

2017

Individuality, the Major Transitions, and the Evolutionary Contingency Thesis

McConwell, Alison K.

McConwell, A. K. (2017). Individuality, the Major Transitions, and the Evolutionary Contingency Thesis (Doctoral thesis, University of Calgary, Calgary, Canada). Retrieved from <https://prism.ucalgary.ca>. doi:10.11575/PRISM/26505

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UNIVERSITY OF CALGARY

Individuality, the Major Transitions, and the Evolutionary Contingency Thesis

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE

DEGREE OF DOCTOR OF PHILOSOPHY

GRADUATE PROGRAM IN PHILOSOPHY

CALGARY, ALBERTA

APRIL, 2017

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Abstract

In this dissertation, I explore the reach of the Evolutionary Contingency Thesis—a view that emphasizes the role of dependency relations and chance in evolution (Gould 1989, Beatty 2006a). Contingency produces diverse biological entities, processes, and mechanisms. I analyze the implications of evolution’s contingency in three areas.

First, I address the problem of evolutionary individuality, which concerns the nature of entities that selection acts on (Godfrey-Smith 2009, Ereshefsky and Pedroso 2015). If we accept Lewontin’s 1970 view that individuals are selected, then what exactly are these individuals? I argue that evolutionary contingency and its diversity of outcomes causes a plurality of individuality types. These types of individuals emerge, evolve, and disappear through evolution.

Second, I defend a disunified model of major transitions in evolution. Major transitions mark pivotal turning points in life’s history, such as the transition from unicellularity to multicellularity. Philosophers and biologists aim to unify evolution’s transitions by establishing a property all major events share. I argue that evolutionary contingency’s emphasis on diversity supports a disunified model of transitions. That is, we should expect numerous kinds of major transitions given the diverse sets of outcomes caused by evolutionary contingency.

Finally, I extend the contingency analysis to a topic in philosophy of medicine: The nature of cancer. It is common to view cancer as a by-product of our evolution as multicelled creatures (Germain 2012, Aktipis et al. 2015). However, Lean and Plutynski (2016) argue that cancer is also a direct product of evolution by selection. In both cases, cancer is characterized in terms of how it functions (or does not function) as an object of selection. I argue that the diversity among cancers suggests philosophers should shift their focus to cancers’ structural differences rather than only their functional similarities.

Preface

Questions concerning biological individuality are truly interdisciplinary in nature. This was part of what drew my attention—not only do individuality questions span across different branches of philosophy, but they also invite philosophically-minded scientists from both biology and physics. Through questions like this, one gains a common language to communicate with others in different fields. Though I argue for three different claims in this dissertation, my work on the nature of individuality is where it started.

Oddly enough, the path began in philosophy of physics where I found individuation problems concerning quantum particles intriguing. I wondered about structural realism, its lack of individual objects, and what biological structuralism could possibly mean. Not long after I turned to evolutionary questions about living individuals and the history of life when suddenly I stumbled upon evolutionary contingency. Drawn in by Gould's ideas and literary style, soon I was on my way. Contingency and individuation led me to large scale macroevolutionary questions concerning major events in the history of life that included a connection with individuality, but also provided another opportunity to explore the reach of the Evolutionary Contingency Thesis. Lastly, I became interested in questions of cancer purely by chance when I received the news that our dog Dazy had mast cell disease. As she went through chemotherapy and successfully into remission, I was reading philosophical work on cancer. At the time, it wasn't obvious how cancer research fit into my broader project. A direction I could take became clearer the better I understood the contingencies of evolution.

The history behind the work of my dissertation involved a series of events that at the outset I could not anticipate where I would end up, and now looking back it's as though it could not be any other way. Such is the nature of historical explanations though, even when the path

taken includes sudden opportunities made available by chance. And at least for the course of my dissertation research, which included an intricate path of sometimes unfortunate yet unexpectedly salient trajectories leading to this outcome, the history mattered.

Acknowledgements

For reading and commenting on the chapters in this dissertation, I am especially grateful to my supervisor Marc Ereshefsky. Words cannot express my gratitude for his guidance and advice over the years that made me a better writer, researcher, teacher, and junior professional in the field. Marc taught me the importance of time management, work-life balance, and the value of having a good philosophical puzzle. His insight and kindness as a mentor proved invaluable during my time as a graduate student. My views on individuality and pluralism have also been shaped through conversations and feedback after presenting material from my dissertation research. For this I thank Megan Delehanty for her astute critiques and catches concerning the biological details and otherwise, as well as Ken Waters for his thoughtful questions that always pushed me to motivate and clarify the pluralism espoused in my work. I am also grateful to Adrian Currie and Jay Odenbaugh for reading drafts about contingency and individuality. I'm pretty sure that often they both knew where I was going before I even did.

There are numerous others who played a supportive role in some capacity over the years, such as the Social Sciences and Humanities Research Council of Canada who helped to provide funds so that I could undertake this research. Additional thanks to Kirsten Walsh, Brian Hanley, Sinan Sencan, Soohyun Ahn, and everyone in the philosophy of biology reading group for sitting through numerous presentations on individuality. They challenged me with great questions every time. And special thanks to Celso Neto who multiple times pressed an objection until I realized my answer. I'm also grateful to new friends Lauren Ross and Derek Turner for their input during the recent presentation of my work, to Kerry McKenzie who initially sparked my interest in individuality, and to Walter Glannon who always engaged with my ideas and research even after I went a different direction. And of course, I must thank my dear friends and colleagues, Justin

Caouette, Aaron Thomas-Bolduc, and Shelley Hulbert for their personal support and friendship—they kept it about the ideas and my PhD experience would not have been the same without them. I have left out too many names on this list as the UCalgary Philosophy Department is truly a community, which is in no small part shaped by Denise Retzlaff's consideration and kindness. I also received valuable emotional support and needed comic relief from friends and family, Chelsea, my parents Pauline and Brian, Loraine, Michelle, Bree-Anne, and Kyrstin.

Finally, I have infinite gratitude for my partner Wade, our dogs Roxy and Dazy, and our cat Casper, who all kept me sane and grounded, especially during the long days and late nights that every grad student knows all too well.

To my best friend and soulmate, Wade McConwell.

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List of Symbols, Abbreviations and Nomenclature

Symbol	Definition
DNA	Deoxyribonucleic Acid
ECT	Evolutionary Contingency Thesis
ETI	Evolutionary Transition in Individuality
LGT	Lateral Genetic Transfer
MTE	Major Transitions in Evolution
TENS	Theory of Evolution by Selection
TPI	Theory of Physiology by Immunology

Epigraph

The epilogue is a final Burgess surprise—vox clamantis in deserto, but a happy voice that will not make the crooked straight or the rough places plain, because it revels in the tortuous crookedness of real paths destined only for interesting ends.

