

ON MECHANISTIC REASONING IN  
EVOLUTIONARY BIOLOGY

by

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## ABSTRACT

The 'New Philosophy of Mechanisms' has been developed in light of dissatisfaction with previous philosophical models of scientific explanation. It comprises a variety of different views regarding the nature of mechanistic explanation, mechanistic strategies of investigation, as well as a mechanistic theory of causation. This dissertation addresses two basic questions regarding this new philosophy of mechanisms. First, what exactly is it? Second, what is its scope? In response to the first question I argue that while the new mechanists are informed by a variety of different cases, defend a variety of different theses, and are motivated by a variety of different problems, all share an emphasis on the value of *mechanistic reasoning* to scientific understanding. In response to the second question, I argue that the new philosophy of mechanisms extends to integrate with *statistical reasoning* in modern evolutionary biology. The upshot is a better picture of the nature, limit, and scope of the most recent and promising philosophical account of scientific reasoning.

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## CHAPTER 1

### INTRODUCTION

#### **1.1 On Mechanistic Reasoning in Evolutionary Biology**

I tackle two basic questions regarding a recent and promising philosophy of science: the so-called ‘new philosophy of mechanisms’. First, what exactly is the new philosophy of mechanisms? Because the new philosophy of mechanisms has emerged primarily in response to dissatisfaction with previous efforts to characterize scientific *explanation*, it is often treated as providing a philosophical account of scientific explanation. A closer look, however, reveals that the new philosophy of mechanisms involves much more than a view about explanation. In addition to views about explanation, new mechanists defend views regarding scientific discovery, methodology, understanding, as well as the metaphysics of causation (Craver & Tabery, 2015). For these reasons, there has been some difficulty in assessing the core commitments of the new philosophy of mechanisms. Therefore, identifying a philosophical thesis that underpins *the* philosophy of mechanisms is the first major goal of this dissertation.

Second, what is the scope of the new philosophy of mechanisms? Much of what has been said about the role and value of mechanistic thinking has been grounded in specific sciences, such as molecular biology and neuroscience. It remains an ongoing effort of the new mechanists to assess the limits and scope of the mechanistic account



across the sciences. Moreover, there appear to be domains of scientific practice that are *nonmechanistic*. Sciences that focus on population-level patterns, driven by statistical methods and making no explicit appeal to mechanisms or mechanistic information (e.g., parts, activities, or organization), are sciences that present challenge cases for the new philosophy of mechanisms. Therefore, the second major task of this dissertation is to assess the scope of the new philosophy of mechanisms, especially as it pertains to those seemingly nonmechanistic domains of investigation.

The first thesis of this dissertation provides an answer to the first question: what is the new philosophy of mechanisms? I argue that the glue that binds the new philosophers of mechanism is an emphasis on the importance of *mechanistic reasoning* to understanding the world. While some new mechanists defend views about mechanistic *explanation*, others defend views about mechanistic *methodology* or *causality*. What is common to each, however, is that their views are driven by *mechanistic reasoning* – i.e., a tendency to conceive of the natural world as composed of causally interacting and organized parts or components. I make my case for this thesis in Chapter 3, where I offer an exhaustive analysis of all the philosophical theses associated with the new philosophy of mechanisms. While various new mechanists defend different views about explanation, methodology, and causality, they are all grounded by mechanistic reasoning.

The second thesis of this dissertation works to answer the second major question: what is the scope of the new philosophy of mechanisms? To that end, I argue that the new philosophy of mechanisms, evidenced by mechanistic reasoning, extends to integrate with, but not overlap or supersede, inherently nonmechanistic, *statistical reasoning* in modern evolutionary biology. Unlike mechanistic reasoning, *statistical reasoning* drives

efforts to mathematically model, evaluate, and predict large-scale (e.g., population-level) patterns. I make my case for this claim in two parts. First, in Chapter 4, I make a case for the role and value of mechanistic reasoning in statistical phylogenetics, which is a historically nonmechanistic subfield of evolutionary biology. There I argue that mechanistic reasoning positively influences tree hypothesis construction via use of ‘embedded mechanisms’ in Maximum Likelihood models of inference. Second, in Chapter 5, I make a case for the role and value of mechanistic reasoning in population genetics. There I argue that the modern application of classical population-genetic, statistical methods is integrated with a family of mechanistic methods used to investigate and understand the relationships between genotypes, phenotypes, and fitness.

With these two positive theses in mind, a few clarifications are in order. The first clarification is to highlight that, although the new philosophy of mechanisms is closely associated with philosophical accounts of scientific *explanation*, my contributions more closely regards scientific *reasoning*. This is because although the new mechanists are motivated by problems facing previous accounts of explanation, the only viable way to tether all of their views is by focusing on reasoning. Moreover, my contribution does not attempt to capture scientific reasoning across the board, but specifically *mechanistic reasoning* – i.e., reasoning about the world as composed of causally-interacting and organized parts. Furthermore, I do not attempt to assess the scope of mechanistic reasoning across all the science. Rather, I target only those specific fields where mechanistic reasoning is both historically and conceptually unexpected; namely, statistical phylogenetics and population genetics. I invite readers to assess whether or not my conclusions extrapolate to a broader domain of scientific practice. For these reasons,

the force of this project regards specifically *the role of mechanistic reasoning in evolutionary biology*.

## **1.2 Summary and Explanation of Chapters**

### **1.2.1 Chapter 2: A Review of Background Literature**

A large part of the motivation for this dissertation project comes from a rich history of philosophical efforts to characterize scientific explanation and problems for each account. Chapter 2 helps make clear this rich history by describing six major philosophical accounts of scientific explanation: (1) the *Deductive Nomological Model*, (2) the *Deductive Statistical Model*, (3) the *Inductive Statistical Model*, (4) the *Unification Model*, (5) the *Statistical Relevance Model*, and (6) the *Causal-Mechanical Model*. Each model provides a highly specified thesis regarding the nature of scientific explanation and each thesis exhibits counterexamples in scientific practice. Chapter 2 also introduces the new philosophy of mechanisms as a conglomeration of philosophies of science designed to resolve many of the issues that beset the six previous models.

### **1.2.2 Chapter 3: What Is the New Philosophy of Mechanisms?**

The goal of Chapter 3 is to make a case for *mechanistic reasoning* as the glue that binds the variety of different views and theses associated with the new philosophy of mechanisms. It does so by engaging an extant account: Arnon Levy's (2013) tripartite model of the new philosophy of mechanisms. Levy construes the philosophy of mechanisms as comprised of three different groups of claims regarding (1) mechanistic explanation, (2) mechanistic methods, and (3) mechanistic causality. I apply Levy's

model to a recent debate regarding whether or not natural selection ‘is a mechanism’ to reveal additional projects and normative challenges that underpin the philosophy of mechanisms.

First, there is the project of fleshing out and articulating *mechanistic explanation*, as a set of philosophical theses regarding the manner in which scientists appeal to mechanisms or mechanistic information (e.g., parts, activities, and organization) in their efforts to explain various natural phenomena. Second, there is the project of fleshing out and articulating *mechanistic methods*, as strategies of investigation in modern scientific practice. Unlike these first two major constituents of the new philosophy of mechanisms, the third project, *mechanistic causality*, regards the metaphysics of causation. The additional project that underpins each of these three primary objectives of the new philosophy of mechanisms is *definitional mechanism*, the fundamental task of articulating exactly what a ‘mechanism’ is in the first place.

Chapter 3 also addresses the *challenge of application*, which is the challenge of aligning one’s definition of mechanism with the manner in which the term is actually used by practicing scientists. In this respect, Chapter 3 introduces a normative component of the new philosophy of mechanisms, as some (but not all) new mechanists have positive views about how practicing scientists should think and talk about mechanisms. The key take-home, however, is that Chapter 3 should be read as answering the question: what is the new philosophy of mechanisms? On the one hand, it makes clear how the new philosophy of mechanisms comprises a variety of projects involving *mechanistic explanation*, *mechanistic methods*, and *mechanistic causality*. In addition to those projects is the more fundamental task of defining what a mechanism is in the first place.

What is common to the three major projects, however, is an emphasis on the importance of *mechanistic reasoning* to understanding the world.

Chapter 3 makes ample use of a locution that calls for some clarification. Throughout the chapter, I make my case in light of the question: “what philosophical theses associated with the new philosophy of mechanisms are *at stake* in light of the debate about natural selection as a mechanism?” I have adopted this ‘at stake’ language in this chapter because there I use Levy as a foil, who is the first to use this particular terminology. If a philosophical thesis is ‘at stake’ in light of the debate about natural selection as a mechanism, it means that that particular philosophical thesis must either be brought into question or completely rejected as a consequence of the conclusion that natural selection is not in fact a mechanism. So, for example, the philosophical thesis that all causal phenomena are mechanisms is ‘at stake’ in light of the debate about natural selection as a mechanism because, if it turns out that natural selection (which is a causal process) is not a mechanism, then it cannot be true that all causal phenomena are mechanisms. In short, readers should note that Chapter 5 treats a philosophical thesis as ‘at stake’ if that thesis must be rejected or brought under scrutiny as a consequence of how one settles the debate regarding whether or not natural selection is a mechanism.

### 1.2.3 Chapter 4: Mechanistic Reasoning in Statistical Phylogenetics

The thesis of this chapter is that there are instances of statistical phylogenetics (an exemplary *nonmechanistic* science) that benefit from mechanistic reasoning. Thus, this chapter should be read as providing an argument that seeks to assess the scope of the new philosophy of mechanisms, which is the second major task of this dissertation. In this

respect, the thesis is that mechanistic reasoning extends to integrate with statistical phylogenetics, via the practice of embedding mechanisms in the mathematical models used to construct phylogenetic tree hypotheses.

#### 1.2.4 Chapter 5: Mechanistic Reasoning in Population Genetics

Like Chapter 4, Chapter 5 works to answer the question: what is the scope of the new philosophy of mechanisms? It does so by addressing the role and value of mechanistic reasoning in population genetics, another exemplar of nonmechanistic science. While classical population genetics is indeed an inherently nonmechanistic approach to the investigation and explanation of evolutionary hypotheses, the modern application of population genetic methods is deeply integrated with a contrasting class of mechanistic methods in evolutionary biology. By integrated, I mean that mechanistic and population genetic methods are combined in current efforts by practicing evolutionary biologists to investigate, explain, and build evidence for hypotheses regarding adaptive evolution. That is, while there was a time when biologists were divided on how best to investigate and build evidence for claims about evolution – population-genetic, statistical vs. organism-oriented, causal-mechanical approaches – today rather large families of mechanistic and statistical methods are applied either in tandem or sequentially in efforts to investigate, explain, and build evidence for claims regarding adaptive evolution in natural populations.

It is important to note that although Chapter 5 is framed as addressing the role of mechanistic reasoning in the field of population genetics, the cases that are considered represent instances in which population genetic methods are applied in modern biology.

The reason for this is that, at the bottom line, what is pertinent to my philosophy of science is not the theoretical and conceptual framework of population genetics, but rather, the manner in which practicing scientists use population genetic methods in modern evolutionary biology. To that end, applied population genetics in modern evolutionary biology, rather than the theoretical foundations of population genetics, is the focus of Chapter 5.

### 1.2.5 Chapter 6: Conclusions

Chapter 6 restates the two major goals tackled by this dissertation. On the one hand, it asks the question: what is the new philosophy of mechanisms? It answers that common to all projects in the new philosophy of mechanisms is an emphasis on the importance of *mechanistic reasoning* to understanding the world. On the other hand, it asks: what is the scope of the new philosophy of mechanisms? It answers that in modern evolutionary biology, the scope of *mechanistic reasoning* extends to integrate with a contrasting class of *statistical reasoning* in both statistical phylogenetics and population genetics.

### 1.3 References

- Craver, C. F., & Tabery, J. G. (2015). Mechanisms in science. *The Stanford Encyclopedia of Philosophy* (Spring 2016 Edition).  
<http://plato.stanford.edu/archives/spr2016/entries/science-mechanisms/>
- Levy, A. (2013). Three kinds of new mechanism. *Biology & Philosophy*, 28(1), 99–114.

## CHAPTER 2

### ON PHILOSOPHIES OF SCIENTIFIC EXPLANATION: FROM NOMOLOGICAL DEDUCTIONS TO MECHANISM ELUCIDATION

#### **2.1 Abstract**

This chapter introduces the background literature that motivates this dissertation project. Because the new philosophy of mechanisms has been developed in light of dissatisfaction with previous philosophical views of scientific explanation, I briefly review six previous ‘models’ of scientific explanation and the primary objections that set their demise. I then briefly introduce the key philosophical moves and contributions that are treated as fundamental to the new philosophy of mechanisms.

#### **2.2 Introduction**

The new philosophy of mechanisms has been developed in light of insurmountable challenges raised against previous models of scientific explanation. In Section 2.2, I will briefly describe six major models of scientific explanation that precede the philosophy of mechanisms, along with the major problems, issues, and objections. In Section 2.3, I will briefly review the key philosophical moves that are attributed to the new philosophy of mechanisms.



## 2.3 Models of Scientific Explanation and Their Pitfalls

I group philosophical efforts to characterize the nature of scientific explanation into two categories. On the one hand, there is a group of models that construe scientific explanations as arguments. On the other hand, there is a group of models that construe scientific explanations as assemblies of information.

### 2.3.1 Explanations as Arguments

The *Deductive-Nomological (DN) Model* construed scientific explanations as deductive arguments (Hempel, 1942, 1965; Hempel & Oppenheim, 1948).<sup>1</sup> To explain a phenomenon is to show how it is “a logical consequence” of premises that express (a) empirical observations and (b) law(s) of nature. On the DN Model, for example, the current position of Mars (**conclusion**) is a logical consequence of Newtonian laws of motion (**premise 1**) and previous observations of the position of Mars (**premise 2**) (Woodward, 2014). This exemplar deductive argument is the explanation of the present position of Mars, according to the DN Model.

The DN Model, however, failed to capture a few key features of scientific explanation and reasoning. First, in its original formulation, the DN Model was unable to accommodate statistical laws. Second, it was unable to accommodate scientific conclusions that are probabilistic. Yet many laws in biology are statistical and rarely are scientific conclusions nonprobabilistic (i.e., certain). To use the first classic example, scientists might appeal to statistical laws in order to assign a high probability that a

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<sup>1</sup> Although core development of the DN Model is best attributed to Hempel and Oppenheim, other proponents include Popper (1935, 1959), Braithwaite (1953), Gardner (1959), and Nagel (1965).

patient who takes penicillin will recover from streptococcus. This argument pattern considers statistical laws and its conclusion considers a *high probability*, but not *absolute certainty*. So Hempel (1965) developed two new models of scientific explanation – the *Deductive Statistical (DS) Model* and the *Inductive Statistical (IS) Model* – to accommodate scientific explanations that appeal to statistical laws or involve uncertain conclusions.

A handful of insurmountable objections set the demise of the DN, DS, and IS Models. Although these three models offer distinct philosophical accounts of scientific explanation, each are problematized by the same set of counterexamples. So, from here on, I will refer to these three models as the ‘DN/DS/IS Model.’ The DN/DS/IS Model, which treated scientific explanations as arguments, ultimately met its demise in light of two basic counterexamples.

First, arguments do not effectively capture the *causal asymmetry* of explanation. Consider this classic counterexample: given the position of the sun and the length of the shadow of a flagpole, one can infer the height of the flagpole (Bromberger, 1966). This inference using basic geometry fits the DN/DS/IS Model quite well. Do we want to say, however, that the length of the shadow explains the height of the flagpole? We do not. Rather, what we want to say is that the reverse is true: that the height of the flagpole (and the position of the sun) explains the length of the shadow. The reason is that the sun *causes* the length of the shadow. Consequently, *causal asymmetry* is embedded in explanation. In other words, the DN/DS/IS Model allows for a problematic counterexample in which one may construct an argument that is not intuitively explanatory.

The DN/DS/IS Model was met with a second classic counterexample. In addition to failing to capture the causal asymmetry of explanation, argument patterns also fail to rule out *explanatorily irrelevant* information. Salmon (1971) devised this problematic argument that fits the DN/DS/IS Model:

**Premise 1:** Mr. Jon Jones takes birth control (empirical observation)

**Premise 2:** Men who take birth control do not get pregnant (law of nature)

**Conclusion:** Mr. Jon Jones will not get pregnant (consequence of P1 and P2)

The problem is that Mr. Jon Jones will not get pregnant regardless of whether or not he takes birth control, so the argument pattern permits information that is explanatorily irrelevant to count as part of the explanation. The philosophical upshot is that a satisfactory account of scientific explanation should restrict cases like these, so the DN/DS/IS Model is inherently problematic.

In an effort to provide a model of scientific explanation that does not succumb to the counterexamples involving causal asymmetry and explanatory irrelevancies, Philip Kitcher (1981, 1989) developed the *Unificationist (U) Model* of scientific explanation.<sup>2</sup> Like the DN/DS/IS Model, the U Model treats scientific explanations as arguments, as it grounds explanatory unification in terms of *schematic arguments*, composed of *schematic sentences*, into triple *argument patterns*. Unlike the DN/IS Model, however, the U Model does not suggest that scientific explanation works by showing that a phenomenon is *to be expected*, given initial conditions. Rather, scientific explanation works by unifying a range of phenomena under a single account.

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<sup>2</sup> Note that Kitcher's U Model was developed in light of a similar Unificationist model provided by Friedman (1974)

The basic idea is this: a major feature of scientific explanation is showing how there are key connections and relationships between phenomena that are treated as unrelated. Newton, for example, unified terrestrial and celestial theories of motion (Woodward, 2014). Maxwell, too, unified theories of magnetism and electricity. Unification seems prominent in the history of evolutionary theory as well. Darwin's theory of natural selection unified a variety of phenomena (e.g., biological diversity and geographical distribution) under a single theory. We might treat the modern evolutionary synthesis as a unification of different fields of biology as well.

While Kitcher (1989) worked to show how the U Model could accommodate the causal asymmetries and explanatory irrelevancies that plagued the DN/DS/IS Model, his account ultimately succumbed to similar objections (Barnes, 1992; Craver, 2007; Woodward, 2003, 2014). Most notably, the U Model fails to capture the *heterogeneity* of unification in science. While it is evident, that is, that unification is an objective of at least some scientists, there are a variety of different ways that scientists unify in practice – and there is no single U Model characterization that can capture the variety of unification across the sciences. So even if scientific explanation works via unification, Kitcher's U Model fails to accommodate all the diverse cases and kinds (i.e., the heterogeneity) of unification across the sciences.

