith 2000). Replicators are entities that faithfully produce copies of themselves that are transmitted across generations. In biological evolution, as far as we know, genes play this role. A vehicle is an entity that interacts with the environment, and whose phenotype has evolved to preserve the replicator that it carries. Since it is the differential survival and reproduction of vehicles that lead to the spread of replicators, selection can be said to act on replicators via their effects on the vehicles that house them. However, since individual organisms and groups are transient occurrences, vehicles cannot be a unit of selection. Genes, on the other hand, are units of selection because they are “potentially immortal” (Dawkins 1982a, p. 97; Bourke 2011).

To see how selfish genetic elements fit into the replicator/vehicle distinction, it is first worth noticing that Dawkins himself changed his mind slightly about the implications of the distinction (Sterelny and Kitcher 1988; Okasha 2008b). In *The Selfish Gene* (Dawkins 1976), he argues that the gene level offers a uniquely correct representation of the causal processes underlying evolutionary change. In *The Extended Phenotype* (Dawkins 1982a), however, he presents a weaker argument. Here, Dawkins argues that the gene's-eye view and the traditional individual centered view as 2 different, equivalent perspectives of evolution—2 orientations of a Necker Cube, as he puts it. Whereas selfish genetic elements are easily accommodated by the first, stronger, argument, the equivalence of the individual and gene's-eye view is more problematic. Selfish genetic elements are the textbook example of a phenomenon not explainable by the traditional individual-centered perspective. A way around this, as has been suggested multiple times (Sober and Wilson 1998; Reeve and Keller 1999; Okasha 2008b; Lloyd 2012), is to treat replicators that are selfish genetic elements also as vehicles. Thus, whereas all genes are replicators, and can only improve their chances of transmission by contributing to the fitness of the vehicle that houses them, selfish genetic elements play a dual role.

Hierarchical views of selfish genetic elements

The relationship between the gene's-eye view as articulated by Williams and Dawkins and the study of selfish genetic elements may thus seem straightforward. The existence of selfish genetic elements has indeed often been seen as one of the strongest arguments for the approach (Okasha 2006), a point emphasized in recent commentary commemorating the 40th anniversary of *The Selfish Gene* (Ridley 2016). For example, when discussing the work of Eberhard (1980)

and Cosmides and Tooby (1981) on the conflicts between the nuclear and organellar genomes, Dawkins (1982a) wrote:

Neither Eberhart nor Cosmides and Tooby explicitly justify or document the genes'-eye view of life: they simply assume it (...). These papers have what I can only describe as the flavour of post-revolutionary normal science.

Dawkins (1982a, p. 178)

We need only to turn to Williams' *Adaptation and Natural Selection* (1966), the first articulation of the gene's-eye view, to see why this is not the whole story. Williams discusses one example of a selfish genetic element, the *t*-allele in mice studied by Lewontin (1962; Lewontin and Dunn 1960). Ironically, however, the inability of the *t*-allele to spread to high frequencies is presented as the only convincing case of group selection in nature (Williams 1966, p. 117). The tension between selfish genetic elements and other levels of selection was also central to one of the strongest proponents of a hierarchical approach to evolutionary theory: Stephen Jay Gould. In his majestic final book, *The Structure of Evolutionary Theory* (2002), he wrote:

When future historians chronicle the interesting failure of exclusive gene selectionism (based largely on the confusion of bookkeeping with causality), and the growing acceptance of an opposite hierarchical model, I predict that they will identify a central irony in the embrace by gene selectionists of a special class of data [i.e. selfish genetic elements], mistakenly read as crucial support, but actually providing strong evidence of their central error.

(Gould 2002, p. 689)

Here, Gould is attacking the strongest version of the gene's-eye view, the argument that a gene level perspective is the only true representation of evolution by natural selection. Gould never warmed to the term “selfish DNA” (as selfish genetic elements have often been called), which he thought privileged the individual organism in an inappropriate way, he did consider selfish genetic elements to be among the strongest evidence for the need of a hierarchical view of evolutionary biology (Gould 1983, 1984, 2002). This link between within-genome selection and hierarchy has later been picked up and expanded by several others (Vrba and Eldredge 1984; Doolittle 1989, 2013; Gregory 2001, 2004, 2005, 2013). The main argument of these papers is that explanations of selfish genetic elements must involve selection at both the level of the selfish genetic element and the level of the individual organism. Thus, like Dawkins and other gene proponents, Gould and his colleagues strive to demote the individual from the central position in evolutionary theory. However, since proponents of multilevel selection models are committed to the organism as one level of explanation they need to invoke an additional level to explain selfish genetic elements. This is in contrast to Dawkins who wants to remove the individual organism completely from evolutionary explanations, as he once put it: “I coined the vehicle not to praise it but to bury it” (Dawkins 1994).