—*Stephen J. Gould, Wonderful Life 1989, p.15*

“Evolution unfolds as though the tree were growing up a funnel, always filling the continually expanding cone of possibilities”—*Stephen J. Gould, Wonderful Life 1989, p. 39*

Chapter One: Introduction

In this dissertation, I explore the reach of the Evolutionary Contingency Thesis. This is a view about the nature of evolution, which emphasizes the diversity of evolutionary outcomes. Contingency in the biological domain produces a variety of biological entities, processes, and mechanisms. I argue for two main claims. First I argue for pluralism concerning evolutionary individuals, which are the objects of natural selection. Second, I defend a disunified model of major transitions in evolution, which are events that mark significant junctures in the history of life. Finally, I take up a third claim and focus on the nature of cancer. I argue that the diversity among cancers suggests philosophers should shift their focus to their structural differences rather than only their functional similarities. In what follows, I introduce these problems and my approach. I use the Evolutionary Contingency Thesis (ECT) as an explanatory framework to address these topics as it provides a platform for pluralism. Here I shall briefly introduce the idea of evolutionary contingency with a more thorough introduction to ECT in Chapter 3.

Current work on evolutionary contingency focuses on the nature of evolution and the shape of life’s history. This shape is due to the dependency relations between events, the processes that cause events, and chance-based factors in how evolution unfolds (Gould 1989, Gould 2002, Beatty 2006a, b, Desjardins 2011a, b, Turner 2011a, b). The Evolutionary Contingency Thesis is in opposition to views that characterize the pattern of evolution as more frequently converging on a particular set of outcomes often defined by environmental challenges (Conway Morris 2003). That is, most evolutionary outcomes that are contingent upon or sensitive to (the order of) prior processes, events, and external factors show how history matters to the existence of

those outcomes. Each evolutionary trajectory with its unique history can yield divergent results even under the same conditions. One reason for the occurrence of divergent outcomes, even in identical conditions, is a general de-emphasis of natural selection's power. Natural selection causes adaptive evolution by acting on traits that are responsive to environmental challenges. If natural selection were *the* driver of evolution, then so long as we have the same environmental conditions we should expect the same outcomes. However, Stephen Jay Gould was suspicious of characterizing evolution in a way that privileges the power of selection alone. Instead, he believed that the patterns of evolution embody the contingencies of history (1989, 2002). My dissertation research is inspired by his work and those who follow Gould.

Overall, I argue that a contingency framework helps us to better understand life's diversity, whether it be the diversity of individuals in the biological domain, the major events in the history of life, or the types of cancer that afflict multicelled creatures. Generally, I argue that this diversity amounts to pluralism: There are many different types of individuals, major events, and cancers, which is supported by the diversity caused by evolutionary contingency. The details of such claims are fleshed out in the following chapters. For now, I aim to motivate the three debates to which I apply the contingency thesis. My contribution to those debates is in the application of contingency as an approach, an approach which could also be construed as an extension of the Evolutionary Contingency Thesis itself.

1.1 Problems of Identity and Individuality in Biology

Though this dissertation focuses on a problem of individuality, there are other problems associated with biological identity more generally where following traditional philosophical reasoning can lead to strange places.

For example, one might think that a thing's identity, e.g. what makes it the thing that it is, is its material constitution. The traditional paradoxical case of this sort is the Ship of Theseus, which undergoes constant change of its parts, yet it appears to remain the same ship, some might say. An analogous case in biology is the renewal of cells in your body. If identity—what both individuates a thing and makes it unique from others—is merely due to what constitutes it, then you lose your identity multiple times over the course of your life. This is because the finite life of your cells and their ability to regenerate cause a large-scale renewal, especially in the lining of your gut that is renewed about every 3-5 days (Pinto and Clevers 2005). How can you be the same object undergoing the loss of parts if the parts that constitute you amount to your identity?¹ Alternatively, one might think that identity is something over and above what constitutes a thing, however, we've generally become suspicious of positing that which we cannot see—the immaterial mind, a mysterious life force or “elan vital,” etc. But what happens when we can ascribe properties to the whole that are not present in the parts which comprise it? Some suggest that “populations of eusocial insect colonies evolve based on adaptations, not of individual workers, but of the colonies of which they are apart” (Gillhooly et al. 2010). The case of eusocial insects may suggest that identity is something over and above constitution if some adaptations can only be attributed to the whole system alone.

¹ For more information about the issues of cell renewal see Alvarado and Yamanaka (2014).

Overall, it should be of no surprise that metaphysical issues of identity and constitution are found in the organic world. Thomas Pradeu (2012, 2ff) defines biological identity as the following: First, individuality is what makes an entity count as one discrete, cohesive, and delineated unit, and second, uniqueness is what makes that entity different from other entities. These two facets of identity are distinct—you may have two identical entities that can nevertheless be distinguished as two individual units. A common example in physics is the case of two electrons, which carry the same intrinsic properties of mass and charge, but are distinguished by their external relationship to one another (i.e. x has opposite spin to y as per McKenzie (2013)). Pradeu’s definition of biological identity clearly follows a Leibnizean theme: individuals may be qualitatively identical to one another, yet discerned by other features, such as extrinsic properties in the case of electrons.² The numerical identity of indiscernible entities, which share all the same qualitative properties, is determined instead by relational properties in that case. In the biological domain, genetically identical twins can be distinguished typically by some phenotypic differences, however, relational properties, such as spatio-temporal location are usually available as well. In the case of electrons in the physical domain, one loses those advantages and the aim is to establish which extrinsic properties successfully individuate.

Physical individuals, such as electrons, however, cause a problem of individuality because of their sameness—they are qualitatively identical by sharing all intrinsic properties so far as we know. Therefore, extrinsic properties are used to individuate instances of the same kind of particle we call ‘electrons’. Sameness in the case of living things can also cause problems, but so does the vast array of heterogeneity in the biological domain. In this dissertation, I focus on

² There is debate over whether discerning individual electrons by their extrinsic or relational properties is a weak characterization of their objecthood (French and McKenzie 2012, McKenzie 2013).

the problem of individuality in evolution. Since about 1970 (re: R.C. Lewontin), it is common ground that selection acts on individuals. And the question is, what are they? Consider the following case.

Armillaria ostoyae, a species of fungi in Oregon, is known as the case of ‘humongous fungus’. I take up this case in more detail in Chapter 2. *A. ostoyae* consists of genetically identical (or homogeneous) fungi clusters called ‘genets’, which spread up to 965 hectares separated by large forests (Worrall et al. 2004). The clones that make up the genet are called ‘ramets’. At first glance, one might think that each ramet is an individual, however, genetic homogeneity is important for natural selection. As long as the parts of an individual are genetically identical, this prevents selection from acting on those parts because there is no distinguishing competition among parts. So, one account of evolutionary individuality is that individuals are genetically homogenous (Janzen 1977, Buss 1987). On this account, *A. ostoyae* is one, very large and spatially disparate, evolutionary individual. However, Hull (1978) argues that individuals are spatially continuous and contiguous, and the parts of an individual function as cohesive, physically integrated wholes. Hull’s account, then, provides a reason to doubt that there is one large and discontinuous individual fungus. So, is *A. ostoyae* one individual or many? Philosophers disagree over the criteria for evolutionary individuality (Godfrey-Smith 2009, Ereshefsky and Pedroso 2015, Clarke 2013, Dupré and Malley 2009, Pradeu 2010).

Rather than give a single criterion (or set of criteria), I argue that evolutionary contingency and its diversity of outcomes causes a plurality of evolutionary individuality types. These types of individuals emerge, evolve, and disappear through evolution. The problem with many contemporary accounts of individuality is that they often abstract away from the details to give a set of necessary conditions to guide individuation. Chapter 2 includes an introduction to these

accounts. My approach involves the use of a contingency framework to better understand life's diversity, namely, the diversity of individuality types in the biological domain.