There is the deeper challenge that although it may be accurate that unification is an objective of scientific practice, it is unclear that the act of unification is actually explanatory. Craver (2007, p. 42), for example, offers instances of unification that are not explanatory, such as the construction of phylogenetic tree hypotheses. Although tree hypotheses unify a variety of phenomena (species, for example) under a single account, it

is not clear that these tree hypotheses are explanatory.

### 2.3.2 Scientific Explanations as Assemblies of Information

All subsequent philosophical accounts of scientific explanation have abandoned one fundamental tenet of the DN/DS/IS Model and the U Model: scientific explanations are arguments. In addition to the challenges of articulating laws (Mitchell, 1997; Woodward, 2000), causal asymmetries, and explanatory irrelevancies, both the DN/DS/IS Model and the U Model failed to capture the fact that, in many cases of scientific explanation, scientists simply are not building arguments. Salmon was the first to push in a new direction that construed scientific explanation not as argumentation, but rather, the assemblage of various kinds of explanatorily relevant information. Because the DN/DS/IS Model and the U Model both struggled with explanatory relevance and low probability explanations (which are ubiquitous in science), Salmon (1971) first devised the *Statistical Relevance (SR) Model*, which construed scientific explanation as the assembly of information that distinguishes statistically relevant relationships and properties from relationships and properties that are statistically irrelevant.

A huge upshot of the SR Model was that it could accommodate both low probability explanations as well as counterexamples (to previous models) involving explanatorily irrelevant information. One of the key examples that broke the DN/DS/IS Model – an argument pattern that cites a male who takes birth control as explaining the male's failure to get pregnant – is handled rather easily with the SR Model. Regardless of whether males take birth control, they will not get pregnant. So the notion that a male takes birth control is statistically irrelevant and ruled out by the SR Model. The SR

Model, that is, restricts information involved in scientific explanations to statistically relevant information.

Eventually, Salmon (1984) bolstered his SR Model in favor of the *Causal-Mechanical (CM) Model*, which focused on an aspect of explanation in fundamental physics missed by all previous models described above: causality. The DN/DS/IS Model failed to capture the asymmetry of causal relationships entirely. The U Model came with the promise that it would make sense of causal relationships via unification, a promise not borne out (Barnes, 1992; Craver, 2007; Woodward, 2003, 2014). It seems as well that Salmon recognized a similar flaw in his SR Model, as statistical relationships (correlations, for example) do not entail causal relationships. Moreover, the identification of causal relationships, Salmon (1984) argues, is what really lies at the heart of scientific explanation.

On the CM Model, a crucial aspect of all scientific explanation is grounded in efforts to distinguish causal relationships and connections from those that are not. For Salmon, to explain a phenomenon is to situate the phenomenon in the causal structure of the world. The CM Model is designed to capture this aspect of scientific explanation at the level of fundamental physics by distinguishing genuine *causal processes* from noncausal *pseudo-processes*. What is unique about causal processes is that they have the capacity to *transmit a mark* (Salmon, 1984).<sup>3</sup> The basic idea is that a causal interaction occurs when two causal processes intersect and leave a ‘mark’. Here, a ‘mark’ is simply a generic term meant to capture some property or feature of causal processes that we can track.

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<sup>3</sup> Salmon (1984, p. 147) attributes the term ‘mark transmission’ to Hans Reichenbach.

On the CM Model, we treat a flying baseball as a causal process because it has the capacity to transmit a mark on other causal processes. So, for example, when a flying baseball strikes the brittle glass window, it leaves a very significant ‘mark’, as the glass shatters. This sort of *causal process* is distinguished from a *pseudo-process* because the latter does not have the capacity to transmit a mark. Feel free to take a moment now and wave your hand in front of the nearest light source. As your hand blocks light, it will leave a shadow across your desk: you will see a shadow move in conjunction with the motion of your hand. Your shadow, however, does not stick – it cannot transmit a mark on your desk. Why? On Salmon’s (1984) CM Model, the reason is that your shadow is a *pseudo-process* that is not causal, because it fails to produce a *mark transmission*.<sup>4</sup>

With the broader picture of an ongoing philosophical attempt to characterize scientific explanation in mind, the CM Model provides the following analysis. That your hand’s shadow is a *pseudo-process* explains why it failed to leave a mark on the table. On the other hand, that the moving baseball is a *causal process* explains why it *did* leave a mark on the pane of glass. While Salmon (1984) does not characterize it in this way, the CM Model construes scientific explanation as the assembly of a certain kind of information: causal information. To explain natural phenomena is to identify and assemble the information that places the phenomena in the causal structure of the world.

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<sup>4</sup> Salmon’s favorite example involved a large, circular room with a spinning spotlight in the center. The light traveling from the spotlight to the wall is a *causal process*, but the spot of light moving along the wall is only a *pseudo process*. This distinction is achieved because the former has the capacity to transmit a mark, but the latter does not. For example, if one inserts a red filter over the spotlight, the beam of light will be red, thus transmitting a mark. As the red spot travels across the wall, however, no red mark is left behind, as it is not a causal process.

The shortcomings of this approach set the basis for many contributions to the new philosophy of mechanisms, which are discussed in the following section.

#### **2.4 The New Philosophy of Mechanisms**

A key goal of this dissertation is to make clear what the ‘new philosophy of mechanisms’ actually is. Here let’s set out some of the key philosophical moves that are often treated as core or foundational to the new philosophy of mechanisms. I will focus as well on the manner in which these philosophical contributions are developed in light of shortcomings of the preceding models of scientific explanation. In a word, this may be the very best way to capture the new philosophy of mechanisms: it is a disparate set of independent attempts to capture the aspects of scientific explanation and reasoning missed by the DN/DS/IS, U, and SR/CM Models.

Many of the contributions constitutive of the new philosophy of mechanisms stem from a basic set of dissatisfactions of all preceding accounts. First, the new philosophers of mechanisms have abandoned the notion that scientific explanations are arguments. While scientists do in fact invoke arguments, it is unclear that arguments are explanatory. Second, the new philosophers have abandoned the notion that scientific explanation in some way must always connect with laws or regularities of nature (Cartwright, 1983). Again, while the search for and identification of laws may be a key component of some scientific practice, genuine laws are few and far between (Beatty et al., 1997). Third, scientific explanation is not reductionistic.<sup>5</sup> Most new mechanists recognize that

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<sup>5</sup> Oppenheim and Putnam (1958) and Sarkar (1992) offer a useful distinction between various kinds of reductionism. To be precise, the kind of reductionsism avoided by the



explanations, especially in biology, are genuinely multilevel. We cannot explain animal cognition or genetic drift by appeal to fundamental physics. Fourth, causality is key. A thorough perspective of what modern scientists are doing demonstrates attention to the causal structure of the world.

#### 2.4.1 Decomposition and Localization

The first thorough articulation of mechanistic explanation traces back to Bechtel and Richardson's (2010) *Discovering Complexity*. Informed by 10 years of research on cognitive neuroscience, Bechtel and Richardson offered an account of '*mechanistic explanation*' very distinct from Salmon's (1984) CM Model. Unlike fundamental physics, cognitive neuroscientists explain the world by searching for and discovering of mechanisms. They outline two basic strategies of investigation and explanation that underpin this practice: *decomposition* and *localization*. Things to be explained are treated as organized systems, composed of functioning parts. *Decomposition* refers to the strategy of breaking a system into functional parts. So, for example, neuroscientists might decompose the brain into various subregions with an eye for divergent functional roles. *Localization*, on the other hand, refers to the strategy of determining which parts of a mechanism (or broader system) are associated with different subfunctions. So, for example, neuroscientists might *localize* the hippocampus as the subregion responsible in

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new mechanists is *epistemological reductionsism*, as opposed to *ontological reductionsism*. That is, while most of the new mechanists likely believe that nothing exists 'over and above' the sum of the constitutive parts of higher-level mechanisms (ontological reductionism), they do not believe that knowledge or explanation of higher-level mechanisms can be 'reduced' to lower level parts or entities.

part for memory. This, however, is only a toy example. Bechtel and Richardson go to great lengths to reveal the intricacies of neuroscientific investigation and localization in light of the mechanistic strategies of decomposition and localization. Details aside, the key take-home of their contribution is the recognition that, over and above appeal to laws, unification, and construction of arguments, neuroscientists have been highly successful in explaining the brain by searching for and discovering the ‘mechanisms’ that are responsible for phenomena.

#### 2.4.2 Organization

Another key contribution to the new philosophy of mechanisms involves attention to the role of *organization* in scientific explanation. In the search for and discovery of mechanisms, the spatial arrangement of biological systems is crucial to its explanation. Genetic mechanisms of replication are not just a jumble of nucleotides, subproteins, proteins, channels, and macromolecules. Rather, mechanisms of replication require a rather specific kind of spatial arrangement, if the system is to function properly. Wimsatt (1997) made a careful conceptual distinction between *organization* and *aggregativity*, which is key to making sense of mechanisms. *Aggregativity* is merely the sum of parts in no particular spatial arrangement. Scoop up a handful of warm beach sand, zoom in with a microscope, and you will see an aggregation of parts into a sum. Feel free to swap out and rearrange various grains of sand in your palm and the behavior of the system will see no change. This is because the palm of sand does not exhibit organization, but only aggregativity. In other words, the spatial arrangement of the parts of aggregative system is irrelevant to the behavior or function of the system as a whole.

Mechanistic *organization*, on the other hand, places constraints on the spatial arrangement of entities or parts constitutive of a larger system. Take apart your clock, swap a few gears, and it most certainly will not work. While new mechanists treat organization as a spectrum phenomenon, all mechanisms exhibit at least some degree of organization. That scientists investigate and explain the world by revealing the *organization* of biological systems is a key point underlying the new philosophy of mechanisms.

### 2.4.3 Thinking About Mechanisms in Molecular Biology and Neuroscience

The most influential contribution to the new philosophy of mechanisms is Machamer, Darden, and Craver's (2000) "Thinking about Mechanisms." They, too, describe the search for and discovery of mechanisms as characteristic of successful practice in neuroscience and molecular biology. They treat 'thinking in terms of mechanisms' as a new framework for addressing a litany of philosophical topics including laws, causality, scientific change, and reduction. The role and value of thinking about mechanisms in molecular biology has been thoroughly analyzed and articulated by Darden (2006). Craver (2007) extends this analysis to neuroscience. Both projects further develop conceptions of 'mechanism' and mechanistic explanation, especially as it contrasts to previous accounts of explanation (i.e., the DN/DS/IS Model, U Model, and the SR/CM Model).

They key take-home for this prominent contribution to the philosophy of mechanisms is the rejection of the views that scientists explain by (a) building arguments,

(b) appealing to laws of nature, and (c) explaining phenomena by reducing it to fundamental physics. In this sense, these contributions demonstrate the autonomy of biological science as a domain of investigation and explanation that is informative, independent of what is going at the level of fundamental physics. At the heart of investigative and explanatory success, moreover, are mechanisms. To explain various aspects of the world is to identify the mechanism responsible for the phenomenon. This requires an elucidation of the various *parts/entities*<sup>6</sup> of a system, the organization of those parts, and the individual *activities/interactions*<sup>7</sup> of the various parts. By elucidating mechanisms, molecular biologists not only reveal *why* systems behave the way they do, but importantly, they reveal *how* systems work.

#### 2.4.4 Mechanisms and Causality

There is a very important sense in which the new philosophy of mechanisms is inspired by Salmon's efforts to associate explanation with the causal structure of the world. The practices of molecular biology and neuroscientists reveal the importance of causal processes and interactions to scientific explanation. On my view, there are two basic ways in which the metaphysics of causality are constitutive of the new philosophy of mechanisms. For most of the new mechanists (but not all), a key feature of mechanisms is that they are causal. Elucidating the mechanism of protein synthesis is

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<sup>6</sup> Some new mechanists treat mechanisms as composed of 'parts', others 'entities'. It is unclear that anything substantial hangs on the distinction. I use 'parts/entities'.

<sup>7</sup> Some new mechanists construe the parts/entities of mechanisms as engaged in 'activities', others 'interactions'. Tabery (2004) reconciles the distinction and makes a proposal for the concept of 'interactivity'.

explanatory partly because it reveals the causal interactions that result in the construction of proteins. An upshot of mechanistic explanation, then, is that it helps us understand the importance of causality to scientific investigation and discovery. So, on the one hand, an important task of the new philosophy of mechanisms is providing a philosophical account of just how it is that mechanisms are causal. In this respect, there is a growing amount of philosophical literature regarding mechanisms and the metaphysics of causation.

Craver and Tabery (2015) couch attempts to account for the causes in mechanisms into four basic camps. First are those who adopt a later version of Salmon's (1984) mark transmission account, which replaces the notion of a 'mark' with the exchange of 'conserved quantities.' This *conserved quantities* account of causation, developed by Salmon (1994) and Dowe (1992), construes causal interactions as only those physical exchanges that involve the exchange and conservation of some quantity of information. So, that the cue ball knocks the eight ball is a causal interaction because the cue ball exchanges a certain quantity of momentum to the eight ball.

There are also those who have adopted a *counterfactual account* of causation in the mechanisms literature. On the counterfactual account, causation is understood not in terms of physical interactions, but rather, what could or would have happened, had things been otherwise. So, the cue ball caused the eight ball to be move because, had the cue ball not struck the eight ball, the eight ball would not have moved. This counterfactual account is most thoroughly developed by Woodward (2001, 2002) and versions of it have been endorsed by both Glennan (2002) and Craver (2007).

Other new mechanists have downplayed the promise of developing a general account of causation and, instead, couched the causal powers of mechanisms in terms of

the ‘activities’ of their parts (Bogen, 2004, 2008; Machamer, 2004). These *activity-based* accounts rest on the view that there are only instances of causal activities in which the parts of mechanisms engage, such as *binding, winding, pushing, pulling*, etc. So, on this view, the cue ball causes the eight ball to move because the cue ball engages in a specific causally powerful activity – perhaps ‘knocking’.

These three basic approaches to causes in mechanisms all apply general views about causation specifically to the concept of mechanism. There is, however, a second manner in which causality is tethered with the new philosophy of mechanisms. A prominent new mechanist, Stuart Glennan (1996, 2002, forthcoming), has gone to great efforts not just to show that mechanisms are causal, but rather, to employ mechanisms as *the* basis of causation. On his view, all causal connections exist in virtue of mechanisms. So, for example, what causes the baseball to break the glass window? A mechanism. Although Glennan’s *mechanistic account of causality* has been met with criticism (Kistler, 2009; Woodward, 2013), the project of developing an account of causality based on the notion of mechanism represents a key move in the new philosophy of mechanisms.

Elsewhere, I argue with Tabery that these various accounts of causality in mechanisms reveal a valuable historical tracing (Matthews & Tabery, forthcoming). For each of the major accounts of causality adopted by the new mechanists, there is a historically analogous response to Hume’s problem of causation. We show, for example, that the activities approach traces back to Anscombe’s (1993) response to Hume, which effectively abandons efforts to provide a general theory of causation. We show as well that the counterfactual approach traces back to Lewis’ (1973) response to Hume, which is grounded in the semantics of counterfactual difference-making. One of the important

upshots of this historical perspective is that it helps alleviate some of the prominent criticisms that trouble accounts of causality in the mechanisms literature. In many cases, that is, it turns out that new mechanists are criticized for failing to meet operational criteria they never endorsed in the first place.

## **2.5 On Solidarity and Scope**

Although the new philosophers of mechanism have done well to develop an account of scientific explanation that resolves the major problems that plagued preceding accounts, the foundational commitments and scope of the new philosophy of mechanisms remain unclear. In the following two subsections, I highlight two aspects of the new philosophy of mechanisms that will be further articulated by this dissertation.

### **2.5.1 Solidarity**

The 20-year span that comprises the foundational projects that I treat as the new philosophy of mechanisms (from 1993 on) is rich. Core contributions to the philosophy of mechanisms come from a variety of different authors (Bechtel, Craver, Darden, Glennan, Machamer, Richardson, etc.). A variety of different case sciences inform the philosophy of mechanisms (e.g., molecular biology, cognitive neuroscience, neurobiology, and neuroscience proper). The various new mechanists tackle a variety of distinct philosophical goals (e.g., some target scientific discovery, others explanation, others causation).

Moreover, there are a variety of problems *within* the new philosophy of mechanisms that divide various proponents. There is, for example, a debate about

whether or not natural selection is a mechanism (Barros, 2008; Havstad, 2011; Matthewson & Calcott, 2011; Skipper & Millstein, 2005). There is a debate about whether mechanistic explanations are ontic or epistemic. Craver (2007), for example, champions an *ontic* account of explanation, which maintains that the things that are explanatory are the actual mechanisms that *exist* in the world. Bechtel (2008), on the other hand, maintains an *epistemic* view of explanation, maintaining that what explains are the *representations* of mechanisms.<sup>8</sup> There is also the more fundamental disagreement as to how to define ‘mechanism’ in the first place (Illari & Williamson, 2012; Matthews, 2016). It is for these reasons that this dissertation addresses the question: what is the new philosophy of mechanisms?

### 2.5.2 Scope

Foundational work in the philosophy of mechanisms starts with neuroscience (Bechtel, 2008; Craver, 2007) and molecular biology (Darden, 2006). However, the scope of the new mechanistic philosophy across the sciences remains unclear. A case has been made for the new mechanistic philosophy in a variety of different disciplines including neuroeconomics, organic chemistry, behavior genetics, cell biology, physics, and astrophysics (Bechtel, 2006, 2008; Craver & Alexandrova, 2008; Illari & Williamson, 2012; Ramsey, 2008; Tabery, 2014; Teller, 2010; Thagard, 2006). The full impact of the new philosophy of mechanisms has not yet been considered in modern evolutionary biology.