In his account of hierarchy, Gould was greatly inspired by Lewontin (1970). In this formulation of the general principles of evolution by natural selection, which argued that evolution will occur in any population of entities, as long as the entities exhibit “heritable variation in fitness”. These basic principles of variation, heredity, and differential fitness are also key to the Price equation (Price 1970) as well as Godfrey-Smith's ‘Darwinian populations’ concept (Godfrey-Smith 2009), which also allow us to partition out selection at multiple levels.

Multilevel selection and the gene's-eye view in practice: genome size variation and the major transitions

The gene's-eye view and multilevel selection models are often presented as rival conceptual frameworks. In reality, they highlight different aspects of the biology of selfish genetic elements. Depending on which perspective one adopts, different aspects of their biology stand out. A multilevel selection model shows how selection on one level will have fitness effects on other levels in the hierarchy and therefore comes in handy when we want to assess the importance phenotypic effects of selfish genetic elements. Taking a gene's-eye view, on the other, offers a way to understand the strategic logic of selfish genetic elements. Two empirical examples that highlight the benefit of maintaining both perspectives are the role of transposable elements in genome size variation and the major transitions.

Transposable element and genome size variation

Genome size correlates with several traits relevant to organismal fitness, such as development and metabolic rate (Gregory 2005, 2013), but much of variation in genome size among closely related species is due to differential accumulation of selfish transposable elements (Ågren and Wright 2011). Thus, while selection at the gene level will push for an increased genome size, this will be counteracted by selection at the individual level (Kidwell and Lisch 2001). A full understanding of the mechanisms governing genome size variation can therefore only come by considering evolutionary processes operating at multiple levels (Gregory 2004, 2013; Gregory et al. 2016). In particular, a multilevel perspective allows us to partition out the strength of selection acting on transposons themselves contra the individual organism. Furthermore, if species with transposon-rich or transposon-poor genomes are formed and/or go extinct at different rates then species level selection may help us to understand why transposons are abundant in some species but not others (Brunet and Doolittle 2015). For other aspects of transposon biology a gene's-eye view can be very helpful. For example, predictions about why transposons will be more common in sexually reproducing species, in groups with low effective population size, and in regions of the genome with low recombination are born out of (diploid) population genetic models. (Whether the gene's-eye view and diploid genotypic models are equivalent is the subject of long and still ongoing debate in the philosophy of biology; see, e.g., the exchange between Brandon and Nijhout 2006; Weinberger 2011).

The major transitions

The study of the major transitions reinvigorated the levels of selection and it has been gathering plenty of interest recently as a way of unifying work on social evolution across the hierarchy of life (Maynard Smith and Szathmáry 1995; Michod 1999; Bourke 2011; Calcott and Sterelny 2011; West et al. 2015). Throughout evolutionary history, evolutionary transitions in individuality have occurred when units that were previously able to reproduce independently now could only do so as part of a new level of individuality (Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1999). This is what has given life its hierarchical structure: genes in genomes, genomes in cells, cells in multicellular organisms, and multicellular organism in eusocial groups. One of the major achievements of the modern study of social evolution is therefore the insight that whatever level in this hierarchy we are interested in, regardless whether we are studying the origin and maintenance of fair meiosis or the policing of worker eggs in social insects, we are faced with similar

conceptual issues (Queller 1997; Bourke 2011; West et al. 2015). Most importantly, what prevents selfish behavior at lower levels from disrupting the functionality of higher levels? Whereas early formulations of the debate took the existence of distinct levels as a given, the major transitions tradition shows that this hierarchy too has an evolutionary origin (Griesemer 2000; Okasha 2005). Thus, the challenge is to explain how selection may act at one or more levels now, and also how the levels evolved to begin with.