As we shall see, this diversity also extends to the macroscale, as well as to our conception of a particular sort of disease. Although a significant portion of this dissertation focuses on individuality and contingency, the final chapter outlines the application of evolutionary contingency within other contexts, namely, major transitions in evolution and cancer.

1.2 A Problem of Classification in Macroeolution: Major Transitions

Major transitions are events occurring at the grand evolutionary scale, which mark drastic turning points in the history of life. These events have significant effects on evolutionary processes along with downstream consequences. An example of a major transition is the shift from unicellular to multicelled life, which also happens to be the emergence of a new type of evolutionary individual. Philosophers and biologists offer unificatory models for major transitions in evolution by establishing a property that all major events share (Szathmáry and Maynard-Smith 1995, Queller 2000, Calcott and Sterelny 2011, O'Malley 2014). These models are supposed to explain major transitions by appeal to what they have in common with one another. For example, all major events might include a new division of labour (Szathmáry and Maynard-Smith 1995, 228). Or perhaps all major transitions involve changes in individuality (Michod and Roze 1999). However, that all transitions are transitions in individuality is challenged by others (O'Malley 2014). Generally, the debate concerning major transitions involves proposals of a common thread to unify events with disagreement over what events are included or excluded as major.

Other philosophers and biologists conclude that we have failed to provide a unified model of transitions and, therefore, we have failed to “get serious about evolution at the macroscale”

(McShea and Simpson 2011, 32). Such a charge assumes that commonalities among major events exist and that unification is the only explanatory framework by which these phenomena can be understood. That claim reflects a consensus on the topic: Although there is disagreement over which property (or properties) all major events share, that unification is required for fruitful explanation is commonly accepted. The identification of a common thread is supposed to reveal something about the robustness of evolutionary processes and their capacity to produce the same types of events over time. It is precisely that common ground I challenge.

In Chapter 5, I reject the unificatory aim concerning models of transitions. I argue that there are many kinds of major transitions given the diverse set of outcomes caused by evolutionary contingency. This diversity of transition kinds yields a disunified model: there is not a single common thread that all major events share. Furthermore, I argue that this disunity is revealing. The lack of a common thread reveals something about the diversity and fragility in evolution, as well as the nature of forces besides natural selection driving the evolutionary process.

In the cases of both individuality and the major transitions, I argue that the diversity of outcomes caused by evolution's contingency results in pluralism: There are many types of individuals in selection, as well as many kinds of major transitions in evolution. Such plurality is achieved by attention to the structural details, which distinguish the types of individuals and events. I conclude this dissertation by briefly exploring a topic in the philosophy of medicine within the framework of contingency.

1.3 The Diversity of Cancers

Finally, in a last chapter section, I focus on the nature of cancer and sketch the application of evolutionary contingency in that context. Generally, I explore whether cancer is the emergence of a new evolutionary individual or an instance of a major transition breakdown.

Specifically, I argue that the diversity among cancers is salient enough for philosophers to focus on their structural differences, rather than on just their functional similarities.

It is common to view cancer as a by-product of our evolution as multicelled creatures (Germain 2012, Aktipis et al. 2015). That is, it is common to view cancer as a side effect of the vast array and rapid evolution of morphological sizes and shapes (Leroi, et al. 2003). However, Lean and Plutynski (2016) argue that cancer is also a direct product of evolution by selection. In both cases, cancer is characterized in terms of how it functions (or does not function) as an object of selection.

I argue that we have an evolutionary reason to pay attention to the diversity of cancers, and that this diversity amounts to a plurality of cancer types. As we shall see, since different kinds of cancers are often distinguished by their different mutational signatures, and since the mutational process is an integral source of evolutionary contingency, philosophers ought to shift focus to those structural differences rather than only analyzing cancer in terms of its function role in the Theory of Evolution by Selection. Under the contingency framework, cancer is a diverse set or heterogeneous disease with a plurality of types.

And so, here is a brief outline of the chapters in this dissertation.

Chapter 2 is primarily expository and provides the landscape of views about evolutionary individuality. These are mostly contemporary views, but I begin the chapter with a historical lens to the problem.

In Chapter 3, rather than proposing particular criteria for the nature of evolutionary individuality, I introduce the Evolutionary Contingency Thesis and begin to explore how one can make sense of individuality pluralism within that context. I argue that evolutionary individuality evolves contingently by identifying the mechanisms responsible for two types of individuals in

selection. Those mechanisms exhibit markers of contingency and I explore processes other than natural selection that affect the evolution of individuality types.

While the two types of evolutionary individuals identified in Chapter 3 support my pluralist aim, more is needed to show that ontological pluralism follows from evolutionary contingency. In Chapter 4, I give a menu of pluralisms for contrast to facilitate an understanding of pluralism concerning evolutionary individuality. I argue that not only does individuality pluralism make sense within the framework of the Evolutionary Contingency Thesis, but also that evolution's contingency *causes* a plurality of individuality types. The chapter concludes with an evolutionary picture of multiple types of individuals at a time and over time.

Chapter 5 focuses on an example of how new types of evolutionary individuals evolve. This example also happens to be a major transition in evolution—the transition to multicellularity. By investigating this transition, not only can we understand the emergence of a new type of individual in selection, but we can also see how evolutionary contingency affects major turning points in the history of life. Chapter 5 ends with a section on the nature of cancer and explores whether it is the emergence of a new individual or if instances of cancer constitute a breakdown in the transition to multicellularity.

A general message of my research is this: The best way to understand concepts in biology is to work from the ground up. Accordingly, I pay attention to the finer, structural details of biological science to inform the philosophical investigations of living things, as well as the events and processes that affect them.

“Living matter always tends to group itself into these closed, independent systems with harmonious parts”—*Julian Huxley 1912, ix*

Chapter Two: The Landscape of Evolutionary Individuality

This chapter addresses the notion of biological individuals, although I focus on the nature of individuals studied in evolution. I outline different views of evolutionary individuality, and explore some puzzles concerning individuation in biology to motivate the problem.

Individuality is one ontological category among others such as classes, natural kinds, processes, relations, substances, properties, structures, living things, and organisms. Generally, individuals are discrete units with spatial boundaries and temporal location. There are physical or quantum individuals, chemical individuals, as well as biological individuals. According to Hull (1978), classes are groups of entities that can function in scientific laws, whereas individuals are historical entities that occupy particular space-time regions (1978, 337). Members of a certain class belong to that class because of the particular attributes they share, e.g. all pieces of gold have the atomic number seventy-nine. They do not exist in part-whole relationships with each other. Parts of an individual, however, do not necessarily share similar attributes, in fact the parts that comprise a whole system can be quite different from one another. For example, an individual organism can be fragmented into structurally-various parts that function together interdependently to sustain an entire organism (Ruse 1987, 225). Hull proposed a notion of individuality that is akin to the integrative nature of organismal parts working together in an organized way, e.g. organs such as the liver, kidneys, etc. comprise such an interconnected system. Metazoa, such as humans, dogs, and polar bears, are examples of organisms with functionally integrated parts that sustain the whole animal. The use of organisms as an intuitive example of individuality is no surprise since ‘individual’ and ‘organism’ were

often considered to be synonymous (e.g. see Buss 1987).³ Traditionally organisms were the paradigm individuals in biology. They were thought to be the exemplar of functionally cohesive wholes with integrated and cooperating parts (Ruse 1987, Hull 1978, Ghiselin 1981, 1987). However, there has been a contemporary push to consider biological individuality as a different ontological category; one that need not include certain organisms (Godfrey-Smith 2009). Different criteria for individuality have been proposed. For example, one might argue that genetic homogeneity is important for individuals in selection because it prevents selection from acting on the parts. Individuals might also have unique genomes—one might say this is how individuals belonging to the same species, for instance, are distinguished from one another. Finally, common criteria for individuals concern their spatial distribution and delineation from the environment, such as physiological unity, spatial contiguity, and autonomy. However, there are numerous problem cases in which the candidates for individuality lack one or more of these attributes (Santelices 1999, 152).