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<sup>8</sup> The distinction between ontic and epistemic accounts of explanation is both subtle and complicated, tracing back to Salmon (1982). See Illari (2013) for a thorough analysis of this distinction and a case for the integration of ontic and epistemic



## 2.6 References

- Anscombe, E. (1993). *Causality and determination: An inaugural lecture*. Cambridge, MA: Cambridge University Press.
- Barnes, E. (1992). Explanatory unification and the problem of asymmetry. *Philosophy of Science*, 59, 558–571.
- Barros, B. D. (2008). Natural selection as a mechanism. *Philosophy of Science*, 75(3), 306—322.
- Beatty, J., Brandon, R., Sober, E., & Mitchell, S. D. (1997). Symposium: Are there laws in biology? *Philosophy of Science*, 64(4), S432–S479.
- Bechtel, W. (2006). *Discovering cell mechanisms: The creation of modern cell biology*. Cambridge, MA: Cambridge University Press.
- Bechtel, W. (2008). *Mental mechanisms: Philosophical perspectives on cognitive neuroscience*. New York, NY: Routledge.
- Bechtel, W., & Richardson, R. C. (2010). *Discovering complexity: Decomposition and localization as strategies in scientific research*. Cambridge, MA: MIT Press.
- Bogen, J. (2004). Analysing causality: The opposite of counterfactual is factual. *International Studies in the Philosophy of Science*, 18(1), 1–26.
- Bogen, J. (2008). Causally productive activities. *Studies in History and Philosophy of Science Part A*, 39(1), 112–123.
- Braithwaite, R. (1953). *Scientific explanation*. Cambridge, MA: Cambridge University Press.
- Bromberger, S. (1966). Questions. *Journal of Philosophy*, 63(20), 597–606.
- Cartwright, N. (1983). *How the laws of physics lie*. Oxford, UK: Oxford University Press.
- Craver, C. F. (2007). *Explaining the brain*. Oxford, UK: Oxford University Press.
- Craver, C. F., & Alexandrova, A. (2008). No revolution necessary: Neural mechanisms for economics. *Economics and Philosophy*, 24, 381–406.
- Craver, C. F., & Tabery, J. (2015). Mechanisms in science. *The Stanford Encyclopedia of Philosophy* (Spring 2016 Edition).  
<<http://plato.stanford.edu/archives/spr2016/entries/science-mechanisms/>>
- Darden, L. (2006). *Reasoning in biological discoveries: Essays on mechanisms, interfield*

- relations, and anomaly resolution*. New York, NY: Cambridge University Press.
- Dowe, P. (1992). Wesley salmon's process theory of causality and the conserved quantity theory. *Philosophy of Science*, 59(2), 195–216.
- Friedman, M. (1974). Explanation and scientific understanding. *Journal of Philosophy*, 71, 5–19.
- Gardner, P. (1959). *The nature of historical selection*. Oxford, UK: Oxford University Press.
- Glennan, S. (1996). Mechanisms and the nature of causation. *Erkenntnis*, 44(1), 49–71.
- Glennan, S. (2002). Rethinking mechanistic explanation. *Philosophy of Science*, 69(S3), S342–S353.
- Glennan, S. (forthcoming). *The Routledge handbook of mechanisms and mechanical philosophy*. New York, NY: Routledge.
- Havstad, J. C. (2011). Discussion: Problems for natural selection as a mechanism. *Philosophy of Science*, 78(3), 512–523.
- Hempel, C. G. (1942). The function of general laws in history. *Journal of Philosophy*, 39, 35–48.
- Hempel, C. G. (1965). *Aspects of scientific explanation: And other essays in the philosophy of science*. New York, NY: Free Press.
- Hempel, C. G., & Oppenheim, P. (1948). Studies in the logic of explanation. *Philosophy of Science*, 15(2), 135–175.
- Illari, P. M. (2013). Mechanistic explanation: Integrating the ontic and epistemic. *Erkenntnis*, 78(2), 237–55.
- Illari, P. M., & Williamson, J. (2012). What is a mechanism? Thinking about mechanisms across the sciences. *European Journal for Philosophy of Science*, 2(1), 119–135.
- Kistler, M. (2009). Mechanisms and downward causation. *Philosophical Psychology*, 22(5), 595–609.
- Kitcher, P. (1981). Explanatory unification. *Philosophy of Science*, 48(4), 507–531.
- Kitcher, P. (1989). Explanatory unification and the causal structure of the world. In P. Kitcher & W. C. Salmon (Eds.), *Minnesota studies in the philosophy of science* (vol. 13, pp. 410–505). Minneapolis, MN: University of Minnesota Press.

- Levy, A. (2013). Three kinds of new mechanism. *Biology & Philosophy*, 28(1), 99–114.
- Lewis, D. (1973). Causation. *The Journal of Philosophy*, 70(17), 556–567.
- Machamer, P. (2004). Activities and causation: The metaphysics and epistemology of mechanisms. *International Studies in the Philosophy of Science*, 18(1), 27–39.
- Machamer, P., Darden, L., & Craver, C. F. (2000). Thinking about mechanisms. *Philosophy of Science*, 67(1), 1–25.
- Matthewson, J., & Calcott, B. (2011). Mechanistic models of population-level phenomena. *Biology & Philosophy*, 26(5), 737–756.
- Matthews, L. J. (2016). On closing the gap between philosophical concepts and their usage in scientific practice: A lesson from the debate about natural selection as a mechanism. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 55, 21–28.
- Matthews, L. J., & Tabery, J. G. (Forthcoming). Mechanisms and the metaphysics of causation. In S. Glennan & P. Illari (Eds.), *The routledge handbook of mechanisms and mechanical philosophy*. New York, NY: Routledge.
- Mitchell, S. D. (1997). Pragmatic laws. *Philosophy of Science*, 64(4), S468–S479.
- Oppenheim, P., & Putnam, H. (1958). Unity of science as a working hypothesis. *Minnesota Studies in the Philosophy of Science*, 2, 3–36.
- Popper, K. (1935). Logik der forschung. *Journal of Philosophy*, 32(4), 107–108.
- Popper, K. (1959). *The logic of scientific discovery*. London, UK: Hutchinson.
- Ramsey, J. L. (2008). Mechanisms and their explanatory challenges in organic chemistry. *Philosophy of Science*, 75(5), 970–82.
- Salmon, W. C. (1971). *Statistical explanation and statistical relevance*. Pittsburgh, PA: University of Pittsburgh Press.
- Salmon, W. C. (1982). Comets, pollen and dreams: Some reflections on scientific explanation. In McLaughlin (Ed.), *Australasian studies in history and philosophy of science* (vol. 1, pp. 155–178). Netherlands: Springer.
- Salmon, W. C. (1984). *Scientific explanation and the causal structure of the world*. Princeton, NJ: Princeton University Press.
- Salmon, W. C. (1994). Causality without counterfactuals. *Philosophy of Science*, 61(2), 297–312.

- Sarkar, S. (1992). Models of reduction and categories of reductionism. *Synthese*, 91(3), 167–194.
- Skipper, R. A., & Millstein, R. L. (2005). Thinking about evolutionary mechanisms: Natural selection. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 36(2), 327–347.
- Tabery, J. G. (2004). Synthesizing activities and interactions in the concept of a mechanism. *Philosophy of Science*, 71(1), 1–15.
- Tabery, J. G. (2014). *Beyond versus: The struggle to understand the interaction of nature and nurture*. Cambridge, MA: The MIT Press.
- Teller, P. (2010). Mechanism, reduction, and emergence in two stories of the human epistemic enterprise. *Erkenntnis*, 73(3), 413–425.
- Thagard, P. (2006). *Hot thought: Mechanisms and applications of emotional cognition*. Cambridge, MA: The MIT Press.
- Wimsatt, W. C. (1997). Aggregativity: Reductive heuristics for finding emergence. *Philosophy of Science*, 64, S372–S384.
- Woodward, J. (2000). Explanation and invariance in the special sciences. *The British Journal for the Philosophy of Science*, 51, 197–254.
- Woodward, J. (2001). Law and explanation in biology: Invariance is the kind of stability that matters. *Philosophy of Science*, 68(1), 1–20.
- Woodward, J. (2002). What is a mechanism? A counterfactual account. *Philosophy of Science*, 69(S3), S366–S377.
- Woodward, J. (2003). *Making things happen: A theory of causal explanation*. New York, NY: Oxford University Press.
- Woodward, J. (2013). Mechanistic explanation: Its scope and limits. *Aristotelian Society Supplementary Volume*, 87(1), 39–65.
- Woodward, J. (2014). Scientific explanation. *The Stanford Encyclopedia of Philosophy* (Winter 2014 Edition).  
<<http://plato.stanford.edu/archives/win2014/entries/scientific-explanation/>>

## CHAPTER 3

### MECHANISMS: METAPHYSICS, EPISTEMOLOGY, METHODOLOGY, AND DEFINITIONS<sup>9</sup>

#### 3.1 Preface

This reprint works to answer the question: what is the new philosophy of mechanisms? It considers an alternative account of the new philosophy of mechanisms: Arnon Levy's (2013) tripartite model. Levy breaks the philosophy of mechanisms into three basic groups: Explanatory Mechanism (EM), Strategic Mechanism (SM), and Causal Mechanism (CM). I apply Levy's tripartite model to a recent debate regarding whether or not natural selection is a mechanism. In light of this debate, I show that Levy's model fails to exhaust all the theses related to new philosophy of mechanisms. In addition to these regarding mechanistic explanation, mechanistic methods, and mechanistic causality, there is a more fundamental project of defining what a mechanism is in the first place, which I call 'Definitional Mechanism'. Closing the gap between definitional accounts of 'mechanism' and how the term is used in scientific practice gives

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rise to *challenge of application*. I reveal a normative component to the philosophy of mechanisms by showing how various new mechanists have addressed the challenge of application. I make a case for pluralism regarding mechanism concepts. The upshot is the view that the new philosophy of mechanisms comprises views about mechanistic explanation, mechanistic methods of investigation, mechanistic causality, definitional mechanism, and norms regarding how scientists use definitional accounts. What is common to all these projects underpinning the new philosophy of mechanisms is that they are driven by *mechanistic reasoning*.



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### On closing the gap between philosophical concepts and their usage in scientific practice: A lesson from the debate about natural selection as mechanism



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#### ABSTRACT

In addition to theorizing about the role and value of mechanisms in scientific explanation or the causal structure of the world, there is a fundamental task of getting straight what a 'mechanism' is in the first place. Broadly, this paper is about the *challenge of application*: the challenge of aligning one's philosophical account of a scientific concept with the manner in which that concept is actually used in scientific practice. This paper considers a case study of the challenge of application as it pertains to the concept of a mechanism: the debate about whether natural selection is a mechanism. By making clear what is and is not at stake in this debate, this paper considers various strategies for dealing with the challenge of application and makes a case for *definitional pluralism* about mechanism concepts.

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#### 1. Introduction

*I honor Darwin's struggles as much as his successes, and I focus on his few weaknesses for entry points of revision—his acknowledged failure to solve the “problem of diversity,” or his special pleading for progress in the absence of any explicit rationale from the operation of his central mechanism of natural selection.*

– Stephen J. Gould, *The Structure of Evolutionary Theory* (2002, p. 47).

It is quite common for scientists to refer to natural selection as a mechanism. Given recent and prevalent philosophical attention to the nature of mechanisms and their role in scientific explanation, one is inclined to ask: is natural selection a mechanism in the technical sense? After all, both scientists and philosophers have already theorized and debated about the nature of natural selection for decades (Bouchard & Rosenberg, 2004; Horan, 1994; Matthen &

Ariew, 2002; Millstein, 2006; Sober, 1984; Walsh, Lewens, & Ariew, 2002). It is perhaps unsurprising that some philosophers of biology are currently engaging in a debate about whether natural selection is a mechanism (Barros, 2008; Havstad, 2011; Illari & Williamson, 2010; Matthewson & Calcott, 2011; Nicholson, 2012; Skipper & Millstein, 2005).

Instead of offering a resolution or answer to the debate about natural selection as a mechanism, this paper works to highlight what philosophers can learn from it. It does this by assessing what is at stake in the debate about natural selection as a mechanism. In other words, it assesses which philosophical theses or positions—if any—might be problematized by the notion that natural selection is not a mechanism. First, Section 2 makes clear what is *not* at stake in the debate. There I consider three proposals from Levy (2013) for what “might” be at stake—theses regarding mechanistic explanation, methods of investigation, and causality—and argue that none of them are actually at issue.

Second, Section 3 makes a case for what is at stake in the debate and what we can learn from it. What is really at stake in the debate

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is something fundamental to any view about the relation between mechanisms and scientific explanation or causality: the concept of a mechanism itself. What we learn from this are three strategies for closing the gap between the manner in which scientists and philosophers think and talk about mechanisms, as well as perks and pitfalls for each. On one strategy, philosophers might offer a definitional account of mechanism that is broad and permissive, in order to capture the sundry uses of the term in scientific practice. On another strategy, philosophers might push highly restrictive conceptions of mechanism with a normative standard, which would render incorrect many uses of the term 'mechanism' in scientific practice. I recommend a third strategy that maintains a kind of *definitional pluralism* about mechanism concepts. On this strategy, distinct conceptions of mechanism are not in competition, but rather designed to capture the manner in which mechanism is used and understood differently in various disciplines or fields of scientific practice.

The three strategies described above consider specifically problems for philosophical conceptions of mechanism and their role in scientific practice. These strategies, however, may be of interest to a broader audience of philosophers of science. 'Mechanism' is just one instance of many in which scientists use a term of philosophical interest in a variety of different ways—'modularity' and 'function,' for example. For those general philosophers of science motivated by the manner in which scientists actually employ these key scientific concepts, the three strategies described in Section 3 may work as a useful guide.

## 2. Three proposals for what is at stake

Levy (2013) considers three kinds of "Mechanism theses"—views associated with the philosophy of mechanisms—as candidates for "what is, or might be, at stake" in the debate about natural selection as a mechanism (p. 109). On Levy's reasoning, a Mechanism thesis is 'at stake' if it might be refuted by the notion that natural selection is not a mechanism. In this section, I consider Levy's model of the philosophy of mechanisms and assess his arguments for why some of these Mechanism theses might be at stake. My analysis differs from Levy's, however, in two important ways. First, Levy's analysis is a noncommittal exploration of the issue. He does not assert what *is* or *is not* at stake, but rather what *might* or *could be* at stake. My analysis, in contrast, offers a full-fledged account of what is and is not at stake in the debate.

The second manner in which my analysis differs from Levy's regards the source of the debate about natural selection as a mechanism: Skipper and Millstein (2005). It will become evident that while Levy and others attribute to Skipper and Millstein a strong claim that "natural selection is not a mechanism," in what follows I defend a weaker reading of their arguments. A closer look at Skipper and Millstein's concerns for natural selection as a mechanism reveals a different sort of philosophical claim—an epistemological worry—regarding the challenges of accurately characterizing natural selection as a mechanism.

### 2.1. Mechanistic explanation and natural selection

Could a mechanistic account of explanation be at stake in light of the debate about natural selection as a mechanism? Levy (2013) tethers the new philosophy of mechanisms to a set of theses regarding the explanatory relevance of mechanisms or mechanistic information to scientific explanation (i.e., EM):

**Explanatory Mechanism (EM)** is a thesis about explanatory relevance: it states that to explain a phenomenon, one must cite mechanistic information, i.e. specify underlying parts and their

organization. EM contrasts with other general accounts of explanation, such as the Deductive-Nomological model. (p. 100).

Proponents of mechanistic explanation in biological science are perhaps the most familiar new mechanists. While the accounts vary in detail and discipline, all can be understood as defending a similar philosophical thesis that successful explanations make explicit appeal to mechanisms or the features/properties of mechanisms, such as parts/entities, activities/interactions,<sup>1</sup> and organization (Bechtel, 2008; Craver, 2007; Darden, 2006; Machamer, Darden, & Craver, 2000).

It is not *prima facie* obvious that a mechanistic account of explanation is at stake with respect to the question of whether natural selection is a mechanism. Levy (2013, p. 112) provides the following argument for why—"potentially at least"—the case of natural selection may cause trouble for the key tenets of mechanistic explanation. First, in some cases (including natural selection), the mechanistic details (e.g., parts and organization) are not explanatorily relevant.<sup>2</sup> In those cases, the best explanatory approaches are probabilistic and populational. Moreover, we might read Skipper and Millstein (2005) as making a related point that natural selection is not composed of parts, nor does it have stable organization. Therefore, if Skipper and Millstein (2005) and Strevens (2008) are right, then natural selection is a case in which parts and organization are not explanatorily relevant and, consequently, it is a case that problematizes the key tenets of mechanistic explanation.

This argument, though, raises two difficult questions. First, Levy assumes a rather strong commitment on behalf of proponents of mechanistic explanation: namely, that a mechanistic approach ought to apply equally well to *all* phenomena of explanatory interest to scientists. But is it a burden of the mechanistic view of explanation that all natural phenomena ought to be explained mechanistically? The foundational projects for mechanistic explanation—Bechtel and Richardson (1993/2010), Machamer et al. (2000), Darden (2006), Craver (2007) and Bechtel (2008)—do not endorse any strong monism about explanation across the sciences. Rather, these contributions highlight the value of mechanistic thinking to specific disciplines; namely, molecular biology and cognitive neuroscience. It does not follow that an account of mechanistic explanation is at stake in the event that natural selection is a phenomenon that is best explained with non-mechanistic methods, such as population statistics. It could simply be that while synapses and protein synthesis are best explained mechanistically, natural selection is not. This would not demand a rejection or reformulation of the new mechanistic account of explanation.

Levy's argument, however, motivates a second important question regarding his interpretation of Skipper and Millstein (2005). He interprets them as providing the argument that natural selection is not a mechanism, because they raise "problems such as whether natural selection has parts, whether it is regular in the requisite ways etc ..." (Levy, 2013, p. 112). It is not uncommon that philosophers of biology read Skipper and Millstein as providing this particularly strong metaphysical claim regarding the nature of natural selection. In posing the question of whether natural selection is a mechanism, Havstad (2011) explains, "Skipper and Millstein (2005) argue that it is not" (p. 512). But do they? While this reading is tempting, Skipper and Millstein do not endorse such

<sup>1</sup> While Machamer et al. (2000) construe the causality in mechanisms in terms of 'activities,' Glennan (2002a, 2002b) in terms of 'interactions.' Tabery (2004) shows how these distinct approaches are not in conflict, but rather, how they complement one another.