The major transitions view is often considered the best vindication of the view that multilevel selection models and the gene's-eye view are complementary (Queller 1997; Okasha 2006; Bourke 2011). For example, the pioneering major transitions models of Michod (e.g., 1997, 1999) are simultaneously multi-level and population genetic. In these hierarchical models, selection at lower levels comes out as transmission bias at higher levels and selfish genetic elements can therefore be treated as genetic entities with a systematic transmission bias (Michod 1999). Using the framework of the major transitions to understand the origin and maintenance of genome cooperation in face of selfish genetic elements has indeed been the theme of several recent papers (Durand and Michod 2010; Ågren 2014; Higgs and Lehman 2015).

Other conceptual consequences of selfish genetic elements

Selfish genetic elements have provided empirical ammunition in the disagreements between proponents of the gene's-eye view and multilevel selectionists. Below I briefly touch on 3 other conceptual issues where selfish genetic elements may contribute: agential thinking, adaptationism, and fitness maximizing models.

In an infamous review of *The Selfish Gene*, Mary Midgley (1979) presented one of the more bizarre misunderstandings of the book:

Genes cannot be selfish or unselfish, any more than atoms can be jealous, elephants abstract or biscuits teleological.

Of course, no one seriously believes that the gene's-eye view is committed to assigning emotions to genes. The heuristic of assigning agency to biological entities has a strong tradition (Dennett 1995, 2011; Wilson 2005). Thinking of genes as agents with the goal to maximize their own transmission is part of this strategy and has been popular especially for problems related to social behavior (Haig 1997, 2012; Queller 2011). A more serious critique of thinking about evolution as a competition between agents is that it may lead to what Francis (2004) in a memorable phrase referred to as "Darwinian paranoia". Godfrey-Smith (2009), picking up on this theme, places the gene's-eye view in the same explanatory family as demonic possessions and Freudian psychology. In each of these approaches, the world is explained by the presence and interaction between agents with competing or overlapping agendas. Moreover, both Francis (2004) and Godfrey-Smith (2009) warn that agential thinking may lead to an overreliance on adaptive explanations at the expense of other evolutionary explanations (although the latter is quick to point out that there is room for non-paranoid adaptationist thinking in evolutionary biology).

By fully accounting for the existence of selfish genetic elements some adaptationist thinking can be counteracted. The modern version of inclusive fitness theory tends to emphasize that individual organisms can be agents designed to maximize their inclusive fitness (West and Gardner 2013 and references therein). Although inclusive fitness can be useful in the study of selfish genetic elements and other

forms of within-individual conflict (Grafen 2006; Bourke 2011), a key assumption in the individual centered models is usually that within-individual conflict can be safely ignored. As Gardner and Grafen (2009) put it “Mendelian outlaws are the exception rather than the rule, at least insofar as we are interested in understanding phenotypic evolution”. This argument can be difficult to stomach for those of us interested in the spread of selfish genetic elements and other examples of within-organism conflicts (Shelton and Michod 2014). Especially given the sheer abundance of evidence of phenotypic effects of selfish genetic elements that has become available by now (Werren 2011; Lisch 2013; Rice 2013). If nothing else, it begs the question of *why* internal conflicts do not get out of hand and the shorthand of the individual as a maximizer and the optimization programme works so well for many evolutionary questions. Indeed, an important lesson from both the gene’s-eye view and the study of selfish genetic elements is the value of downplaying the organism and pushes to explain how it can persist in face of internal conflicts. The very existence of individual organism is a “paradox” (Dawkins 1990) or an “adaptive compromise” (Haig 2006, 2014). Or, as Maynard Smith (1985) puts it:

How did it come about that most genes, most of the time, play fair, so that a gene’s fitness depends only on the success of the individual that carries it? (Maynard Smith 1985)

In general, selfish genetic elements can act as a counterweight to naïve kinds of adaptationist thinking. Given the growing appreciation of the phenotypic consequences of selfish genetic elements (Burt and Trivers 2006; Werren 2011; Ågren 2013; Lisch 2013; Rice 2013), it becomes more difficult to ignore the existence of competing genes within individuals, at least if our goal is to develop a general account of adaptation. As discussed above, the idea that individual organisms act to maximize their inclusive fitness is based on the assumption that all genes share the same fitness interests, or that when they do not such disagreements can be discarded (Haig 2014). Selfish genetic elements show that instead of being a cohesive fitness maximizer, the individual organism is a compromise of several fitness interests (Cosmides and Tooby 1981; Dawkins 1990; Hurst 1996; Haig 2014). Individuals will still appear to be well adapted to their environments, as maximizing individual fitness will serve the majority of the genes in the organism.