2.1 Case Studies as Counterexamples: The Humongous Fungus and a Bobtail Squid

Recall the case of *Armillaria ostoyae* briefly discussed in the introduction. This fungus spreads clonally underground and kills tree roots (Worrall et al 2004, 191). In eastern Oregon, groups of fungi are comprised of isolates (or clones) which bear identical genotypes and those groups can span up to 965 hectares separated by large forests that appear not to be occupied by *Armillaria* (ibid, 204). Fungi groupings are referred to as a ‘genets’ to indicate a genetically identical unit of a fungal population (Dettman and van der Kamp 2001, 614). Notably, “this definition of a genet does not denote spatial contiguity of all the isolates: it is possible for a genet

³ Perhaps more accurately though, Buss (1987) considered evolutionary individuality as a very organized case of the organism.

to be fragmented into several non-contiguous patches” (ibid, 614-15). Previously, the visible clusters were thought to be individually discrete fungi until it was established that those clusters were genetically identical. If genetic sameness and uniqueness are the signposts of individuality, then one ought to consider an entire genet of *A. ostoyae* as one individual despite the physio-spatial disparity that is often observed among the isolate mushrooms.

Consider an additional example. Symbionts are heterogeneous, i.e. members from different species, in a collective of entities that often work together in a way that is evolutionarily advantageous for all organisms involved. One symbiotic consortium consists of both the *Vibrio fischeri* and Hawaiian sepiolid (Bobtail) squid (Nishiguchi 2002). The Bobtail squid ingests *V. fischeri* at night, then vents the bacteria during the day. The squid can avoid predators via bioluminescence or the emission of light gained from the luminous bacterial symbionts. Conversely, “if environmental transmission increases the competitive abilities of a particular bacterium to infect only one type of host, then that particular host must have some mechanism(s) that allows the symbiont to increase its fitness as a benefit of the mutualism” (Nishiguchi 2002, 15). Such benefits to the bacteria are inferred from the observation that particular strains of *Vibrio* bacteria have very specific relationships to different types of squids (ibid, 16). This mutual relationship yields evolutionary benefits to both parties and the specificity of their relationships may suggest that coevolution is occurring despite young squids being born asymbiotic with no vertical transmission of the bacteria. Regardless, both the squid and bacteria work together. They depend on the mutualistic relationship that exists between them for aspects of survival. To consider the squid-*Vibrio* pair an individual though violates the criteria of genetic homogeneity, and both symbionts do not always remain spatially contiguous or physiologically unified either.

The two cases above as instances of clonal cases and symbiotic relationships are ubiquitous in nature. They are counterexamples to typical criteria proposed for individuality.⁴ However, there is an ambiguity concerning whether all biological individuals are evolutionary. That is, when addressing the problem of biological individuality, is one just asking which biological entities are the object(s) of natural selection? Although Thomas Pradeu (2010, 2012) seems to think that the problem of biological individuality amounts to determining individuals in selection, this is not necessarily a sentiment shared in the mainstream literature. For example, Ereshefsky and Pedroso (2013, 2016) propose a sortal view of biological individuality inspired by the work of Wiggins' (2001) sortal view of identity.⁵ They argue that there are different sorts of individuals and one must clarify which type of individual is under consideration (Ereshefsky and Pedroso, 2016). That is, there are different sorts of biological individuals of which evolutionary individuality is just one type. Such a pluralistic view captures the variety of biological individuals that have been identified by other philosophers, such as immunological individuals (Pradeu 2010) and metabolic individuals (Dupré and O'Malley 2009). But one can ask the additional question of whether immunological and metabolic individuals can be objects of selection or if individuals in selection have some additional feature(s) shared with those sorts of non-evolutionary individuals. Evolutionary individuality concerns the entities or collectives of entities that selection acts on.⁶ In other words, evolutionary individuals are the objects of

⁴ Besides *A. Ostoyae* and squid-*Vibrio*, there are other examples that challenge intuitions about biological individuality, such as the quaking Aspen trees found in Utah and the aphid-*Buchnera* symbiotic relationship that exhibits vertical transmission and strong interdependence between the aphid and bacteria.

⁵ Wiggins' sortal view of identity distinguishes between phase sortals and substance sortals. Phase sortals pick out a certain phase of an object's existence, which is different from sorting objects according to different substances (2001).

⁶ Is there a difference between individuals in selection and individuals in evolution?? Defining 'evolutionary individuals' as individuals upon which selection acts might be confusing. Yet Hull briefly distinguishes between the

natural selection; by undergoing selection pressures and mutations, among other evolutionary processes, populations of evolutionary individuals evolve through time. For example, although the squid-*Vibrio* consortium violates traditional individuality criteria such as physiological unity and genetic homogeneity, it does engage in activity that is evolutionarily advantageous for both parties. And so, it is controversial whether selection acts on the squid-*Vibrio* pair at the level of the pair, that is, it is controversial if together these entities constitute an evolutionary individual. Another way to ask the question is whether the squid-*vibrio* counts as one unit of selection. It is important to note that although this construal of the problem is related to the units of selection debate, rather than disagreement over which level selection acts on (i.e. species, organisms, genes, etc.) the focus here is on *the nature* of evolutionary individuality. I return to this in section 2.2.

Generally, philosophers of biology suggest that evolutionary individuals have certain attributes or they function in a particular way. In what follows I detail their views of evolutionary individuality to provide a sense of the philosophical landscape. The chapter ends with a comparative analysis of the views presented, and an exploration of how notions of pluralism and monism fit into the debate.

units of selection and the units of evolution by saying that both are individuals (1978 338). He says that even if species are not units of selection, they are entities that evolve as a result of selection at lower levels and as so they form lineages of “evolutionary unity” and these lineages can be individuated by spatiotemporal location and continuity (344). Hull thinks that species as units of evolution are historical entities—they form lineages just like genes form lineages by copying themselves, single organisms form historical lineages too. They are “historical entities persisting while changing indefinitely through time” (341). Therefore, the term ‘evolutionary individuality’ could be misleading if we mean the sort of individuals in selection rather than those individuals which count as units of evolution. This is unfortunate, but regardless I will continue to use ‘evolutionary individuality’ as referring to the object of selection even though arguably Hull outlined grounds for distinguishing two concepts.