<sup>2</sup> Levy cites Strevens (2008) as providing the groundwork for this premise.



a strong metaphysical claim about the nature of natural selection. In fact, at no point do they claim strictly, “natural selection is not a mechanism.” Rather, their arguments provide a slightly weaker epistemic point; specifically that none of the main accounts of mechanism can *adequately characterize* natural selection as a mechanism.

Skipper and Millstein’s strategy is to highlight major features of the primary accounts of mechanisms<sup>3</sup> and then to assess whether those features accurately capture or “get at” the general process of natural selection. First, mechanisms exhibit some degree of *organization*, which involves some constrained spatial relation between parts or entities. Yet, because there are so many different possible ‘organizations’ of natural selection, and the parts/entities could be so many different phenomena (e.g., organisms, groups, populations, environments, etc.), no single characterization of the organization of natural selection may suffice:

In other words, we can give no *general* account of organization in populations undergoing natural selection. And if that is right, then there is no general mechanism, *sensu* MDC and Glennan, of natural selection to be found. (pp. 338–339; emphasis original)

What is key here is that Skipper and Millstein’s point is about the viability of a general *characterization* of natural selection, and not natural selection *itself*. This distinction is akin to the difference between making a claim about the *model* of a phenomenon as opposed to the phenomenon *itself*. If they wanted to make a point specifically about natural selection, then they would claim specifically that “natural selection is not a mechanism”—but they do not. Rather, in every instance of their analysis, Skipper and Millstein (2005) qualify their claims about natural selection. They do not claim that natural selection does not exhibit organization or regularity *simpliciter*. Rather, they claim that natural selection does not exhibit organization or regularity *in the senses outlined by either Machamer et al. (2000) or Glennan (2002a, 2002b)*.

The point is analogous to making a claim about the viability of a certain conception of art or music. In a similar way that there is much difficulty in characterizing *art* so that it captures all possible instantiations—everything from Michelangelo’s *David* to Duchamp’s *Fountain*—there is difficulty in characterizing all possible instantiations of natural selection as a mechanism. The point, then, is epistemic and not metaphysical, as the challenge regards one’s *characterization* of the phenomenon and not the phenomenon *itself*. Skipper and Millstein (2005) should be read as making an epistemic point about the difficulties of characterizing natural selection as a mechanism *in Machamer et al.’s sense* or a mechanism *in Glennan’s sense* and not as showing that natural selection is not a mechanism.

While it is important that we get straight Skipper and Millstein’s (2005) original argument, there is a more general assumption underlying Levy’s (2013) argument on this point. The assumption is that a mechanistic explanatory framework will only be fruitful when applied to phenomena that are, in fact, *mechanistic* (e.g., phenomena that have parts). Is it the case that the limits of mechanistic explanation are contingent on whether the phenomenon of interest is mechanistic? Matthewson and Calcott’s (2011) contribution to the debate about natural selection as a mechanism is helpful here. They argue that the “relevant question is not whether any population-level phenomenon such as natural selection is a mechanism, but whether it can be usefully modelled as though it were a particular type of mechanism” (p. 737). They offer interesting examples of mechanistic models of inherently non-

mechanistic phenomena, such as the Monetary Nation Income Analogue Computer (MONIAC) in Fig. 1. MONIAC is a mechanical model of an economy designed by economists to understand the causal structure of economic interactions. Examples like these provide evidence in favor of the claim that there is value in a mechanistic explanatory approach to inherently non-mechanistic phenomena.

MONIAC provides evidence for the value of mechanistic explanations of non-mechanistic phenomena in economics, but what about the case of natural selection? Is it equally valuable to model natural selection as a mechanism? That Futuyma’s (1997, p. 350) textbook explanation of evolution in Fig. 2 depicts natural selection as a toy “sieve mechanism” lends evidence to the view that mechanistic modeling of natural selection has epistemic merit:

The natural selection sieve mechanism (adapted from Sober, 1984) represents the general process of natural selection as a mechanical device in which marbles of various sizes and colors are sifted through various screens, so that only marbles of a specific size make it to the bottom. On this explanation the marbles represent, for example, organisms and their varying size represents

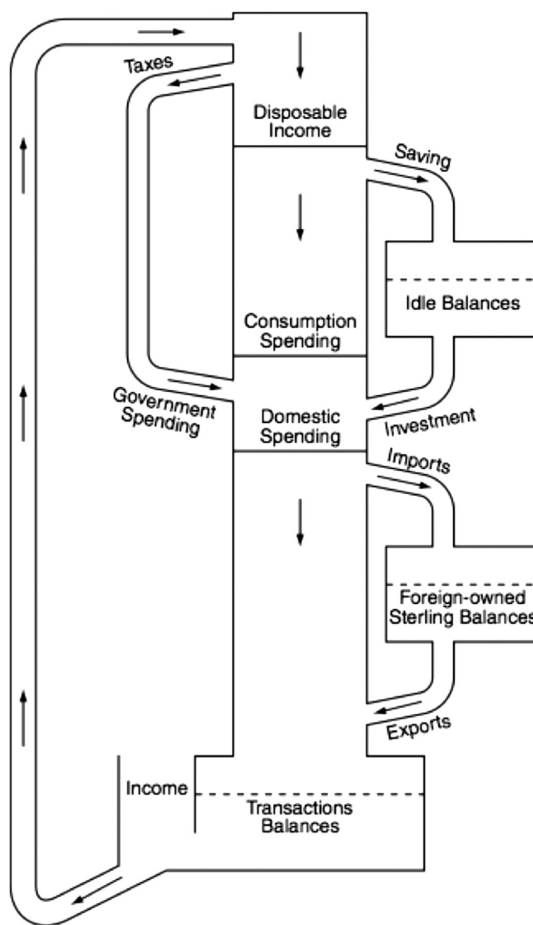


Fig. 1. Modified MONIAC from Matthewson and Calcott (2011).

<sup>3</sup> The two primary conceptions/accounts of mechanism addressed by Skipper & Millstein (2005) are Glennan (2002a, 2002b) and Machamer et al. (2000) as two main conceptions of mechanism.

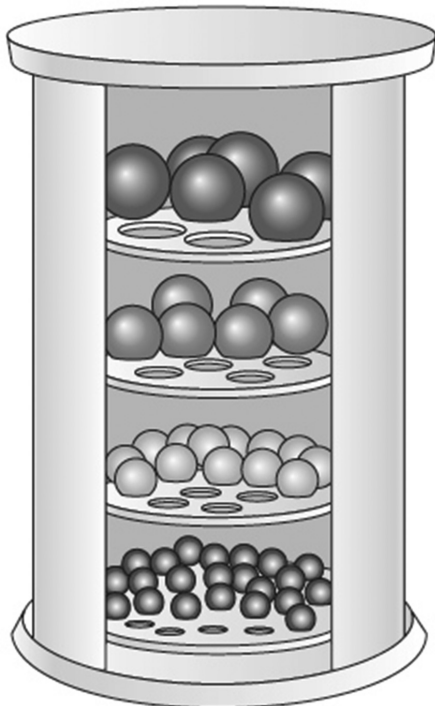


Fig. 2. Toy sieve mechanism of natural selection.

trait variation. The sieve mechanism represents a clear-cut case of a mechanistic explanation of natural selection.

In light of the above considerations, there is minimal evidence that the new mechanistic account of explanation is really at stake in the debate about natural selection as a mechanism. On the one hand, it is important that we clarify Skipper and Millstein's (2005) original challenge as one about the difficulties of characterizing natural selection as a mechanism; and not as showing that natural selection is in fact not a mechanism. On the other hand, even if natural selection were in fact not a mechanism, it would not follow that a mechanistic account of explanation would be at stake.

## 2.2. Mechanistic methods and natural selection

So far I have argued that an account of mechanistic explanation is not really at stake in the debate about natural selection as a mechanism. On Levy's (2013) model, distinct from these regarding mechanistic explanation are these regarding various mechanistic strategies of scientific investigation:

**Strategic Mechanism (SM)** concerns the cognitive-epistemic power of mechanistic modelling and related scientific methods. It asserts that certain phenomena are best handled mechanistically. Discussions of SM tend to construe 'mechanism' fairly narrowly, in machine-like terms. (p. 100)

Notable SM methodologies include Bechtel and Richardson's (1993/2010) account of *decomposition* and *localization* strategies. The bottom line for these strategies is that they treat the target system as though it were a mechanism. This involves breaking a

system into parts and elucidating, for example, their function in the system as a whole. Does the viability of this particular class of mechanistic methods hinge on the notion that natural selection is mechanism?

The arguments for why mechanistic methods might be at stake here are the same that Levy gives for why mechanistic explanation might be at stake. It assumes—as it did earlier—that we might read Skipper and Millstein (2005) as showing either that natural selection is not a mechanism, or merely that it is non-mechanistic.<sup>4</sup> I have already shown that a closer look at their arguments and conclusion do not warrant this strong reading, so I will not belabor the point. But what of the question of whether mechanistic methods are only valuable when applied to mechanistic phenomena? Is it possible to break a system into parts if the system is not actually composed of parts? Even if this method were possible, would it also be valuable?

Again, Matthewson and Calcott's (2011) discussion of MONIAC—the mechanistic modeling of national economies—is relevant. It is not my task here to assess whether a national economy is composed of parts, but the case of MONIAC lends evidence to the view that modeling national economies *as though they are composed of parts* is a fruitful method of investigation for practicing economists. In effect, the case of MONIAC supports the more general view that it is valuable to approach non-mechanistic phenomena, such as national economies, using mechanistic methods.

The more pertinent question asks whether mechanistic methods are in fact fruitfully applied to scientific investigations of natural selection. What happens when we look at scientific practice with respect to investigations of natural selection? Regardless of whether it is a force, a process, a statistical pattern, or a mechanism, Kuorikoski (2009) argues that mechanistic strategies are in fact applied to scientific investigations of natural selection. Illari and Williamson (2010) also argue that scientists employ the same mechanistic strategies to investigate the mechanism of protein synthesis as they do to investigate natural selection. Elsewhere, I argue that "embedded mechanisms"—i.e., mechanisms that are built into mathematical models—enhance statistical phylogenetics, a case that further strengthens the view that mechanistic methods are fruitful even when applied to non-mechanistic phenomena.

Even practicing evolutionary biologists Pardo-Diaz, Salazar, and Jiggins (2015, p. 445), take themselves to be in the business of 'mechanism-elucidation,' which is a key mechanistic method of investigation on Tabery's (2014) account. Elsewhere I argue that statistical phylogenetics benefits from 'embedded mechanisms' (Matthews, 2015). These are causal-mechanical explanations built into mathematical models that are used for phylogeny estimation. This too is evidence for the value of mechanistic approaches to non-mechanistic phenomena. In light of weaknesses in Levy's (2013) argument, such as his strong reading of Skipper and Millstein (2005), and also the aforementioned arguments from philosophers of biology and claims from practicing evolutionary biologists, it simply is not the case that mechanistic methods are really at stake in the debate about whether natural selection is a mechanism.

## 2.3. Mechanistic causality and natural selection

Because at least a few philosophers have discussed the relationship between mechanisms and the causal structure of the world, it could be that what is at stake in the debate about natural

<sup>4</sup> An anonymous reviewer questioned my distinction between 'mechanistic' and 'a mechanism.' If all things that are mechanistic were also mechanisms, then there would no need for the term 'mechanistic.' I used 'mechanistic' to capture those phenomena that are mechanism-like, but do not qualify as proper mechanisms.

selection as mechanism is a philosophical view about *mechanistic causality*. Glennan (1996) claims that his “theory of mechanisms could provide the foundation for a theory of causation” (p. 17). On this view, mechanisms are at the source of causal interactions. Levy (2013) deploys the concept of ‘Causal Mechanism’ (CM) to capture views of this ilk:

**Causal Mechanism (CM)** is the view that causal relations, at least outside the domain of fundamental physical phenomena, exist in virtue of underlying mechanisms. CM rivals other accounts of causation, such as regularity views. It is best seen as a contribution to metaphysics. (p. 100)

On Levy’s view, CM is a competitor to alternative accounts of causality. It states that causal relations exist in virtue of mechanisms—as opposed to, say, laws, regularities, counterfactual truths (Lewis, 1973), mark transmissions (Salmon, 1984), the exchange of conserved quantities (Dowe, 1992), or what might be revealed by counterfactual interventions (Woodward, 2003).

Could this specific account of mechanistic causality—i.e., Glennan’s (1996) view that causal relations exist in virtue of mechanisms—hinge on the notion that natural selection is a mechanism? In other words, can natural selection work as a counterexample to the mechanistic account of causality? Perhaps, but only if it were both the case that (1) natural selection is a causal process and that (2) natural selection is not a (causal) mechanism. Even Glennan (1996), however, concedes that his sense of mechanistic causality may not capture *all* causal relations. For example, he admits that at lower levels of analysis, Salmon’s process theory more accurately captures the causal structure of the world. It is perfectly plausible that natural selection is not a mechanism, and yet Glennan’s strong sense of mechanistic causality is a perfectly viable account of causality.<sup>5</sup>

On the potential for conflict between mechanistic causality and the notion that natural selection is not a mechanism, I completely agree with Levy (2013). In this case, more likely at stake is “probably a reformulation of the notion of mechanism, but not an abandonment of the mechanist view of causation” (Levy, 2013, p. 111). In other words, to abandon Glennan’s mechanistic account of causality because natural selection does not meet the criteria for mechanismhood would be to throw the baby out with the bathwater. Instead, what is needed is a bit of tinkering with the concept of a mechanism itself, so as to accommodate the case of natural selection. While Levy only mentions this point about the concept of a mechanism in passing, in what follows I argue that it is precisely the concept of a mechanism itself that is what is at stake in the debate about natural selection as a mechanism.

### 3. An alternate proposal for what is at stake

In the previous section I argued that none of the three Mechanism theses outlined by Levy (2013) are really at stake in the debate about natural selection as a mechanism. If views about mechanistic causality, mechanistic explanation, and mechanistic methods of investigation do not hinge on the notion that natural selection is a

mechanism, then what does? Answering this question requires a return to the source of the debate about natural selection as a mechanism: the dissonance between the way scientists and philosophers think and talk about mechanisms.

On the one hand are the practicing scientists who investigate and explain natural selection, and commonly refer to it as a mechanism. On the other hand are the conceptual experts on mechanisms—the new philosophers of mechanism—who defend a variety of different theses regarding the nature of mechanisms and their role in scientific reasoning. That there is a debate about natural selection as a mechanism in the first place highlights this very discord between ‘mechanism-talk’—i.e., use of the term ‘mechanism’ by scientists—and theoretical conceptions of mechanisms developed by philosophers. Skipper and Millstein’s (2005) ignition of the natural selection as a mechanism debate was motivated by the combination of the facts that (a) scientists talk about natural selection as though it were a mechanism and (b) the new mechanists are committed to accommodating the manner in which scientists talk about mechanisms.

In what follows, I show how the project of accommodating scientific mechanism-talk actually characterizes a significant project in the philosophy of biology. In addition to the project of developing philosophical accounts of mechanistic causality, explanation, and methods of investigation, the new mechanists are also concerned with the concept of a mechanism itself—and this is a fundamental element of the philosophy of mechanisms that is missed by Levy’s (2013) tripartite taxonomy. Philosophical development of the mechanism concepts faces what we might call a *challenge of application*: the challenge of aligning one’s philosophical understanding of ‘mechanism’ with the manner in which the term is used by scientists. At the bottom line, what is really at stake in the debate about natural selection as a mechanism is the concept of a mechanism itself.

In the theme of Levy’s tripartite model, this grouping of mechanism theses should be characterized in the following way:

**Definitional Mechanism (DM):** any thesis that makes claim to the key features, properties, or criteria for what a mechanism is – ‘mechanismhood,’ for lack of a better term. This category should capture philosophical disputes about mechanism ‘senses,’ ‘conceptions,’ ‘characterizations,’ or ‘frameworks.’

Articulating the conditions for mechanismhood, or simply the nature of mechanisms, is a large part of the philosophy of mechanisms. So what is really at stake in the debate about natural selection as a mechanism are competing accounts of DM, such as those from Machamer et al. (2000) or Glennan (2002a, 2002b).

#### 3.1. Three strategies for resolving the challenge of application

Above I introduced the *challenge of application* as the true source of the natural selection as a mechanism debate. At the heart of this particular question is the fact that there is dissonance between scientific mechanism-talk and the conceptions of mechanism developed by Glennan (2002a, 2002b) and Machamer et al. (2000). How have the new mechanists dealt with this challenge of application?

##### 3.1.1. Definitional permissivism

At the source of the challenge of application is the fact that, across the sciences, the term ‘mechanism’ can mean many different things. One intuitive solution is to develop a conception of mechanism that accommodates the myriad of uses of the term in practice. Illari and Williamson (2012), for example, provide the following catchall definition of mechanism:

<sup>5</sup> Note that there are many contributions to the philosophy of mechanisms that regard causality, but do not truly fit with Levy’s CM category. There are those, for example, who construe causal relations in mechanisms in terms of ‘activities’ (Bogen, 2005, 2008; Illari & Williamson, 2013; Machamer et al., 2000; Machamer, 2004). There are also those who defend a counterfactual/interventionist account of causality in mechanisms (Craver, 2007; Glennan, 2002a, 2002b; Joffe, 2013; Woodward, 2002, 2011). In any case, there is no obvious way in which these views should come in conflict with the notion that natural selection is or is not a mechanism.

A mechanism for a phenomenon consists of entities and activities organized in such a way that they are responsible for the phenomenon. (p. 120)

The broad scope of this definition is not incidental. Illari and Williamson make explicit their attempt to “defend a characterization that gives an understanding of what is common to mechanisms in all fields” (p. 120, *emphasis original*). This evinces a kind of *definitional permissivism*, in which the mechanism concept is intentionally designed to capture as many uses of the term as possible.

An advantage of *definitional permissivism* is that it mitigates the challenge of application by leaving few cases to question. On Illari and Williamson’s definition, both the mechanisms described by astrophysicists as well as those described by molecular biologists count as proper mechanisms. Interestingly, even a definition as permissive as Illari and Williamson’s does not clearly accommodate the notion that natural selection is a mechanism. It would seem that any conception of mechanism that accommodates the case of natural selection must allow that the parts, activities, and organization changes over time, as it is an inherent feature of evolution by natural selection that the organisms, the environments, and all their sundry interactions are constantly changing from one generation to the next. Illari and Williamson (2012), however, do not address the question as to whether the parts of a mechanism can change over time.