Although it is easy to recognize that the same conceptual problems of conflict and cooperation exist at all levels in the hierarchy, moving between levels is not without problems. For example, the population genetic models used in studies of transposable elements have been said to have little in common with the game theoretical approaches of researchers of parent–offspring conflict (Charlesworth 2000; but see, e.g., Haig 1992, 1996). The lack of similarity is expressed in several ways. For example, the fitness-maximizing approach of behavioral ecology has had tremendous empirical success (Davies et al. 2012), but the take-home message of modern population genetics is that fitness is rarely if ever maximized (Ewens 2004). Moreover, whereas traditional Hamiltonian models have been designed under assumptions of weak selection, selfish genetic elements cause strong selective effects so that the application of such models may be difficult (Hamilton 1995; Keller 1999; Wenseleers and Ratnieks 2001).

Is it a problem that our modeling frameworks are based on such fundamentally different assumptions? On the one hand, both population genetic and game theory frameworks have enjoyed great empirical success, which arguably is ultimately what matters for any theoretical framework. On the other hand, it can be unsatisfactory

to have such fundamental disagreement at the heart of evolutionary theory. Addressing this is the goal of Alan Grafen’s admirable and ambitious Formal Darwinism Project (Grafen 1999, 2007, 2008, 2014). Making use of Grafen’s Formal Darwinism approach, Gardner and Welch (2011) developed a “gene as maximizing agent” analogy. This allowed them to link optimization models with the Price equation, thus providing a link between gene-level intentionality and the dynamic change in gene frequencies. Furthermore, several researchers have successfully taken modeling tools from behavioral ecology and applied them to selfish genetic elements (Bohl et al. 2014; Haig 2014). For example, Wenseleers and Ratnieks (2001) used a hawk and dove game theory approach to model meiotic drive, showing that insights from population genetics can be expressed in game theory terms. Similarly, Wagner (2006) used game theory to argue that there is little reason to expect transposable elements to cooperate. Finally, Haig and Grafen (1991) used game theory to model the evolution of recombination and fair meiosis as a defence against meiotic drive. Later, Haig (1996) showed how meiotic drive and parent–offspring conflict could be modeled with the same mathematical approach.

Concluding remarks

Close to a century of empirical advances mean that the days of considering selfish genetic elements as irrelevant oddities of limited evolutionary significance are long gone. Instead the last few decades has seen a rapid increase in our understanding of their biology. This review highlights how several alternative, but not necessarily mutually exclusive, concepts within the levels of selection tradition can be used to make sense of the evolutionary dynamics of selfish genetic elements. Most importantly, the gene’s-eye view helps us follow the strategic logic of selfish genetic elements, whereas focus on the levels of selection highlights how selection on selfish genetic elements will affect selection at other levels.

The gene’s-eye view and the multilevel selection models are not the only theoretical frameworks available. Additional conceptual insights to the biology of selfish genetic elements have also come from research on host–parasite interactions (Nee and Maynard Smith 1990; Brookfield 2011), political philosophy (Okasha 2012), epidemiology (Wagner 2009), and community ecology (Venner et al. 2009; Linquist et al. 2015). Different ways of modeling the same evolutionary process can often yield the same empirical prediction (Maynard Smith 1987; Waters 2005; Foster 2006). Occasionally some models may better represent the causal structure (Okasha 2015). Often, however, different models highlight different aspects of the phenomena in question and the empirical study of selfish genetic elements is better off keeping different conceptual approaches.

Acknowledgments

Many thanks to Andrew G. Clark, Tyler A. Elliott, David Haig, and Samir Okasha for comments and discussion. I am also grateful to 2 anonymous reviewers, Manus Patten, and Tom A.R. Price, who provided extensive comments on earlier versions that greatly improved the paper.

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