2.2 The Historical Landscape: Accounts of Evolutionary Individuality

So how does one discern evolutionary individuals? As the object of natural selection, evolutionary individuals are discrete biological phenomena visible to processes that drive evolution, such as selection.⁷ Generally speaking, different theories of natural selection might yield different, and often competing, approaches to evolutionary individuality (Booth 2014, 13). Different approaches to evolutionary individuality cite various biological features as important markers of individuals, such as reproduction, replication, collaboration, integration, immunology, policing and demarcation mechanisms, and interaction schemes (Godfrey-Smith 2009, 2013, Pradeu 2010, 2012, Dupré and O' Malley 2009, Ereshefsky and Pedroso 2013, 2015, 2016, Clarke 2013, Huneman 2014a, b)

First I will outline the view of Leo Buss (1987), an evolutionary biologist, who uses the notion of an individual organism in modelling the organic structure of world. Then I turn to Lewontin's recipe for evolutionary change and his contribution to the issue of evolutionary individuality (1970, 1983). Third, I discuss the work of David Hull (1976, 1978, 1980, 1992), who theorizes about biological individuality and identifies units of selection as individuals. I will outline his view in Section 2.5. Together these inform how the problem of evolutionary individuality arose by introducing those selected historical instances. From there, I turn to more contemporary answers to the problem. Section 2.6 includes work from Godfrey-Smith (2009, 2013) and is followed by Pradeu's (2010, 2012) immunological perspective of individuality. A comparison of Godfrey-Smith and Pradeu's views exemplifies how different accounts of evolutionary individuality often cross-classify biological entities. Thereafter, I discuss

⁷ There may be other entities besides individuals that are important to processes that drive evolution.

Ereshefsky and Pedroso's (2013, 2016) account of evolutionary individuality, which is inspired by Hull, and I outline the metabolic account of individuality from Dupré and O'Malley (2009). Finally, Clarke's (2013) functional view of individuals in selection is discussed in Section 2.8, and I finalize with Huneman's (2014a, b) critique of evolutionary individuality from ecology and his account of individuals in biology. In making their case, some of these philosophers and biologists suggest that their views are pluralistic, whereas others seek one unified account of evolutionary individuality. The end of this chapter will contain some brief remarks about monism and pluralism in the literature.

Notably, up to this point I have excluded two issues of relevance and I am compelled to give reasons for their exclusion. First, a well-known historical figure who theorizes about the notion of individuality in biology is Sir Julian Huxley (1912). He articulates biological individuals as entities made up of heterogeneous parts that function together to sustain the whole system; a system with a degree of independence from external factors in the environment (28). I have not devoted a section to Huxley, but this does not reflect any misgivings about his role in concerning individuals in biology. As the title of his book suggests, *The Individual in the Animal Kingdom*, it contains ideas about individuality, but those ideas focus on animals of the Metazoa division. Furthermore, Huxley was not specifically concerned with individuals in selection as much as he worried about individuating biological entities more generally. This exclusion does not imply that Huxley's work concerning individuality is not important, rather I have chosen to focus on contemporary accounts.

Second, instead of the more general aim to discern individuals in biology, one might ask whether the units of selection are individuals. The anticipated complaint here is an objection to the exclusion of the units of selection debate, which is commonly associated with debate over

which level of organization selection acts on (e.g. genes, organisms, groups of organisms, etc.). Evolutionary individuality can be conceived of in isolation, although its roots draw from the traditional units of selection debate. One may object that when discussing evolutionary individuality and organisms, it is best to consult the units of selection research (e.g. Dawkins 1976, Lewontin 1970, Sober 1991, Okasha 2006). Here is one reason why the levels of selection debate does not receive my direct attention: A brief glance into the history surrounding the development of individuality as distinct from organismality shows the development of a distinct research programme. There is enough to work with just by focusing on individuality literature alone. Both the units of selection debate and the individuality literature have developed somewhat independently with issues from one side only mildly constraining the other. Despite such constraints, each side focuses on different research problems.

The units of selection debate does not directly address the nature of evolutionary individuality. David Hull made the case that units of selection are individuals and argued that units of evolution—those entities that through selection and mutation drive the evolutionary process—are individuals too (1978, 338). Later I propose that Hull may have been the first to articulate *evolutionary* individuality as a concept that warranted clarification apart from worrying about the levels of selection. Hull argued that just like organisms species can be individuals too, but he also identified the need for conceptual clarification concerning the role individuals play in selection and evolutionary theory generally, especially given the general consensus on multi-level selection theory (Okasha 2006). The nature of evolutionary individuality is a distinct concern from which level of organization—genes, chromosomes, genomes, organisms, colonies, populations, species, ecosystems—selection operates on since the nature of evolutionary individuality may be identified on a basis that includes characteristics satisfied on multiple levels

of organization. Hull gives his own view concerning the special sort of individuals involved in the evolutionary process, the details of which will be explained later. For now, the point is that we can focus on evolutionary individuality without diving too far into debates concerning levels of selection that were raised in the latter half of the 20th century. And so, I turn to a disentangling of individuality and organismality concepts found in the work of two evolutionary biologists.

As a rule of thumb, Lewontin (1970, 1983) and Buss (1987) treat ‘individual’ and ‘organism’ as synonyms, but sometimes use ‘individual’ to denote something akin to entities that are tokens of a single type of biological entity, e.g. individual chromosomes, individual genes, etc. The work of Lewontin and Buss secured the foundation for the problem of evolutionary individuality as it is known today. Through a historical lens we gain some insight concerning how individuals fit into a larger biological picture, which includes evolutionary theory and the organization of life.

2.3 An Evolutionary Biologist and the Individual Organism

In *The Evolution of Individuality*, Leo Buss addresses the evolution of hierarchical organization, and he views the “history of life [as] a history of transitions between different units of selection (1987, 171). In the final chapter of his book, Buss explores how organisms fit into that framework and he uses the notions of ‘individual’ and ‘organism’ rather loosely sometimes referring to organisms as ‘individuals’ (180). Recently, the ontological category of individuality in biology is treated as a different category, which may or may not include organisms (see Godfrey-Smith 2009). However, Buss often used the concepts interchangeably and helped to develop the notion of an individual organism as situated on a certain level within the nested hierarchy model of life's organization. In this model, higher levels of organization are more

inclusive—they in some sense contain lower levels. However, Buss was primarily interested in how a new level in the hierarchy came to be—i.e. processes or mechanisms at the higher-level limiting variation at the lower level—as well as why life was organized in a hierarchical fashion (1987, 183). He proposed an illuminating account of individual organisms and their place in the history of life. Buss states:

That life is hierarchically organized, with species composed of populations, populations of individuals, individuals of cells, cells of organelles, organelles of genomes, genomes of chromosomes, and chromosomes of genes, is so obvious an observation that it is quite remarkable that we have no general explanation of why this is so. Life beginning as self-replicating molecules, did not persist in this initial state. Rather, it sequentially elaborated “vehicles” in which the original heritable units became increasingly distanced from direct interaction with the external environment. Why is life hierarchical? (1987, 183).