*Definitional permissivism*, however, is a double-edged sword, as there is the worry that a permissive conception of mechanism might capture too much. It is not my goal here to assess Illari and Williamson’s definitional account of mechanism in detail, but one should recognize the ease with which many natural phenomena meet the criteria for mechanismhood on their account. So long as some set of entities and activities—both of which are broad concepts—are responsible for a phenomenon, then that set of entities and activities is a mechanism. This may permit things to count as mechanisms that denigrate the value of the concept. Take, for example, Jay, the philosophy department janitor who vacuum-cleans the floors regularly each week. Jay and his tools (e.g., vacuum cleaner) are responsible for the phenomenon of philosophy department cleaning—is this particular set of entities (Jay and his vacuum) and activities (vacuuming) the ‘mechanism of philosophy department cleaning’? The underlying worry is that a permissive definition of mechanism will capture so much that usage of the term ‘mechanism’ no longer indicates something unique or informative about the world. The challenge then becomes showing what is *not* a mechanism.<sup>6</sup>

### 3.1.2. Definitional restrictivism

On the approaches that work to construe mechanisms broadly, the strategy is to cater to the manner in which the concept of a mechanism is used in all the sciences. There is, however, an opposite strategy to dealing with the challenge of application evinced by recent contributions to the philosophy of mechanisms. On this alternative approach one develops an intentionally narrow and restrictive conception of a mechanism that puts the burden of accommodation on the scientists. Woodward’s (2002) counterfactual account of mechanism exemplifies a highly specific and narrow mechanism concept:

(MECH) a necessary condition for a representation to be an acceptable model of a mechanism is that the representation (i) describe an organized or structured set of parts or components, where (ii) the behavior of each component is described by a generalization that is invariant under interventions, and where (iii) the generalizations governing each component are also independently changeable, and where (iv) the representation allows us to see how, in virtue of (i), (ii) and (iii), the overall output of the mechanism will vary under manipulation of the input to each component and changes in the components themselves. (p. S375)

There are at least a few arguments that favor *definitional restrictivism* over *definitional permissivism*. First, the former is strong precisely where the latter is weak. While one might worry that Illari and Williamson’s (2012) catchall definition of mechanism might capture too much, Woodward’s (2013) narrow conception is highly restrictive. Woodward, too, provides the argument that restrictive conceptions are useful in that they provide a tool for distinguishing actual mechanisms from phenomena that are referred to as mechanism, but are not actually mechanisms (p. 64). For example, the mechanisms of planet formation described by astrophysicists are not likely to count as mechanisms on Woodward’s account, and natural selection most certainly would not count as a mechanism.

Another advantage of *definitional restrictivism* is that a narrow conception of mechanism allows one to assess the scope of broad philosophical views about mechanisms. Because many natural phenomena will not qualify as mechanisms on a restricted definition, we have access to a relatively clear boundary for distinguishing the scope of, for example, a mechanistic account of explanation. One might also argue that a restricted mechanism concept could facilitate interfield discourse. Because ‘mechanism’ could have different meanings in different contexts, there is room for miscommunication between scientists from different fields. If ‘mechanism’ meant the same thing in all contexts, however, it is possible that such potential for miscommunication would be mitigated.

Yet *definitional restrictivism* about mechanisms has pitfalls as well. There is the obvious worry that a narrow conception of a mechanism will not capture enough. If the astrophysical mechanisms of planet formation described by astronomers are not mechanisms, then what are they? And how are we to make sense of all the mechanism talk across the sciences? There is perhaps a deeper challenge found in the execution of, first, devising a satisfactory and narrow conception, and second, finding a way to enforce it in scientific practice. Will most philosophers and scientists across all disciplines and in every field agree to use the term ‘mechanism’ in a specific way? If anything, restrictivism about definitions of mechanism will exacerbate the challenge of application. That is, a highly specific and normative conception of mechanism will increase the gap between the way scientists and philosophers think and talk about mechanisms.

### 3.1.3. Definitional pluralism

Permissivism and restrictivism about mechanism definitions have opposing pitfalls—one seems to capture too much while the other does not capture enough. In developing a *functional sense of mechanism*, Garson (2013) hints at a third option: a “modest pluralism with respect to mechanism” (p. 319). Garson only mentions pluralism about senses of mechanism in passing, but I take it to be the groundwork for the most promising solution to the challenge of application. Working from Garson’s (2013) notion, I recommend *definitional pluralism* as the view that mechanism concepts should not necessarily be in competition; but rather,

<sup>6</sup> Note that this particularly worry—about capturing too much—hinges on whether the conditions for mechanismhood outlined by Illari & Williamson (2012) are sufficient or necessary. If their account describes necessary but not sufficient conditions for mechanismhood, then the problem of capturing too much is mitigated. Illari and Williamson, however, do not make this distinction explicit—Hat tip to Matt Haber for highlighting this worry.

designed to capture distinct senses of mechanism and the fields in which they are most applicable.

*Definitional pluralism* accepts that there are many different senses or concepts of mechanism across the sciences. Instead of adjudicating toward a specific mechanism concept, the task of philosophers of science is to articulate and refine these distinct senses of mechanism and to assess their most fruitful domains of application. On this approach, the mechanisms described by biologists should fit a concept of *biological mechanism* and the mechanisms described by astrophysicists should fit a concept of *astrophysical mechanism*. While it is not a goal here to flesh out these alternative conceptions of mechanism, one can imagine that proteins are the relevant parts of biological mechanisms and astral bodies are the relevant parts of astrophysical mechanisms.

*Definitional pluralism* about mechanisms has distinct advantages over *definitional permissivism* and *definitional restrictivism*. While the former approach over-generalizes the mechanism concept, the pluralist approach can maintain a set of specific and meaningful conceptions of mechanism. While the latter approach fails to capture countless uses of the term 'mechanism' across the sciences, the pluralist approach should accommodate most of them. Moreover, while *definitional restrictivism* faces an important challenge of achieving consensus—the problem of convincing most philosophers and scientists to use the term 'mechanism' in a specific manner—*definitional pluralism* has a minimal requirement of consensus.<sup>7</sup>

What are the pitfalls of mechanism concept pluralism? There is a familiar worry that pluralism will mitigate conceptual development by minimizing competition between theories. With singular or monistic approaches to mechanism, like Illari and Williamson's (2012) and Woodward's (2013), there is competition between mechanisms in ongoing efforts to develop the best concept of a mechanism. By dealing and receiving challenges from competing mechanism conceptions, each contributor works to develop stronger conceptions of mechanism. Yet on the pluralist approach there is less need to continue developing one's mechanism concept, as it may be that not everyone is competing for the same resources. But we should still expect competition and conceptual development between those working toward specific mechanism concepts on the pluralist approach. That is, we should still expect philosophers of biology (and biologists) to work toward the best conception of *biological mechanism*.

There is an additional worry that the pervasive and variable use of 'mechanism' across the sciences hints at something robust and distinct about scientific theorizing, and *definitional pluralism* would mean giving up on the pursuit to figure out precisely what links all senses of mechanism.<sup>8</sup> But this need not be the case. In addition to the challenging philosophical project of identifying and articulating a plurality of mechanism concepts across the sciences, we should anticipate the ongoing and deeper philosophical project of identifying and articulating what is common to all senses of mechanism. *Definitional pluralism* is a tactic for dealing with the challenge of application, which is effectively a normative problem. Getting to the philosophical bedrock of 'mechanism', on the other hand, should remain an ongoing task for philosophers interested in the concept of a mechanism.

#### 4. Conclusion

This paper is an exploration of the debate about natural selection as a mechanism. It does not try to answer whether natural selection is, in fact, a mechanism. It elucidates instead the value of the debate. The central question is: what can we learn from the ongoing philosophical assessment of whether natural selection is a mechanism? The underlying force of this project is the idea that there is something valuable for philosophers of biology—and philosophers of science in general—in identifying what is and is not at stake in this particular debate.

First, I made a negative point about what is *not* at stake in the debate. Contra Levy's (2013) analysis, theses or philosophical views about the relation between mechanisms and explanation, scientific methods of investigation, and causality are not really at stake in the debate about natural selection as a mechanism. Second, I made a positive case for what *is* at stake in the debate, which is something fundamental to all the theses considered by Levy: the concept of a mechanism itself. In addition to theorizing about the role and value of mechanisms in scientific explanation or the causal structure of the world, an important task for philosophers interested in mechanisms is getting straight the concept of a mechanism itself.

Third, I made a point about what benefit can be derived from this exploration of the debate about natural selection as a mechanism. At the heart of this issue is a more general problem facing philosophers of science: this is the challenge of aligning one's philosophical account of a scientific concept with the manner in which the concept is actually employed by scientists. The *challenge of application*, that is, is the challenge of closing the gap between how scientists and philosophers think and talk about key scientific concepts, such as 'mechanism.' While I describe three strategies for dealing with the challenge of application, as it pertains to the concept of a mechanism, these strategies may also be valuable alternative scientific concepts of philosophical interest, such as 'modularity' or 'function.'

On one approach, which I term *definitional permissivism*, the strategy is to define a concept loosely so that it captures most uses of the term across the sciences. A major pitfall of this approach is that it might capture too much, thereby devaluing what is informative about a technical concept. On a second approach, which I term *definitional restrictivism*, the strategy is to develop a highly specific and narrow concept with normative bite, so that only a subset of scientists using the term are using it appropriately. I adjudicated toward a third approach, *definitional pluralism*, in which strategy is to accept that there are distinct senses of the same concept used across the sciences. On this approach the task of the philosopher of science is not to adjudicate toward a single sense of 'mechanism,' for example, but to delineate and refine each unique sense, and to identify the most fruitful scientific disciplines or fields of application.

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#### References

- Barros, B. D. (2008). Natural selection as a mechanism. *Philosophy of Science*, 75(3), 306–322.
- Bechtel, W. (2008). *Mental mechanisms: Philosophical perspectives on cognitive neuroscience*. New York: Taylor & Francis.
- Bechtel, W., & Richardson, R. C. (2010). *Discovering complexity: Decomposition and localization as strategies in scientific research*. Cambridge, MA: MIT Press.

<sup>7</sup> On *definitional pluralism*, the problem of consensus will only regard agreeing on, for example, a satisfactory conception of *biological mechanism*.

<sup>8</sup> Thanks to an anonymous reviewer for noting this issue.

- Bogen, J. (2005). Regularities and causality: generalizations and causal explanations. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 36(2), 397–420. Mechanisms in biology.
- Bogen, J. (2008). Causally productive activities. *Studies in History and Philosophy of Science Part A*, 39(1), 112–123.
- Bouchard, F., & Rosenberg, A. (2004). Fitness, probability and the principles of natural selection. *The British Journal for the Philosophy of Science*, 55(4), 693–712.
- Craver, C. F. (2007). *Explaining the brain*. Oxford: Oxford University Press.
- Darden, L. (2006). Reasoning. In *Biological discoveries: Essays on mechanism, inter-field relations, and anomaly resolution*. New York, NY: Cambridge University Press.
- Dowe, P. (1992). Wesley salmon's process theory of causality and the conserved quantity theory. *Philosophy of Science*, 59(2), 195–216.
- Futuyma, D. J. (1997). *Evolutionary biology* (3rd ed.). Stanford, Connecticut: Sinauer Associates.
- Garson, J. (2013). The functional sense of mechanism. *Philosophy of Science*, 80(3), 317–333.
- Glennan, S. (1996). Mechanisms and the nature of causation. *Erkenntnis*, 44(1), 49–71.
- Glennan, S. (2002a). Contextual unanimity and the units of selection problem. *Philosophy of Science*, 69(1), 118–137.
- Glennan, S. (2002b). Rethinking mechanistic explanation. *Philosophy of Science*, 69(S3), S342–S353.
- Gould, S. J. (2002). *The structure of evolutionary theory*. Cambridge, Massachusetts: The Belknap Press of Harvard University Press.
- Havstad, J. C. (2011). Discussion: Problems for natural selection as a mechanism. *Philosophy of Science*, 78(3), 512–523.
- Horan, B. L. (1994). The statistical character of evolutionary theory. *Philosophy of Science*, 61(1), 76–95.
- Illari, P. M., & Williamson, J. (2010). Function and organization: Comparing the mechanisms of protein synthesis and natural selection. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 41(3), 279–291.
- Illari, P. M., & Williamson, J. (2012). What is a mechanism? Thinking about mechanisms across the sciences. *European Journal for Philosophy of Science*, 2(1), 119–135.
- Illari, P. M., & Williamson, J. (2013). In defense of activities. *Journal for General Philosophy of Science*, 44(1), 69–83.
- Joffe, M. (2013). The concept of causation in biology. *Erkenntnis*, 78(2), 179–197.
- Kuorikoski, J. (2009). Two concepts of mechanism: Componential causal system and abstract form of interaction. *International Studies in the Philosophy of Science*, 23(2), 143–160.
- Levy, A. (2013). Three kinds of new mechanism. *Biology & Philosophy*, 28(1), 99–114.
- Lewis, D. (1973). Causation. *The Journal of Philosophy*, 70(17), 556–567.
- Machamer, P. (2004). Activities and causation: The metaphysics and epistemology of mechanisms. *International Studies in the Philosophy of Science*, 18(1), 27–39.
- Machamer, P., Darden, L., & Craver, C. F. (2000). Thinking about mechanisms. *Philosophy of Science*, 67(1), 1–25.
- Matthen, M., & Ariew, A. (2002). Two ways of thinking about fitness and natural selection. *The Journal of Philosophy*, 99(2), 55–83.
- Matthews, L. J. (2015). Embedded mechanisms and phylogenetics. *Philosophy of Science*, 82(5), 1116–1126.
- Matthewson, J., & Calcott, B. (2011). Mechanistic models of population-level phenomena. *Biology & Philosophy*, 26(5), 737–756.
- Millstein, R. L. (2006). Natural selection as a population-level causal process. *The British Journal for the Philosophy of Science*, 57(4), 627–653.
- Nicholson, D. J. (2012). The concept of mechanism in biology. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 43(1), 152–163.
- Pardo-Diaz, C., Salazar, C., & Jiggins, C. D. (2015). Towards the identification of the loci of adaptive evolution. *Methods in Ecology and Evolution*, 6(4), 445–464.
- Salmon, W. C. (1984). *Scientific explanation and the causal structure of the world*. Princeton, NJ: Princeton University Press.
- Skipper, R. A., & Millstein, R. L. (2005). Thinking about evolutionary mechanisms: Natural selection. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 36(2), 327–347.
- Sober, E. (1984). *The nature of selection*. Chicago: Chicago University Press.
- Strevens, M. (2008). *Depth: An account of scientific explanation*. Harvard University Press.
- Tabery, J. G. (2004). Synthesizing activities and interactions in the concept of a mechanism. *Philosophy of Science*, 71(1), 1–15.
- Tabery, J. G. (2014). *Beyond versus: The struggle to understand the interaction of nature and nurture*. Cambridge, Massachusetts: The MIT Press.
- Walsh, D. M., Lewens, T., & Ariew, A. (2002). The trials of life: Natural selection and random drift. *Philosophy of Science*, 69(3), 429–446.
- Woodward, J. (2002). What is a mechanism? A counterfactual account. *Philosophy of Science*, 69(S3), S366–S377.
- Woodward, J. (2003). *Making things happen: A theory of causal explanation*. New York, NY: Oxford University Press.
- Woodward, J. (2011). Mechanisms revisited. *Synthese*, 183(3), 409–427.
- Woodward, J. (2013). Mechanistic explanation: Its scope and limits. *Aristotelian Society Supplementary Volume*, 87(1), 39–65.

## CHAPTER 4

### MECHANISTIC REASONING IN STATISTICAL PHYLOGENETICS<sup>10</sup>

#### 4.1 Preface

This reprint works to answer the second major question undertaken by this dissertation: what is the scope of the new philosophy of mechanisms? It addresses this question in the context of statistical phylogenetics – the branch of evolutionary biology that constructs ‘tree hypotheses’ regarding evolutionary relationships. I show how the development of mathematical models evinces a shift from purely statistical models to models positively influenced by *mechanistic reasoning*. By using ‘embedded mechanisms’, mechanistic reasoning positively influences statistical phylogenetics by constructing stronger tree hypotheses, as measure by *LogL*.

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# Embedded Mechanisms and Phylogenetics

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A strong case has been made for the role and value of mechanistic explanation in neuroscience and molecular biology. A similar demonstration in other domains of scientific investigation, however, remains an important challenge of scope for the new mechanists. This article helps answer that challenge by demonstrating one valuable role mechanisms play in phylogenetics. Using the transition/transversion (ti/tv) rate parameter as a case example, this article argues that models embedded with mechanisms produce stronger phylogenetic tree hypotheses, as measured by maximum likelihood  $\log L$  values. Two important implications for the new mechanistic account of explanation are considered.

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**1. Introduction.** A recent trend in philosophy of science focuses on the central importance of mechanisms to scientific investigation, explanation, and understanding (Machamer, Darden, and Craver 2000). This is typically cast in terms of the value and role of either mechanistic explanations or strategies to scientific discovery, modeling, explanation, and understanding (Craver and Tabery, forthcoming). Yet this new mechanistic account of explanation faces important challenges.<sup>1</sup> One such challenge regards scope. The new mechanists have done well to make their case in specialized disciplines, such as neuroscience (Bechtel and Richardson 1993/2010; Craver 2007; Bechtel 2008) and molecular biology (Darden 2006).<sup>2</sup> Yet these life sciences are process oriented in that they investigate proximate systems that are highly amenable to mechanistic thinking (i.e., systems composed of interacting and

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1. Sometimes called the “new mechanical philosophy,” the “New Philosophy of Mechanism (NPM),” or simply the “philosophy of mechanisms.” Here I refer to this general project as the *new mechanism* and its proponents as *new mechanists*.

2. Work has been done to extend the new mechanism to behavioral genetics (Tabery 2014), cell biology (Bechtel 2006), cognitive science (Thagard 2006), neuroeconomics (Craver and Alexandrova 2008), organic chemistry (Ramsey 2008), social science (Hedström and Swedberg 1998; Hedström 2005; Hedström and Ylikoski 2010), and physics (Teller 2010).

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organized parts). Making a similar case for the value of mechanisms to other domains of scientific investigation is the challenge of scope for the new mechanism.

This article works to resolve the challenge of scope by revealing a role for mechanisms in a paradigmatically nonmechanistic science: statistical phylogenetics. Unlike the proximate, process-oriented sciences mentioned above, phylogenetics is a ‘pattern-oriented science’ in that the explanandum phenomena are patterns in nature (e.g., phenotypic traits or nucleotide sequences) rather than underlying processes (e.g., DNA replication or protein syntheses) (see Sober 1988; Haber 2009; Velasco 2013). Moreover, unlike the process-oriented life sciences, phylogenetics is a science driven by statistical methods and mathematical models.<sup>3</sup> There is no obvious sense in which practicing phylogeneticists appeal to mechanisms or mechanistic information in the manner outlined by the new mechanists. Despite this lack of explicit appeal or representation, here I show that mechanisms play a valuable role in maximum likelihood (ML) methods of phylogeny estimation. I argue specifically that molecular mechanisms (or the breakdown thereof) can be ‘embedded’ in mathematical model parameters to strengthen phylogenetic tree hypotheses. I discuss Kimura’s (1980) estimation of the transition/transversion (ti/tv) rate ratio as an *embedded mechanism* of DNA mutation, the application of which produces stronger tree hypotheses, as measured by ML  $\log L$  values.

Section 2 shows how ML methods of phylogeny estimation are enhanced by embedded molecular mechanisms, such as the ti/tv rate ratio. Section 3 fleshes out the concept of an embedded mechanism and its implications for the new mechanism and the challenge of scope. Section 4 gives conclusions.

## 2. From Molecular Mechanisms to Maximum Likelihood

### 2.1. Phylogenetics Tree Hypothesis Testing and Strengthening.

Broadly, phylogenetics is a science of patterns in that it makes inferences about evolutionary history from observed patterns of biodiversity or character distribution in nature. The products of these efforts are tree hypotheses, which graphically represent evolutionary-relatedness of groups of taxa. Phylogenetic hypotheses are valuable to any scientific explanation regarding life history, such as human epidemiology (Ou et al. 1992; Harvey and Paul 1994), ecology (Brooks 1991), and evolutionary biology (Harvey and

3. Note that this is not to confuse statistical phylogenetics with alternative cladistics approaches, such as pattern cladism. At least some proponents of the latter reject statistical approaches entirely. This analysis, however, engages specifically approaches that incorporate models of evolution into their statistical methods of phylogeny estimation. For more on this distinction see Haber (2009).

Pagel 1991). Here I focus on one prominent approach to phylogeny estimation: the ML method.

Fisher (1922) developed ML as a statistical tool estimating the probability of observing the data, given the model. Modern forms construe ML as the probability of the evidence (E), given the hypothesis (H). ML methods of phylogeny estimation assign a *logarithmic likelihood* ( $\log L$ ) value to tree hypotheses given (a) observed nucleotide sequences and (b) model assumptions (parameters) of evolutionary change. In other words, ML methods allow for the construction of competing tree hypotheses, given various assumptions about evolutionary processes and observed genetic data.

The history of ML methods of phylogeny estimation is marked by an informative trend. While observed nucleotide sequences remain the same, phylogenetic tree hypotheses get stronger over time. In other words, phylogenetics improves tree hypotheses by analyzing the same data with better models of evolution. Here 'better models' are understood as those that more accurately accommodate subtleties of evolutionary change, often at the molecular level (Felsenstein 2004). Each tree hypothesis has a  $\log L$  value, which is treated as a measure of strength. The lower the  $\log L$  value, the stronger the hypothesis. These quantitative values of tree hypotheses allow for a simple method of hypothesis testing in which phylogeneticists pit competing hypotheses against one another (Huelsenbeck and Crandall 1997). In effect, phylogeneticists can run the same data using different models or the same model but with different parameters. Each analysis allows for a new tree hypothesis to be assessed against the others. In short, altering model assumptions and achieving greater  $\log L$  values strengthen phylogenetic tree hypotheses.

*2.2. Strengthening Tree Hypotheses with Mechanistic Model Parameters.* In order to compare tree hypotheses, phylogeneticists must analyze the same data using different models and assumptions. This generates competing hypotheses that phylogeneticists use to reconstruct the best phylogenetic tree. Models that estimate  $t_i/t_v$  rates are an excellent example of how more accurate model assumptions result in stronger tree hypotheses. One of the earliest models, JC69, made two important assumptions about fundamental evolutionary processes. It assumed both (a) equal nucleotide frequencies and (b) equal rates of change between nucleotides (Jukes and Cantor 1969). Yet practicing phylogeneticists soon realized that these assumptions failed to capture real processes of DNA substitution. For example, molecular biologists recognize unique ways in which substitutions may occur as either transitions or transversions (Freese 1959). In order to more accurately capture biological details, Kimura (1980) developed a valuable method of  $t_i/t_v$  rate estimation for ML tree reconstruction. More importantly, analyzing the same nucleotide sequences with  $t_i/t_v$  rate parameters produces tree hypotheses

with improved  $\log L$  values (Huelsenbeck and Crandall 1997, 455). Thus, phylogenetic models that accommodate ti/tv rate biases produce stronger tree hypotheses, given the data.

But what exactly is the ti/tv rate bias? Why does estimation of the bias strengthen tree hypotheses? Although these sorts of questions are often black-boxed by practicing phylogeneticists, their answers have important implications for the philosophy of science. A ti/tv rate bias is essentially an effect caused by subtleties of DNA substitutions, which occur at the molecular level. *Transitions* are spontaneous purine–purine or pyrimidine–pyrimidine substitutions. *Transversions* are spontaneous purine–pyrimidine or pyrimidine–purine substitutions. What distinguishes these two types of nucleotides is molecular ring structure. Purines have a double-ring structure, while pyrimidines take a single-ring structure. Moreover, these unique structural features play an important role in how molecular biologists explain ti/tv rates of DNA substitution (see fig. 1).<sup>4</sup>

While various mechanisms of mutagenesis have been proposed over the years (e.g., *tautomeric shifts* and *link slippage*), most scientists today attribute DNA replication errors to Crick's (1966) *wobble hypothesis* (Pray 2008). While a typical base pairing involves cytosine–guanine, the wobble hypothesis explains a unique pairing of cytosine–adenine in the event that adenine contains an extra hydrogen atom, for example. While these are often referred to as 'mechanisms', such phenomena are more accurately described as the *failure* or *breakdown* of DNA error recognition and repair mechanisms (see, e.g., Kolodner 1995; Iyer et al. 2006).

While there are many subtle differences between various scientific explanations for DNA replication error, what they all have in common are mechanistic details. On this point Illari and Williamson's catchall definition of mechanism is useful: "A mechanism for a phenomenon consists of entities and activities organized in such a way that they are responsible for the phenomenon" (2012, 120). There should be little dispute that any explanation for the ti/tv bias involves appeal to entities, activities, and organization. Moreover, Darden (2006) offers a systematic and persuasive case for the mechanistic nature of molecular biology. For the purposes of this article, the pertinent claim is that any explanation for the ti/tv rate bias will be molecular biological and inherently mechanistic. It will either describe an explicit mechanism (or the breakdown thereof) or appeal to mechanistic details or information, such as parts/entities, activities/interactions, or organization.

In this light, explanations for the ti/tv rate bias are inherently mechanistic in the sense of interest to the new mechanists. These explanations show precisely how errors in the mechanism of DNA replication can give rise to per-

4. The figure is courtesy of ATDbio Nucleic Acids Book, <http://www.ATDbio.com/nucleic-acids-book>.

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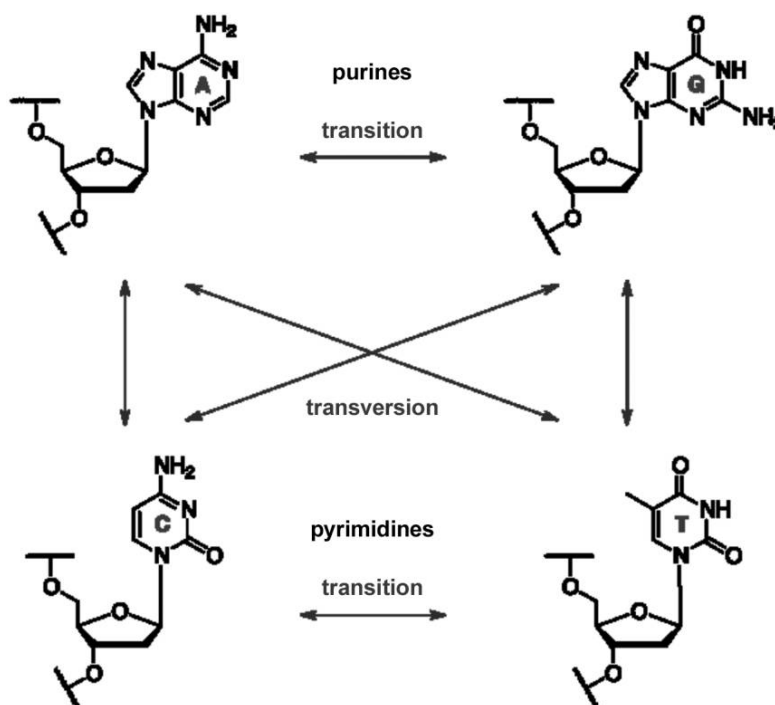


Figure 1. Transitions involve purine–purine or pyrimidine–pyrimidine mutations ( $A \leftrightarrow G$  and  $C \leftrightarrow T$ ), while transversions involve purine–pyrimidine or pyrimidine–purine mutations ( $A \leftrightarrow C$ ,  $A \leftrightarrow T$ ,  $G \leftrightarrow C$ , and  $G \leftrightarrow T$ ). Color version available as an online enhancement.

manent mutations. Subtle details in the manner in which various mutations occur give rise to a nearly universal bias in favor of transitions over transversions. That is, by virtue of the mechanical details of DNA replication, transitions occur at a higher rate than transversions.<sup>5</sup> Phylogenetic models, in turn, accommodate these mechanistic details with the addition or manipulation of parameters. The effect of this bias is then estimated, mathematically, for accurate phylogenetic modeling. Thus, the effects of molecular-level mechanisms (or the breakdown thereof) are accommodated in models using  $t_i/t_v$  rate parametric values. In other words, mechanisms, mechanistic details, or mechanistic explanations are ‘embedded’ in phylogenetic model parameters, such as the  $t_i/t_v$  rate bias. More importantly, however, models us-

5. It is worth noting that some evidence suggests that this bias in favor of transitions is not universal. See Keller, Bensasson, and Nichols (2007).

ing  $t_i/t_v$  parametric values produce tree hypotheses with greater  $\log L$  values. Thus, models embedded with mechanisms produce stronger phylogenetic tree hypotheses.

**3. Embedded Phylogenetic Mechanisms.** The previous section shows how models using embedded mechanisms provide stronger phylogenetic tree hypotheses. Yet this notion of embedded mechanisms raises important questions. How are embedded mechanisms distinct from those of interest to the philosophers of mechanism? How does this notion of strengthening phylogeny estimation by embedding mechanisms bear on the challenge of scope for the new philosophy of mechanisms? In this section I flesh out this new notion of mechanism and show how it affects the prospective scope of mechanistic explanation.

*3.1. Understanding Embedded Mechanisms.* Above I use the term ‘embedded mechanism’ to capture the fact that the mechanistic details that facilitate ML phylogeny estimation are entirely implicit; they are built into mathematical model parameters of DNA substitution ( $t_i/t_v$  bias). While it is not the goal of this article to construct a complete account of embedded mechanisms, here I will clarify a few important points. First, I do not mean to claim that because phylogenetics benefits from embedded mechanisms, it is a mechanistic science. There is a clear sense in which molecular biology and neuroscience are mechanistic in that their explanations often elucidate mechanisms and often use mechanistic strategies of investigation, such as decomposition, localization, and recombination. But phylogenetics does not share these characteristics. Broadly, the new mechanists are interested in the value and role of mechanisms to scientific investigation, discovery, modeling, and explanation more generally. So the claim is not that phylogenetic methods or hypotheses are inherently mechanistic—it remains unclear whether this is the case. Rather, the claim is that mechanistic explanations elsewhere (molecular biology) positively contribute to phylogenetic tree construction.

It might also be helpful to think about embedded mechanisms in light of Salmon’s (1984) ontic/epistemic distinction, which highlights a point of contention among new mechanists (Illari 2013). That distinction is meant to capture the source of explanatory power for those thinking about mechanisms. On the ontic conception of mechanisms, it is the physically embodied mechanism ‘out there in the world’ that explains.<sup>6</sup> On the epistemic conception of mechanisms, however, it is the representation or exhibition of the mechanism that explains.<sup>7</sup> With this framework in mind, one should conceive of an embedded mechanism as a unique kind of epistemic mechanism. While

6. The ontic view is most commonly attributed to Craver (2007).

7. The epistemic view is most commonly attributed to Bechtel (2008).

it is not precisely clear that embedded mechanisms *explain*, the above analysis demonstrates a distinct sense in which they strengthen phylogenetic tree hypotheses. Yet proponents of the epistemic conception of mechanism make claim to the value of visuo-spatial representations to explanation and understanding (Bechtel and Abrahamsen 2005). On that view, it is by virtue of the fact that visual representations can accommodate parts/entities, causal relations, and organization that they facilitate scientific explanation and understanding. Yet embedded mechanisms are unique in that they lack precisely this kind of visual representation. Rather, the embedded mechanism is—in the case described above—a mathematical model parameter. Thus, embedded mechanisms are uniquely epistemic in that they facilitate scientific understanding sans explicit representation.

It may also be useful to think about the notion of embedded mechanisms in light of Levy's (2013) tripartite characterization of the philosophy of mechanisms. He distinguishes three kinds of new mechanism theses, regarding the metaphysics of causation (causal mechanism), scientific explanation (explanatory mechanism), and scientific methods of investigation (strategic mechanism):

**Causal mechanism (CM)** is the view that causal relations, at least outside the domain of fundamental physical phenomena, exist by virtue of underlying mechanisms. CM rivals other accounts of causation, such as regularity views. It is best seen as a contribution to metaphysics.

**Explanatory mechanism (EM)** is a thesis about explanatory relevance: it states that to explain a phenomenon, one must cite mechanistic information, that is, specify underlying parts and their organization. EM contrasts with other general accounts of explanation, such as the deductive-nomological model.

**Strategic mechanism (SM)** concerns the cognitive-epistemic power of mechanistic modeling and related scientific methods. It asserts that certain phenomena are best handled mechanistically. Discussions of SM tend to construe 'mechanism' fairly narrowly, in machine-like terms (Levy 2013, 2).

My analysis of embedded mechanisms in phylogenetics is not meant as a contribution to the metaphysics of causation, nor is it clear that it has implications for such. Hence, CM does not capture the significance of embedded mechanism.

Levy's characterization of EM represents an interesting candidate for capturing the notion of embedded mechanism. On the one hand, there is a sense in which the practice of embedding mechanisms into one's model counts as citing mechanistic information. On the other hand, however, it

remains an open question whether phylogenetic tree construction qualifies as explanation. While I believe that a case could be made for such a view, it is beyond the purview of this article. Thus, for present purposes, Levy's characterization of EM fails to adequately capture the unique manner in which embedded mechanisms contribute to ML phylogeny estimation.

Does Levy's characterization of SM capture my notion that embedded mechanisms positively influence phylogenetic tree construction? If one treats the practice of building mechanistic details into mathematical models—that is, embedding mechanisms—as a mechanistic method, then SM is relevant here. However, the practice of embedding mechanisms is markedly unique from exemplar SM methods, such as decomposition, localization, and recombination. Thus, the notion of embedding mechanisms in one's mathematical model is a good candidate for fleshing out Levy's characterization of SM.

*3.2. On the Challenge of Scope.* Earlier I framed this contribution as one that works to resolve a challenge of scope. Moss (2012) offers the most explicit presentation of this challenge by questioning the value of the 'mechanistic metaphor' to some areas in biomedical research, such as intrinsically unstructured proteins:

By means of what kind of knowing can and should the biomedical scientist and biologist approach the kinds of strikingly nonmachine like empirical realities revealed in studies of the pleiomorphic ensembles and intrinsically unstructured proteins that constitute the woof and warp of systematic cellular signaling and adaptive regulation? Is it possible that where the 'rods and pistons' of the mechanistic metaphor have run out of steam that a transition to alternative forms of understanding will be in order? Where philosophers of mechanism, largely focused on the science of a bygone era, have yet to recognize this as a problem, it has not escaped the notice of contemporary biomedical investigators. (Moss 2012, 170)

Although Moss's concern targets a specialized case, it hints at a more general problem for explanandum phenomena that are not amenable to mechanistic explanation. Strevens (2008, chap. 2) raises a similar concern, arguing that some phenomena are inherently probabilistic, populational, and, consequently, unsusceptible to mechanistic explanation. Lastly, Woodward notes that limits of scope are a feature of all accounts of explanation: "My view is that mechanistic explanations are most likely to be successful when the systems to which they are applied satisfy certain empirical presuppositions . . . [yet] as one moves away from contexts in which these presuppositions are satisfied, mechanistic explanation becomes a less promising strategy. This is not intended as a criticism of mechanistic explanation in

those circumstances in which it is appropriate, but rather simply reflects the point that, like virtually all explanatory strategies and structures, there are limits on its range of application” (2013, 64).

The concerns expressed by Moss, Strevens, and Woodward indicate a limited scope for the new philosophy of mechanisms on the grounds that there are some explanandum phenomena to which mechanistic thinking or strategies of investigation are not applicable. How does the notion of an embedded mechanism bear on this general worry? While it does not answer these concerns directly, it does provide a different way of thinking about how mechanistic thinking facilitates scientific investigation and explanation of inherently nonmechanistic phenomena. While Moss, Strevens, and Woodward may have in mind sciences that make no explicit appeal to mechanisms or mechanistic information, it remains an open question whether these sciences implicitly appeal to embedded mechanisms in the manner of statistical phylogenetics. At the very least, the notion of embedding mechanisms extends the scope of mechanistic thinking beyond those sciences in which appeal to mechanisms is both explicit and ubiquitous.