Buss thinks that transitions to higher levels in the hierarchy are facilitated by whatever mechanism(s) maintains selection on the higher unit and suppresses lower level variation. Almost a decade later, and in line with thinking that a new level of organization arises by suppression of variation at a lower level, Szathmáry and Maynard-Smith (1995) proposed genetic identity and homogeneity as markers of those transitions between levels in the hierarchy. They identified what they thought to be major events, or major transitions in evolution, caused by the mechanisms responsible for a decrease in variation and an increase in identity and sameness at many levels. The major transitions in evolution (MTEs) will be addressed in Chapter 5 with a focus on the transition to multicellularity as a transition in individuality. For present purposes, the importance of Szathmáry and Maynard-Smith’s follow-up to Buss is that they tried to account for how transitions to new levels took place. Situated within the context of biological organization and transitions between levels, Buss illustrates a conception of the individual

organism as it has been conceived of in evolutionary theory. He says that the “evolution of individuality is but one such transition” and the theory of evolution was originally formulated with individual organisms in mind, specifically Metazoa (189, 195). Buss calls for the accommodation of units of selection other than individual organisms, such as species, but carefully notes that determining the sequence of transitions to new levels in the hierarchy will be a separate matter (195). Though it is helpful to see that the individual organism is situated within one of the top-tiered levels in the hierarchy of life, as Buss describes it, this is not an account concerning the *nature* of individuals per se. Rather, he focuses on where individual organisms are situated in biological ontology.

Throughout his book, Buss gives detailed descriptions concerning the ontogeny of organisms in addition to grander questions about the hierarchy (and history) of life. Though he does not address the nature of individuality directly, the interchangeable use of ‘individual’ and ‘organism’ throughout the book suggests that Buss considered individuals as organisms, or at least that organisms are the paradigm examples of individuality. However, it is through the work of Richard Lewontin that one gains more information concerning the role of individuality in evolution.

2.4 Lewontin and the Theory of Evolution by Natural Selection

Lewontin identifies the organism as the object of evolutionary forces, such as mutation and selection (1983, 87). The organism is the “nexus of internal and external factors, it is also the locus of their interaction (89). According to Lewontin, the object of selection replicates, and through replication it generates heritable variation, which in turn yields differential fitness when selection distinguishes among those variants (1970). More specifically, a population will undergo evolutionary change if three principles hold. First, individuals within a population must

exhibit phenotypic variation. Second, the varying phenotypes must have rates of survival and reproduction, which indicate how those phenotypes make a difference to the fitness of individuals. Third, fitness must be heritable, though no mechanism of heritability is specified as Lewontin wishes to offer a general principle (1970, 1). And so, individuals in selection exhibit varying heritable traits that make a difference to their fitness. From Lewontin one learns that “the primary focus of evolution by natural selection is the individual” (7).

In line with Buss, Lewontin does not focus specifically on the nature of evolutionary individuality, but his analysis begins to constrain the boundaries of such a concept. Importantly, Lewontin states that natural selection acts on individuals, although he focuses on the genotype as sufficient to understand individuals in selection (1970, 7). He thinks that in “individual selection, it is sufficient to know the genotype of the individual and all the relevant environmental variables, without inquiring how [to come] by that genotype or what the genotype of his offspring will be” (8). It is important to note that in this statement Lewontin is concerned about how evolution *by selection* works and the functional role individuals play in that context. Though as we shall see in following chapters, there is more to evolutionary change than just selection alone. Additionally, it is contentious as to whether largescale evolution exhibits patterns one should expect from selection at the microscale, if it were indeed the most significant driver of evolutionary change. However, what is important for the purposes of this dissertation is how Lewontin identifies the objects of selection as individuals. This means that particular sorts of individuals hold an indispensable role within evolutionary theory. Moreover, he thinks that what facilitates evolution by selection—variation, heredity, and differential fitness—can be applied “equally to genes, organisms, populations, species, and at opposite ends of the scale, prebiotic molecules and ecosystems” (2). This means that evolutionary individuality has

characteristics that are not necessarily found only at one specific level in the biological hierarchy.⁸

In sum, both Buss and Lewontin provide models that show how individuals are situated within evolutionary theory. On the one hand, Buss proposes a model of biological organization that places individuals on various levels in the nested hierarchy of life. He concerns himself with how new levels emerge. On the other hand, Lewontin articulates a particular recipe for the Theory of Evolution by Selection (TENS) that identifies the objects of selection as individuals. The work of Lewontin and Buss provides a foundation for more recent accounts of evolutionary individuality, which will be the subject matter from here forward. I now turn to the role David Hull's work plays in further shaping the notion of individuals in selection.

2.5 David Hull on Individuality in Biology

The importance of Hull's contribution to the topic of individuality should not be understated. Not only did he famously argue that species are individuals instead of classes, in doing so he identified a special sort of individuality that takes part in the evolutionary process (1976, 1978, 1980, 1992).⁹ I defend three claims about Hull's publications in this area: First, his transition to thinking about the nature of individuals in selection is an illuminating conceptual development to track. Second, he articulates a broad sense of individuality for thinking about units of selection as individuals. And finally, Hull's notion of organisms in addition to his account of evolutionary individuality are both very important for this chapter.

⁸ Lewontin was critical of selection operating on lower levels so perhaps it would be better to describe his sentiment as 'individual *organisms* as the objects of selection occupy a particular place in TENS,' however, this does not capture his view concerning higher level selection of colonies, populations, and species.

⁹ Ghiselin (1974) first argues for the consideration of species as individuals and Hull later develops the idea.

2.5.1 Tracking Hull's Conceptual Development of Individuality

Tracking the conceptual development and usage of the term 'individual' in Hull's work proves to be a worthwhile endeavour. Although additional historical legwork may be needed to affirm the following claim, I suspect that the contemporary usage of 'evolutionary individuality' has roots that were articulated by, and perhaps even originated with, Hull (1976, 1978, 1980, 1992).¹⁰ One of the best instances of Hull's insight that evolutionary individuality as a concept needs clarification is when he says:

Entities at various levels of organization can function as units of selection if they possess the sort of organization most clearly exhibited by organisms; and as such, units of selection are individuals, not classes...like mutation and selection, evolution occurs at more than one level of organization (1980, 131).

This passage distinguishes objects of selection as individuals instead of classes, and it indicates that organisms are not the only objects of selection. That is, one finds individuals in selection on multiple biological levels. Organismality, then, is only one example of evolutionary individuality. Hence, we see in Hull's work how the notion of individuality becomes at least a wider category than that of an organism as it denotes any spatiotemporally localized and well-integrated entity (ibid).

If one accepts that selection can act on multiple levels, e.g. from genes to populations to entire species, then the object of selection has characteristics that entities on multiple levels exhibit. One need not assume that selection acts on every level simultaneously, rather selection

¹⁰ I am in good company identifying Hull as a source of contemporary conceptions of how individuals function in evolutionary theory: Gould (2002, 615) says, "David Hull formalized this distinction in a manner that has...organized the professional discussion on units of selection ever since." Notably, Gould's consideration of individuals is similar to Hull's.

as an operation may wander from one level to the next. The entities at each level that selection takes as its object may vary, but to count as individuals they share certain features. Hull aimed to identify those shared features. While Lewontin proposed that selection acts on individuals, Hull illustrates that it is individuals of a certain sort which take on such a role.¹¹ And those particular individuals have features that genes and organisms, for example, both demonstrate (e.g. spatiotemporal location) despite organisms residing on a more inclusive level of organization. This brings me to the second point of discussion: Hull's broader notion of individuality.