**4. Conclusion.** This article makes a case for the role and value of embedded mechanisms in phylogenetics. At the molecular level, the  $t_i/t_v$  rate bias is an effect best explained by the mechanistic details of DNA replication error, recognition, and repair. This mechanistic effect, however, is of particular value to accurate phylogeny estimation using ML methods. Models embedded with these mechanistic details produce stronger phylogenetic tree hypotheses, as measured by  $\log L$  values. In other words, implicit ‘embedded’ mechanisms strengthen the science of phylogeny estimation. That embedded mechanisms play a valuable role in phylogenetics has two important implications for the new philosophy of mechanisms. First, it suggests a unique and subtle mechanistic strategy characterized by statistical models bolstered with embedded mechanisms. Embedded mechanisms are unique to those discussed by the philosophers of mechanism in that they lack explicit, visuo-spatial representation. Second, it helps answer the important challenge of scope, extending the value and role of mechanisms to the pattern-oriented science of phylogenetics. Extrapolating from this case to additional sciences using mathematical models of mechanistic processes is the next step toward a better understanding of the scope and limits of the new philosophy of mechanisms.

#### REFERENCES

- Bechtel, William. 2006. *Discovering Cell Mechanisms: The Creation of Modern Cell Biology*. Cambridge Studies in Philosophy and Biology. Cambridge: Cambridge University Press.



- . 2008. *Mental Mechanisms: Philosophical Perspectives on Cognitive Neuroscience*. New York: Taylor & Francis.
- Bechtel, William, and Adele Abrahamsen. 2005. "Explanation: A Mechanist Alternative." *Studies in History and Philosophy of Science C* 36 (2): 421–41.
- Bechtel, William, and Robert C. Richardson. 1993/2010. *Discovering Complexity: Decomposition and Localization as Strategies in Scientific Research*. Repr. Cambridge, MA: MIT Press.
- Brooks, Daniel R. 1991. *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. Chicago: University of Chicago Press.
- Craver, Carl F. 2007. *Explaining the Brain*. Oxford: Oxford University Press.
- Craver, Carl F., and Anna Alexandrova. 2008. "No Revolution Necessary: Neural Mechanisms for Economics." *Economics and Philosophy* 24:381–406.
- Craver, Carl F., and James G. Tabery. Forthcoming. "Mechanisms." *Stanford Encyclopedia of Philosophy*.
- Crick, Francis H. C. 1966. "Codon—Anticodon Pairing: The Wobble Hypothesis." *Journal of Molecular Biology* 19 (2): 548–55.
- Darden, Lindley. 2006. *Reasoning in Biological Discoveries: Essays On Mechanism, Interfield Relations, and Anomaly Resolution*. New York: Cambridge University Press.
- Felsenstein, Joseph. 2004. *Inferring Phylogenies*. Sunderland, MA: Sinauer.
- Fisher, Ronald A. 1922. "On the Mathematical Foundations of Theoretical Statistics." *Philosophical Transactions of the Royal Society of London A* 222:309–68.
- Freese, Ernst. 1959. "The Specific Mutagenic Effect of Base Analogues on Phage {T4}." *Journal of Molecular Biology* 1 (2): 87–105.
- Haber, Matthew H. 2009. "Phylogenetic Inference." In *A Companion to the Philosophy of History and Historiography*, ed. Aviezer Tucker, no. 41 in Blackwell Companions to Philosophy, chap. 20, 231–42. Malden, MA: Wiley-Blackwell.
- Harvey, Paul H., and Mark D. Pagel. 1991. *The Comparative Method in Evolutionary Biology*. Oxford Series in Ecology and Evolution 1. New York: Oxford University Press.
- Harvey, Paul H., and Sean N. Paul. 1994. "Phylogenetic Epidemiology Lives." *Trends in Ecology and Evolution* 9 (10): 361–63.
- Hedström, Peter. 2005. *Dissecting the Social: On the Principles of Analytical Sociology*. New York: Cambridge University Press.
- Hedström, Peter, and Richard Swedberg. 1998. *Social Mechanisms: An Analytical Approach to Social Theory*. Studies in Rationality and Social Change. Cambridge: Cambridge University Press.
- Hedström, Peter, and Petri Ylikoski. 2010. "Causal Mechanisms in the Social Sciences." *Annual Review of Sociology* 36 (1): 49–67.
- Huelsenbeck, John P., and Keith A. Crandall. 1997. "Phylogeny Estimation and Hypothesis Testing Using Maximum Likelihood." *Annual Review of Ecology and Systematics* 28:437–66.
- Illari, Phyllis M. 2013. "Mechanistic Explanation: Integrating the Ontic and Epistemic." *Erkenntnis* 78 (2): 237–55.
- Illari, Phyllis M., and Jon Williamson. 2012. "What Is a Mechanism? Thinking about Mechanisms across the Sciences." *European Journal for Philosophy of Science* 2 (1): 119–35.
- Iyer, Ravi R., Anna Pluciennik, Vickers Burdett, and Paul L. Modrich. 2006. "DNA Mismatch Repair: Functions and Mechanisms." *Chemical Reviews* 106 (2): 302–23.
- Jukes, Thomas H., and Charles R. Cantor. 1969. "Evolution of Protein Molecules." *Mammalian Protein Metabolism* 3:21–132.
- Keller, Irene, Douda Bensasson, and Richard A. Nichols. 2007. "Transition-Transversion Bias Is Not Universal: A Counter Example from Grasshopper Pseudogenes." *PLOS Genetics* 3 (2): e22.
- Kimura, Motoo. 1980. "A Simple Method for Estimating Evolutionary Rates of Base Substitutions through Comparative Studies of Nucleotide Sequences." *Journal of Molecular Evolution* 16:111–20.
- Kolodner, Richard D. 1995. "Mismatch Repair: Mechanisms and Relationship to Cancer Susceptibility." *Trends in Biochemical Sciences* 20 (10): 397–401.
- Levy, Arnon. 2013. "Three Kinds of New Mechanism." *Biology and Philosophy* 28 (1): 99–114.

- Machamer, Peter, Lindley Darden, and Carl F. Craver. 2000. "Thinking about Mechanisms." *Philosophy of Science* 67 (1): 1–25.
- Moss, L. 2012. "Is Philosophy of Mechanism Philosophy Enough?" *Studies in History and Philosophy of Science C* 43 (1): 164–72.
- Ou, Chinyi, et al. 1992. "Molecular Epidemiology of HIV Transmission in a Dental Practice." *Science* 256 (5060): 1165–71.
- Pray, Leslie. 2008. "DNA Replication and Causes of Mutation." *Nature Education* 1 (1): 214.
- Ramsey, Jeffrey L. 2008. "Mechanisms and Their Explanatory Challenges in Organic Chemistry." *Philosophy of Science* 75 (5): 970–82.
- Salmon, Wesley C. 1984. *Scientific Explanation and the Causal Structure of the World*. Princeton, NJ: Princeton University Press.
- Sober, Elliot. 1988. *Reconstructing the Past: Parsimony, Evolution, and Inference*. Cambridge, MA: MIT Press.
- Strevens, Michael. 2008. *Depth: An Account of Scientific Explanation*. Cambridge, MA: Harvard University Press.
- Tabery, James G. 2014. *Beyond Versus: The Struggle to Understand the Interaction of Nature and Nurture*. Cambridge, MA: MIT Press.
- Teller, Paul. 2010. "Mechanism, Reduction, and Emergence in Two Stories of the Human Epistemic Enterprise." *Erkenntnis* 73 (3): 413–25.
- Thagard, Paul. 2006. *Hot Thought: Mechanisms and Applications of Emotional Cognition*. Cambridge, MA: MIT Press.
- Velasco, Joel D. 2013. "Philosophy and Phylogenetics." *Philosophy Compass* 8 (10): 990–98.
- Woodward, James. 2013. "Mechanistic Explanation: Its Scope and Limits." *Aristotelian Society Supplementary Volume* 87 (1): 39–65.

## CHAPTER 5

### MECHANISTIC REASONING IN POPULATION GENETICS

#### **5.1 Preface**

This chapter works to further answer the question: what is the scope of the new philosophy of mechanisms? It addresses this question in the context of a second field of evolutionary biology that is historically and conceptually treated as *nonmechanistic*: population genetics. I use two frameworks for thinking about mechanistic reasoning to show how the modern application of statistical methods is integrated with a family of mechanistic methods in evolutionary biology. In building evidence for claims about adaptations, evolutionary biologists use statistical methods to build evidence for associations between genotypes and phenotypes, which are then bolstered with a family of methods driven by mechanistic reasoning.

#### **5.2 Introduction**

What is a mechanism? Why are mechanisms so pervasive in biological science? These sorts of questions set the groundwork for what is often referred to as the new philosophy of mechanisms – a philosophical account of scientific reasoning (Craver & Tabery, 2015). This chapter advances that project by assessing the scope of mechanistic reasoning in a field of biology that is intuitively nonmechanistic: population genetics.

The advent of population genetics, through the synthesis of Darwinism and Mendelism, roots back to Fisher's (1918, 1930) application of statistical thermodynamic methods to evolutionary theory (Provine, 1971). That synthesis represents a shift from causal-mechanical reasoning about interactions between organisms and their environments to a pattern-oriented and population-perspective, which is inherently mathematical and driven by statistics.

Here I argue that, while the field of population genetics is indeed nonmechanistic, the practical application of population genetic methodologies is integrated with mechanistic methodologies. Modern evolutionary biology, that is, strongly informs the view that ideal and satisfactory investigations of adaptive evolution call for both statistical evidence from population genetic methods as well as mechanistic evidence from interventionist manipulations. The philosophical upshot is that, in practice, the scope of mechanistic reasoning does not border (i.e., form a boundary), but rather, integrates with population genetics. By this I mean that it is not the case that the fruitful application of mechanistic methods is excluded from the field of population genetics. Rather, it is the case that, in practice, both mechanistic and statistical methods are combined in modern efforts to investigate, explain, and build evidence for scientific hypotheses regarding adaptive evolution. This result is valuable, first, because it further develops our understanding of the role and value of mechanistic reasoning across the science and, second, because it bridges the gap between two investigative approaches often understood to be at odds.

### **5.3 Population Genetics as a Nonmechanistic Methodology**

Population genetics is often treated as a field of biology that studies evolution using mathematical models and statistical methods at the level of populations (Okasha, 2012). Classical population genetics is seemingly nonmechanistic. Instead of tracking the causal interactions between individual organisms and their environments, population genetics was the study of distributions of genes in populations. Classical population genetics constructed mathematical models for the purpose of thinking about how, in theory, distributions of genes will change in populations in various contexts. An early discovery of population genetics, for example, was the Wright-Fisher model-driven hypothesis that, in relatively small populations, genetic drift is more likely to sweep a population.

There is much discussion of population genetics in the context of philosophy of science. There is, for example, a dispute about the value of population genetics. On the one hand are those who have criticized population genetics for a variety of reasons, such as the notion that population genetic models are too idealized and abstract to confer legitimate knowledge about real biological evolution (Gildenhuys, 2011; Lewontin, 1980; Pigliucci, 2008; Wade, 2005). Others have defended population genetics on a variety of points, arguing that – at the very least – population genetic methods are central to understanding evolution (Lynch, 2007; Millstein, 2013; Morrison, 2004). It is not the goal here to take a stance on this particular issue, although the analysis in Section 5.4 undoubtedly favors the view that population genetic methods are central to modern investigations of adaptive evolution.

For the purpose of this analysis, which seeks to understand the relation between

population genetic methods and mechanistic methods in modern evolutionary biology, population genetics will not be treated as a field of study in biology, but rather, a family of statistical and mathematical methods of investigation that consider genes in populations, both real and theoretical. For that purpose, the standard application of population genetic methods involves the development of mathematical models of evolution for a variety of purposes. A key premise of this argument is that, today, population genetic methods are most often used to develop statistical evidence regarding genotype-phenotype and genotype-fitness associations. That is, the modern application of population genetic methods is most often geared toward narrowing down the genome of living organisms in search of associations between specific genes correlated with adaptive fitness. Section 5.4 treats forward genetics, reverse genetics, and candidate gene approaches as modern applications of population genetics.

## **5.4 Mechanistic Methods and Mechanism**

### **Elucidation in Compositional Biology**

As described in the previous section, population genetics represents a challenge case for the philosophy of mechanisms. Given the framework of mechanistic explanation developed in neuroscience and molecular biology, there is no obvious way in which population geneticists appeal to mechanisms and mechanistic information in their investigations of the world. So what does one look for in assessing the use of mechanistic reasoning to population genetics? To this question, there are two frameworks that quite effectively capture mechanistic reasoning in modern evolutionary biology: Tabery's (2014) account of *mechanism-elucidation* and Winther's (2006) account of *compositional*

*biology.*

Both Tabery and Winther describe a division between two approaches or theoretical perspectives in behavior genetics and biology respectively. Tabery distinguishes the *variation-partitioning* approach, which seeks to answer ‘*how-much*’ questions about variation in populations by using statistical methodologies to identify and measure the causes of variation, and the *mechanism-elucidation approach*, which seeks to answer *how* questions by using interventionist manipulations in order to reveal underlying developmental processes. Winther, on the other hand, distinguishes two theoretical perspectives in biology: *formal biology*, which “relies on mathematical laws and models”, and *compositional biology*, which “investigates the concrete structures, mechanisms, and functions through developmental evolution and evolutionary time, of material parts and wholes” (p. 472).

These two frameworks may be used to effectively capture population genetic and mechanistic methods of investigation in modern evolutionary biology. On the one hand, population genetic methods are well-captured by Tabery’s *variation-partitioning approach*, as they are often applied to distinguish how much variation in a population is a result of various forces of evolution (e.g., drift or selection), and Winther’s account of *formal biology*, as population genetic methods comprise the development and application of mathematical models and laws. On the other hand, mechanistic methods in modern biology are well-captured by Tabery’s *mechanism-elucidation approach*, as experimental interventionist manipulations play a key role in modern investigations of adaptive evolution, and Winther’s account of *compositional biology*, as these investigations target the etiological pathway from genotype, to phenotype, to fitness.

## **5.5 On the Integration of Population Genetic and Mechanistic Methods**

### **5.5.1 Applications of Population Genetic Methods**

In modern evolutionary biology, scientists use population genetic methods to develop statistical evidence for associations between genotypes, phenotypes, and fitness (Okasha, 2012; Pardo-Diaz, Salazar, & Jiggins, 2015). These applications are an excellent fit for Tabery's *variation-partitioning approach* and Winther's account of *formal biology*. Broadly, there are two primary applications of modern population genetic methods: forward and reverse genetics. Each of these approaches represent a host of mathematical models and statistical methods for associating genotypes, phenotypes, and fitness. *Forward genetics* represents the search for genotypes associated with a phenotype already believed to be adaptive. This is achieved through Genome Wide Association Studies (GWAS), Quantitative Trait Loci (QTL) mapping, and Linkage Disequilibrium (LD) studies – all of which involve applications of population genetic, statistical analyses and mathematical models (Hunter, Wright, & Bomblies, 2013; Shimizu & Purugganan, 2005; Stinchcombe & Hoekstra, 2008). Shimizu and Purugganan (2005), for example, applied QTL mapping and GWAS techniques to Rockress (*Aradibopsis*) genomes, a weedy coastal plant. Their analyses proceeded from the hypothesis that the quantifiable trait, flowering time, was undergoing selection. In this case, application of GWAS and QTL mapping provided statistical evidence that the *CRY2* gene both underpins flowering time and also that it was subject to selection in wild *Aradibopsis* populations.

In other cases, modern evolutionary biologists use *reverse genetics* to investigate a genotype with no prior information or knowledge regarding the adaptive significance of said genotype. Sometimes, however, biologists investigate a genotype without prior



knowledge or information regarding its phenotypic or adaptive significance. This practice represents a modern application of population genetic methods for the purpose of building statistical evidence for specific genotype-phenotype or genotype-fitness associations (Balding & Nichols, 2008; Foll & Gaggiotti, 2008; Joost et al., 2007; Luikart et al., 2003; Nicholson et al., 2002; Vitalis et al., 2003).

The culmination of these efforts is the development of statistical evidence for an association between a specific genotype and a specific phenotype that is believed to be adaptive. Ideally, practicing biologists seek to employ both forward and reverse genetic approaches to the investigation of the same adaptive locus of evolution (Stinchcombe & Hoekstra, 2007). Colosimo et al. (2005), for example, used both forward and reverse genetics to develop evidence for the relation between *Eda* alleles and armor plating in the threespined sticklebacks (*Gasterosteus aculeatus*).

### 5.5.2 Mechanistic Approaches to Adaptive Evolution

While the application of population genetic methods, such as forward and reverse genetics, plays a key role in how biologists investigate adaptive evolution, this practice is only part of the story. A large part of scientific practice in this respect is building evidence for a variety of claims about the relation between a specific genotype, an associated phenotype, and adaptive fitness. At the bottom line, the statistical evidence produced by population genetic methods is insufficient in presenting a strong case for a scientific claim about the adaptive value of a trait and the genotype that underpins it. Consequently, in conjunction with population genetic, statistical methods, today evolutionary biologists employ a variety of interventionist methods to further bolster

claims about adaptive evolution. Evolutionary biologists Pardo-Diaz, Salazar, and Jiggins (2015), for example, describe a multistep methodology that integrates both population genetics with experimental interventions:

First, it is necessary to corroborate that a trait affects fitness in the field and is in fact adaptive. Then, the region(s) of the genome in which genotypes are correlated with adaptive phenotypes should be defined either with classical genetic tools or applying new genomic approaches. . . Ultimately, functional experiments are required to prove that a gene or mutation is actually responsible for the phenotype observed. Once individual genes or SNPs have been identified, it is important to quantify their effect in the 'trait value' (i.e. how much variation in the phenotype is explained by the candidate SNPs/genes). Finally, the genetic variation in the genes shaping those adaptive traits should be evaluated in field selection experiments in order to establish a definite connection between genotype, phenotype and fitness. (pp. 457—458)

The sort of integrative methodology prescribed by Pardo-Diaz, Salazar, and Jiggins fits the mold of both Tabery's account of *mechanism-elucidation* and *variation-partitioning* approaches as well as Winther's (2006) distinction between *formal biology* and *compositional biology*. Pardo-Diaz, Salazar, and Jiggins (2015), for example, claim that establishing "the genetic and molecular basis underlying adaptive traits is one of the major goals of evolutionary geneticists in order to understand the connection between genotype and phenotype and **elucidate the mechanisms** of evolutionary change" (p. 445; **emphasis mine**).