2.5.2 Hull's General Notion of Individuality

Hull's general concept of individuality is important because functional integrity is a feature peculiar to biological individuals. For example, quantum particles do not have the sort of inherent structures that can be used to individuate them (McKenzie 2013, 10).¹² Organisms have a variety of different parts working together that helps to distinguish one organism from another in many cases.

What features do organisms have that make them a paradigm case of individuality? Hull argued that if species share such features, then they should be considered individuals too.¹³ That is, if species are located in a particular time and a place as organisms are, and they demonstrate the degree of functional integrity that organisms do, then species should also be considered

¹¹Although related more to the units of selection debate, interestingly one motivation Hull provides for the S-A-I thesis is that evolutionary theory requires species to be considered as individuals. This is because if species are classes, it's not clear how they could evolve and permit change (1976, 175). If the idea here is that individuals must withstand change, what might follow from this is that individuality concepts need to somehow incorporate change as well.

¹² French and McKenzie (2012) also discuss the difficulties concerning individuating quantum particles such as electrons, which must be done terms of their opposite spin to one another (extrinsic properties) rather than by mass or charge (intrinsic properties).

¹³ Hull points out that the analogy between organisms-as-individuals and species-as-individuals breaks down in situations where the organisms possess a largely fixed makeup that constrains their development (1976, 174).

individuals as well (1976, 174). Spatiotemporal localization and functional unity are notions associated with a general notion of individuality used by Hull (1992). Often, Hull emphasizes spatiotemporal location as the distinguishing feature between entities that are otherwise identical. No matter how similar they are, identical entities or groupings of entities can be distinguished by the time and place they occupy. Spatiotemporal location is what makes something unique and permits individuation on that basis, namely, that there are two individuals instead of just one (1976, 176). Organisms exhibit this kind of spatio-temporal continuity, but what else renders organisms as paradigmatic individuals?

Hull states, “organisms retain their identity by means of a constant change of substance: new cells are manufactured, old cells are sloughed off” (1976, 176). As Hull indicates, “the retention of a certain substance can hardly be necessary for individuality in organisms” (ibid).¹⁴ Rather, a more relevant factor for individuating organisms is internal organization or integral functional component parts that act together in some unified fashion to sustain the whole organism.¹⁵ Parts of a whole are different from members of a class: Entities are members of a class because they are similar, e.g. all pieces of gold, as members of the class of all gold things, have the atomic number 79. However, parts of an individual are often both heterogeneous and organized to work together in varying degrees of mutual dependence to sustain the whole system (178). This organization yields a “togetherness” bounded from factors considered external to the system. The organization and function of our own organs is a great example of how

¹⁴ In contrast to a constant change of substance, a more traditional view of what makes something the thing that it is and different from others is the following: That entity has an essence—some identifying feature that persists always, which makes that feature (or set of features) the defining characteristic(s) of the entity in question.

¹⁵ Hull anticipates a problem in identifying the difference between groups and individuals when he points out the difficulties of establishing how “closely knit” a group of organisms needs to be before they lose their separate individualities and become one individual, as well as how loosely organized an organism can become before its parts are free-living organisms (1976, 177).

interdependent function of parts is necessary to maintain continued existence, bodily function, and external boundaries of a whole system.

In summary, Hull uses organisms as a starting point to build a general concept of individuals in the biological domain. He chooses features that ground an organism's individuality and extrapolates to other cases. In doing so, Hull demonstrates how an organism's spatiotemporal location and continuity as a marker of its individuality coincides with broader metaphysical notions of individuals across domains, although functional integration sets individuals in biology apart (1980).¹⁶ In contrast to broad metaphysical concepts of individuality, the peculiar feature of heterogeneous and functionally unified parts is noted as a striking feature of biological individuals in particular. But what can we say about biological individuals that are also evolutionary? Hull argues that "not all individuals can function as units of selection, but only individuals can be selected" (1980, 313). And those individuals in selection must engage in particular processes. Individuals that replicate themselves and individuals that interact with the environment are special sorts of biological individuals, namely, they are individuals required for selection to work (1980).

2.5.3 Hull's Replicator-Interactor Theory of Individuals in Selection

Hull maintains that both replication and interaction with the environment are the precise characteristics needed for natural selection (1980, 315). In other words, replicators and interactors are both needed for selection to occur (1992). Replicators pass on their structure from generation to generation mostly intact, and they either interact with their environment or produce more inclusive entities that do (1980, 315). One most obvious case of interactors and replicators

¹⁶ When Hull argues that functional integration sets apart biological individuals from other sorts of individuals that cannot be broken down into more basic units, he likely has in mind basic physical particles, perhaps particles like quarks and leptons, which have no internal structure.

is organisms and genes, respectively. Genes replicate copies of themselves and as such many genes produce characteristics that exist directly at the level of the functional whole of which they are a part of, namely, the organism.¹⁷ In turn, an organism's interaction with the environment uniformly affects that interactor's constituent genetic replicators. Additionally, replicators only need to last long enough to copy themselves and retain their structure through descent (1980, 318).¹⁸ But TENS requires that individuals in selection interact with their environment as well. Replicators and interactors engage in two different processes and so "become separated into different individuals at different levels of organization" (ibid). Moreover, Hull defines the process of selection as a process in which differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them (318).¹⁹ According to Hull, genes are the most fundamental replicators. Although most organisms can replicate, as functionally-organized wholes organisms are the paradigm case of interactors. However, in cases of chromosomes, entire genomes, as well as colonies, populations, and species, it may be more difficult to determine what sort of individual they are, if any. Although one might argue, as Hull does, that the kind of structural and functional unity needed for replicators and interactors can be found on both more and less inclusive levels of organization.

¹⁷ Although many genes produce characteristics at the level of the whole organism, some genes in an organism are not expressed.

¹⁸ Hull identifies longevity, fecundity, and fidelity as necessary features of replicators: They need to last long enough to make copies, they need to retain structure, and they descend from previous replicators from within the same ancestral history (1980, 318).

¹⁹ Hull's view is in contrast to Dawkins (1976, 1978) who argues that the gene is the unit of selection and not the organism. Hull disagrees and thinks that although evolution could result from replication, evolution by natural selection needs the interplay between replication and interaction with the environment (1980, 320).

On Hull's account, selection occurs when there are two individuals of two different types: ones that replicate themselves and ones that interact with their environment.²⁰ These cases also satisfy the broader metaphysical notions of individuality of spatio-temporal location and continuity, as well as the internal structure and functional organization characteristic of individuals in the biological domain specially. Finally, through replication and interaction, some biological individuals have a place in evolution. This leads us to Godfrey-Smith's view of Darwinian individuals.

2.6 Godfrey-Smith's Darwinian Individuals

Peter Godfrey-Smith uses Lewontin's recipe of TENS to develop his own account of individuals in selection (2009, 2011, 2013). Three aspects of Godfrey-Smith's account are important for this chapter: First is his appeal to Lewontin's version of TENS, which in turn lays a foundation for his conception of individuals in selection, as well as for the conceptual space that is left for organisms. I will take each in turn.