The integration of mechanistic and population genetic methods is borne out by the manner in which modern biologists investigate adaptive evolution in living populations. Here the focus is the manner in which biologists conduct experimental interventionist manipulations of biological systems for the purpose of revealing the development processes underlying evolution. There are two primary relationships apt for interventionist manipulations. On the one hand, biologists seek to elucidate the

mechanism(s) that link a given genotype-phenotype relationship. This is achieved through a variety of techniques designed to reveal the molecular function of specific genotypes. The experimental development of *transgenic organisms* represents a key interventionist tactic. Here an exogenous gene is inserted into the genome of an embryo after which the phenotypic effects are tracked. Rebeiz et al. (2009), for example, conducted experimental interventions on the genome of *Drosophila melanogaster* by introducing *ebony* transgenes light (U62) and dark (U76). In other cases, a candidate gene will be removed from the genome of an undeveloped embryo, the phenotypic effects of which are then tracked after development. These *gene knockouts*, too, represent an interventionist manipulation for the purpose of investigating and testing the molecular function of specific genes. In other cases, instead of the complete removal of a candidate gene from an undeveloped embryo, gene expression is reduced in *gene knockdown* experimental interventions. A fourth experimental intervention for the purpose of elucidating molecular function involves *gene replacement*. These experimental interventions represent the application of mechanistic methods toward the investigation of adaptive evolution via assays of molecular function.

In addition to these mechanistic methods applied to genotype-phenotype associations, biologists employ similar methods to the investigation of phenotype-fitness associations. In order to further develop evidence for hypotheses regarding adaptive evolution, that is, biologists conduct ecological experimental interventionist manipulations. Most notably, this is achieved through *field selection experiments* (Barrett & Hoekstra, 2011). On this approach, biologists manipulate a variable in a natural environment for the purpose of observing fitness effects. This can be achieved through

$Q_{ST}$ — $F_{ST}$  comparison studies, which involve an analyses between measurement of genetic differentiation within a population ( $F_{ST}$ ) and analogous genetic variance among populations (Leinonen et al., 2013). In other cases, biologists might intervene on a natural system in order to determine which physiological mechanisms might contribute to adaptive divergence in a population. Lowry et al. (2009), for example, combined QTL mapping with reciprocal transplant experiments of the Yellow Monkeyflower plant (*Mimulus guttatus*) to track response to sodium concentration. Still in other cases, biologists will intervene on natural systems to investigate phenotype-fitness relations by the controlled introduction of organisms into novel environments (Barrett & Schluter, 2008; Irschick & Reznick, 2009; Kapan, 2001; Reznick et al., 1997). Gompert et al. (2014), for example, sought to quantify the relative contributions of selection and genetic drift by introducing wingless, stick insects (*Timema cristinae*) into a novel environment. Another experimental manipulation of phenotype-genotype relationships involves the introduction of artificial characteristics to natural environments. These assays of ecological function allow for the manipulation of evolutionary traits (Irschick & Reznick, 2009; Linnen et al., 2013; Losos, Warheitt, & Schoener, 1997). Merrill et al. (2012), for example, created artificial butterflies (*Heliconius*), altered wing patterns, introduced them to natural environments, and then tracked frequency of attacks from birds.

It is worth mentioning that extant philosophical perspectives evince a similar claim regarding the integration of mechanistic and population genetic methods. Millstein (2006) makes a case for natural selection as a population-level causal process. A key premise in her argument involves a demonstration that biologists understand natural selection as a causal process. In making her case, Millstein describes evolutionary

investigations of the montane willow leaf beetle (*Chrysomelidae*) (Dahlhoff & Rank, 2000; Rank, 1992; Rank & Dahlhoff, 2002). Her account of Rank and Dahlhoff's investigations of the Phosphoglucose Isomerase (PGI) locus further evince the view that, in modern biology, satisfactory evidence of hypotheses regarding adaptive evolution involve the integration of both population genetic, statistical methods as well as mechanistic methods:

We need either to perform a laboratory experiment to demonstrate that the selective agent indeed acts on the phenotype in the way we think it does, or we need to provide the underlying mechanism to show that the genotypes have the abilities that we say that they do, or both. Rank and Dahlhoff do both; the laboratory experiment is described above, and they explain that the different PGI genotypes' differing abilities to withstand heat and cold are the result of the production of differing amounts of heat shock protein at different temperatures. This causal and mechanistic information, together with the other information presented, provides strong evidence for Rank and Dahlhoff's conclusions. (p. 640)

The picture that emerges is one of mechanism-elucidation approaches in modern compositional biology. The manner in which biologists intervene on genotype-phenotype relationships represents mechanistic methodologies via assays of molecular function, such as *gene knockouts*, *gene knockdowns*, *transgenics*, and *gene replacements*. The manner in which biologists intervene on phenotype-fitness relationships represents the mechanistic methods via assays of ecological function, such as *field selection experiments*.

## **5.6 Conclusion**

This chapter is about the scope of the new philosophy of mechanisms. In most cases, the value of mechanistic reasoning is well represented in those process-oriented fields of scientific investigation that target biological systems composed of interacting

and organized parts. Fields of evolutionary biology that focus on patterns, primarily use mathematical models and statistical methods, and make no explicit appeal to mechanisms or mechanistic information, then, present a challenge case for the scope of the new philosophy of mechanisms across the sciences. Here I argue that in modern evolutionary biology, population genetic methods are most fruitfully applied in tandem with mechanistic methods in building evidence for hypotheses regarding adaptive evolution.

I characterize population genetics using Tabery's (2014) conception of the *variation-partitioning* approach and Winther's (2006) account of *formal biology*. I characterize mechanistic methods using Tabery's conception of *mechanism-elucidation* and Winther's account of *compositional biology*. The view that emerges is one of an integration of mechanistic and population genetic methods of investigating adaptive evolution in living populations. On the one hand, biologists use mathematical models and statistical methods to develop genotype-phenotype and genotype-fitness associations. On the other hand, however, evolutionary investigations do not cease with these modern applications of population genetics. Rather, they proceed from statistical evidence to causal-mechanical evidence. In order to make a strong case for a scientific hypothesis regarding adaptive evolution in living populations, statistical associations must be tested and bolstered using mechanistic methods, such as experimental interventionist manipulations. Thus, while the scope of the new mechanistic philosophy may not extend directly into population genetics as a field of biology, both mechanistic and population genetic methods are integrated in the practice of building evidence for hypotheses about adaptive evolution.

## 5.7 References

- Balding, D. J., & Nichols, R. A. (2008). A method for quantifying differentiation between populations at multi-allelic loci and its implications for investigating identity and paternity. *Genetica*, *133*(1), 107–107.
- Barrett, R. H., & Hoekstra, H. E. (2011). Molecular spandrels: Tests of adaptation at the genetic level. *Nature Reviews Genetics*, *12*, 767–780.
- Barrett, R. H., & Schluter, D. (2008). Adaptation from standing genetic variation. *Trends in Ecology & Evolution*, *23*, 38–44.
- Colosimo, P. F., Hosemann, K. E., Balabhadra, S., Villarreal, G., Dickson, M., Grimwood, J., . . . Kingsley, D. M. (2005). Widespread parallel evolution in sticklebacks by repeated fixation of ectodysplasin alleles. *Science*, *307*, 1928–1933.
- Dahlhoff, E. P., & Rank, N. E. (2000). Functional and physiological consequences of genetic variation at phosphoglucose isomerase: Heat shock protein expression is related to enzyme genotype in a montane beetle. *Proceedings of the National Academy of Sciences*, *97*(18), 10056–10061.
- Fisher, R. A. (1918). The correlation between relatives on the supposition of mendelian inheritance. *Transactions of the Royal Society of Edinburgh*, *52*, 399–433.
- Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford, UK: Oxford University Press.
- Foll, M., & Gaggiotti, O. (2008). A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: A bayesian perspective. *Genetics*, *180*, 977–993.
- Gildenhuys, P. (2011). Righteous modeling: The competence of classical population genetics. *Biology & Philosophy*, *26*(6), 813–835.
- Gompert, Z., Comeault, A. A., Farkas, T. E., Feder, J. L., Parchman, T. L., Buerkle, C. A., & Nosil, P. (2014). Experimental evidence for ecological selection on genome variation in the wild. *Ecology Letters*, *17*, 369–379.
- Hempel, C. G., & Oppenheim, P. (1948). Studies in the logic of explanation. *Philosophy of Science*, *15*(2), 135–175.
- Hunter, B., Wright, K. M., & Bomblies, K. (2013). Short read sequencing in studies of natural variation and adaptation. *Current Opinion in Plant Biology*, *16*(1), 85–91.
- Irschick, D., & Reznick, D.N. (2009). Field experiments, introductions, and experimental

- evolution. In T. Garland & M. R. Rose (Eds.), *Experimental evolution: Concepts, methods, and applications of selection experiments* (pp. 173–193). Oxford, UK: Oxford University Press.
- Joost, S., Bonin, A., Bruford, M. W., Despre, S. L., Conord, C., Erhardt, G., & Taberlet, P. (2007). A spatial analysis method (SAM) to detect candidate loci for selection: Towards a landscape genomics approach to adaptation. *Molecular Ecology*, *16*, 3955–3969.
- Kapan, D. D. (2001). Three-butterfly system provides a field test of mullerian mimicry. *Nature*, *409*, 338–340.
- Leinonen, T., McCairns, R. S., O'Hara, R. B., & Merila, J. (2013). QST-FST comparisons: Evolutionary and ecological insights from genomic heterogeneity. *Nature Reviews Genetics*, *14*, 179–190.
- Lewontin, R. C. (1980). Theoretical population genetics in the evolutionary synthesis. In E. Mayr & W. B. Provine (Eds.), *The evolutionary synthesis: Perspectives on the unification of biology* (pp. 58–68). Cambridge, MA: Harvard University Press.
- Linnen, C. R., Poh, Y. P., Peterson, B. K., Barrett, R. H., Larson, J. G., Jensen, J. D., & Hoekstra, H. E. (2013). Adaptive evolution of multiple traits through multiple mutations at a single gene. *Science*, *339*, 1312–1316.
- Losos, J. B., Warheitt, K. I., & Schoener, T. W. (1997). Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature*, *387*, 70–73.
- Lowry, D. B., Hall, M. C., Salt, D. E., & Willis, J. H. (2009). Genetic and physiological basis of adaptive salt tolerance divergence between coastal and inland *mimulus guttatus*. *New Phytologist*, *183*, 776–788.
- Luikart, G., England, P. R., Tallmon, D., Jordan, S., & Taberlet, P. (2003). The power and promise of population genomics: From genotyping to genome typing. *Nature Reviews Genetics*, *4*(12), 981.
- Lynch, M. J. (2007). *The origins of genome architecture*. Baltimore, MD: Sinauer Associates.
- Merrill, R. M., Wallbank, R. R., Bull, V., Salazar, P. A., Mallet, J., Stevens, M., & Jiggins, C. D. (2012). Disruptive ecological selection on a mating cue. *Proceedings of the Royal Society B: Biological Sciences*, *22*, 4907–4913.
- Millstein, R. L. (2006). Natural selection as a population-level causal process. *The British Journal for the Philosophy of Science*, *57*(4), 627–653.
- Millstein, R. L. (2013). Exploring the status of population genetics: The role of ecology.



- Biological Theory*, 7(4), 346–357.
- Morrison, M. (2004). Population genetics and population thinking: Mathematics and the role of the individual. *Philosophy of Science*, 71(5), 1189–1200.
- Nicholson G., Smith, A. V., Jónsson, F., Gústafsson, O., Stefansson, K., & Donnelly, P. (2002). Assessing population differentiation and isolation from single-nucleotide polymorphism data. *Journal of the Royal Statistical Society*, 64(4), 695–715.
- Okasha, S. (2012). Population genetics. *The Stanford Encyclopedia of Philosophy*. <http://plato.stanford.edu/entries/population-genetics/>
- Pardo-Diaz, C., Salazar, C., & Jiggins, C. D. (2015). Towards the identification of the loci of adaptive evolution. *Methods in Ecology and Evolution*, 6(4), 445–464.
- Pigliucci, M. (2008). The proper role of population genetics in modern evolutionary theory. *Biology & Philosophy*, 3(4), 316–324.
- Provine, W.B., (1971). *The origins of theoretical population genetics*. Chicago, IL: University of Chicago Press.
- Rank, N. E., & Dahlhoff, E. P. (2002). Allele frequency shifts in response to climate change and physiological consequences of allozyme variation in a montane insect. *Evolution*, 56(11), 2278–2289.
- Rank, N. E. (1992). A hierarchical analysis of genetic differentiation in a montane leaf beetle *Chrysomela aeneicollis* (coleoptera: Chrysomelidae). *Evolution*, 46(4), 1097–1111.
- Rebeiz, M., Pool, J. E., Kassner, V. A., Aquadro, C. F., & Carroll, S. B. (2009). Stepwise modification of a modular enhancer underlies adaptation in a drosophila population. *Science*, 326, 1663–1667.
- Reznick, D. N., Shaw, F. H., Rodd, F. H., & Shaw, R. G. (1997). Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science*, 275, 1934–1937.
- Shimizu, K. K., & Purugganan, M. D. (2005). Evolutionary and ecological genomics of *Arabidopsis*. *Plant Physiology*, 138(2), 578–584.
- Stinchcombe, J. R., & Hoekstra, H. E. (2008). Combining population genomics and quantitative genetics: Finding the genes underlying ecologically important traits. *Heredity*, 100, 158–170.
- Tabery, J. G. (2014). *Beyond versus: The struggle to understand the interaction of nature and nurture*. Cambridge, MA: The MIT Press.

- Vitalis, R., Dawson, K., Boursot, P., & Belkhir, K. (2003). DetSel 1.0: A computer program to detect markers responding to selection. *Journal of Heredity*, *94*, 429–431.
- Wade, M. J., (2005). Evolutionary and ecological genetics. *The Stanford Encyclopedia of Philosophy* (Spring 2005 Edition).  
<<http://plato.stanford.edu/archives/spr2005/entries/evolutionary-genetics/>>.
- Winther, R. G. (2006). Parts and theories in compositional biology. *Biology & Philosophy*, *21*, 471–499.

## CHAPTER 6

### CONCLUSION

What is good scientific reasoning? This dissertation addresses two questions related to the most prominent and promising recent effort to answer this question: the new philosophy of mechanisms. First, what is the new philosophy of mechanisms? Second, what is its scope? I have argued in answer to the first question that the new philosophy of mechanisms is a rather wide array of philosophical projects all driven by the value and importance placed on *mechanistic reasoning* to understanding the natural world. I have argued in answer to the second question that the scope of the new philosophy of mechanisms extends to integrate with statistical approaches applied in modern evolutionary biology.

I have made my case in the following ways. In Chapter 2, I set the groundwork for the project by reviewing six models of explanation that precede the new philosophy of mechanisms: the *Deductive Nomological Model*, the *Deductive Statistical Model*, the *Inductive Statistical Model*, the *Unification Model*, the *Statistical Relevance Model*, and the *Causal-Mechanical Model*. By highlight the shortcomings of these six models, I introduced the new philosophy of mechanisms as a sundry set of efforts to develop a new account of explanation that better captures scientific practice.

In Chapter 3, I made my case for *mechanistic reasoning* as the glue that binds the

philosophy of mechanisms. There I elucidated the key tenets and projects of the new philosophy of mechanisms in light of the debate about whether or not natural selection is a mechanism. In Chapters 4 and 5, I make a case for my answer to the question of scope. I argue, first, that that mechanistic reasoning positively influences statistical phylogenetics via the practice of embedding mechanisms in mathematical models of tree hypothesis construction. This warrants the conclusion that, in statistical phylogenetics, mechanistic reasoning positively influences a modern evolutionary biological science that is often understood as inherently nonmechanistic. I argue, second, that mechanistic reasoning positively influences modern population genetics, another modern evolutionary science often treated as inherently nonmechanistic.

The upshot of the project as a whole is a better picture of the latest philosophical understanding of scientific reasoning, as well as its scope and limits. While new mechanists defend a variety of different theses, are motivated by a variety of different case studies, and tackle different philosophical challenges, they are all unified by the importance of *mechanistic reasoning* to understanding the natural world. With respect to its scope, I have gone straight to the most difficult cases: the deeply mathematical and statistical sciences that are seemingly nonmechanistic. The results are promising. Even in those places of scientific investigation where mechanisms and mechanistic information are not explicitly mentioned or represented, mechanistic reasoning is positively influential. In some cases, mechanistic reasoning plays an important role in the construction of mathematical models characteristic of statistical reasoning. In other cases, mechanistic reasoning drives the investigate practices toward the search for and discovery of evidence underpinning evolutionary adaptations.

The results of these arguments indicate directions for future work. On the question of scope, there is still much to be addressed for the new philosophy of mechanisms. Although I have made a case for the role and value of mechanistic reasoning in two fields of modern evolutionary biology – statistical phylogenetics and population genetics – there has not yet been an assessment of mechanistic reasoning in developmental biology. Moreover, the notion that statistical phylogeneticists make use of embedded mechanisms introduces a broader question regarding the role and value of embedded mechanisms across the sciences. Presumably, wherever scientists are developing mathematical models that accommodate physical mechanistic information, there may be a presence of embedded mechanisms. An identification of additional cases and kinds of embedded mechanisms across the sciences is a future project that I believe is well-motivated by what has been achieved above.

Although I have tried to identify the core of the new philosophy of mechanisms as an emphasis on the value of *mechanistic reasoning*, a thorough philosophical analysis of the nature of mechanistic reasoning is left wanting. Moreover, implicit in these arguments is the view that *statistical reasoning* is the contrast of mechanistic reasoning. A thorough distinction between these two kinds of reasoning in the sciences as well as an assessment of the existence of different kinds of scientific reasoning is another future project motivated by this dissertation.

While I have introduced the *challenge of application* in Chapter 3 as a subsidiary problem for new mechanists interested in closing the gap between how philosophers and scientists think and talk about mechanisms, this challenge only hints at a broader set of *normative components* related to the new philosophy of mechanisms. One of the things

that really distinguishes the mechanistic account of scientific explanation from previous accounts is special attention to the activities of practicing scientists. In this light, there are additional questions regarding how the new mechanistic philosophy might work as a model for positively influencing scientific practice.