2.6.1 TENS and Reproduction

As we shall see in later chapters, Godfrey-Smith plays a significant role in shaping the debate over the nature of evolutionary individuality through his analysis of Darwinian populations. He builds on the classic Lewontin three-fold framework for the theory of evolution by natural selection (TENS), which includes variation, heredity, and differences in fitness among individuals in a population (Godfrey-Smith 2011, 65). Recall that such features are required for populations of individuals to evolve. According to Lewontin, the object of selection transmits traits, which generates heritable variation that yields differential fitness when selection

²⁰ Sometimes a replicator is an interactor as well—organisms can replicate themselves in some fashion.

distinguishes among those variants (1970). Lewontin identifies individuals as the objects of selection, whereas Godfrey-Smith outlines their nature. Godfrey-Smith says: “Darwinian populations are collections of [individuals] that vary, reproduce at different rates, and inherit some of this variation” (2009, 107). Heredity is important for passing on variations of advantageous phenotypic traits, and heritability tracks how a population responds to differences in fitness (25). Important processes such as reproduction ensure that traits are transmitted, which results in differential fitness, as well as the continuity of that differential fitness (64). For example, if trait x has differential fitness y , then trait $x+1$ will have differential fitness $y+1$, and so on.

As we’ll see, Godfrey-Smith specifies that individuals in selection transmit traits through a particular form of reproduction.²¹ He argues that evolution by natural selection is connected with differences in how much individuals reproduce (2009, 21). The process of reproduction forms a chain of reproducers. This chain of reproducers provides a vehicle for heritable traits to be passed to individuals in subsequent generations (2013, 20). For Godfrey-Smith, reproduction as a mechanism for heredity is important for individuality because it is the making of a new individual (18). Reproduction in the intuitive sense includes the notion that parents are causally responsible for the existence of the offspring (2009, 79). In order to be an individual in selection, that entity (or collection of entities) must reproduce in the way described below.

²¹ At this point one might be tempted to use ‘evolutionary individual’ and ‘Darwinian individual’ interchangeably, however, given arguments in later chapters, it’s better to think of Godfrey-Smith’s Darwinian individuality as just one type of evolutionary individuality. So not all evolutionary individuals are Darwinian in the sense specified by Godfrey-Smith in this section.

2.6.2 *Criteria for Darwinian Individuals*

According to Godfrey-Smith, thinking of the organic world as structured in terms of populations provides a means to understanding large scale structure (2009, 11). Darwinian individuals are members of Darwinian populations and they play an important role in the evolution of those populations.²² Importantly, however, Darwinian individuals need not be organisms: “genes, chromosomes, and other fragments of organisms can all form Darwinian populations” (2009, 85). However, at minimum, for an entity to be a Darwinian individual, it needs to reproduce. How is reproduction tied to individuality? Reproduction yields lineages of particular things—whether they are duplicates or genetically distinct, they are still “distinct, countable things” (ibid). It involves the creation of a new entity and “this [new entity] will be a countable individual” that is distinguishable from mere growth of the same (86). Godfrey-Smith gives the conditions for the sort of reproduction under which some evolutionary individuals are formed (Bouchard and Huneman 2013, 7). He identifies different modes of reproducing—there are different ways in which entities can produce new material and reshape old material (2009, 87). And so, there are different sorts of reproducers: Collective, simple, and scaffolding reproducers. Collective reproducers engage in the sort of reproduction that includes the distinctive features important for Godfrey-Smith’s view of Darwinian individuality. These distinctive features are reproduction, germ-line specialization, and integration. But first, a general understanding of the differences between collective reproducers compared to simple and scaffolding reproducers will be useful.

²² Godfrey-Smith proposes three corresponding grades of Darwinian populations: *Paradigm* populations are evolving populations in which novel variation emerges. A *minimal* Darwinian population is a collection of causally connected individual with variation in character which leads to a difference in reproductive output; a difference that is inherited. *Marginal* cases do not satisfy minimal requirements, but only approximate them (2009, 39, 41).

Some collective entities can reproduce, such as many multicellular organisms, but they also contain at least some other parts that can reproduce in a simpler sense, such as cells that make more of themselves by utilizing machinery internal to them. Simple reproducers, such as a bacterial cell, can reproduce on their own often within an environmental context, which allows for the nutrients and energy they need to get the job done. The general rule is that if something has simple reproducers as its parts, then it is a collective, but there can also be collectives of collectives, such as social groups containing multicellular organisms (2009, 88-89).²³

Viruses and chromosomes are examples of scaffolding reproducers that reproduce themselves by means of structures or mechanisms external to them (see 2009, 88 and 2013, 20-21).²⁴ So, similar to how construction workers utilize scaffolding structures as a platform for building something else, scaffolding reproducers utilize structures external to them in order to replicate themselves. Simple reproducers can have reproducing parts only if they are scaffolding reproducers. As a result, genes, chromosomes, cells and organisms can all exhibit fitness and heredity because they are part of parent-offspring network of relations (2009, 90). As such, these can all form Darwinian populations to some degree.

Finally, Godfrey-Smith identifies three features of collective reproducers, which come in degrees and help to distinguish between paradigm and marginal cases of Darwinian individuality. Collective reproducers are important because the parameters identified below make the most sense within that context (2009, 100). Furthermore, Godfrey-Smith views collective entities as the result of de-Darwinization, that is, the evolution of lower-level entities

²³ Even if there are collectives that include other collectives, there is likely not collectives ‘all the way down’.

²⁴ Godfrey-Smith thinks that the replicator concept is too broad as it includes enzymes used for gene expression because pre-existing structures are in the same vicinity. He argues that on his view, enzymes are just part of the machinery (2009, 90).

can be suppressed by evolution taking place at a higher level of biological organization. The breakdown of this process is signified by evolutionary activity at the lower-level, such as rapid replication of cancerous cells within an organism (see 2009, 100-103 for a discussion of de-Darwinization). And so, collective evolutionary—or Darwinian—individuals reproduce according to the process of reproduction that includes the following: A reproductive bottleneck and the presence of germ cells, in addition to appropriate integration (2013, 19). Importantly, Godfrey-Smith admits that there may be cases which do not fit the types of reproducers just described: “Order is being imposed on an unmanageable menagerie, and this is being done in part via idealization” (2009, 89). He focuses on collective reproducers because he thinks that the following three features—bottlenecks, germ-lines, and integration—are not helpful with regards to simple and scaffolding reproducers (2009, 100). These three features set the parameters for his view of individuals in selection.

A reproductive bottleneck, is an evolutionary event that reduces genetic variation and marks the divide between generations. It forces the process of growth and development to start anew (2009, 91). Godfrey-Smith says “when a large organism starts life small and simple, it creates a window of opportunity for wholesale reorganization and change” (2009, 91). Bottlenecks are linked to evolutionary novelty and yield the kind of variation available to natural selection (ibid). One example is any organism that begins as a one-celled zygote.²⁵ The existence of a bottleneck presents itself within a gradient from the single-celled small beginnings to the absence of a bottleneck altogether. Since reproduction and growth are often confused, the

²⁵ A less intuitive example of the presence of a bottleneck is when groups of plants or fungi consist of genetically identical clones—these ramets have runners that can result in a new clonal fragment. Godfrey-Smith points out that the thinner the runner, the less likely it is that the new fragment is a mere continuation of the old clone (92).

bottleneck requirement rules out cases that appear to be growth, such as the clonal dandelion ramets that remain genetically identical despite spatial discontinuity (Janzen 1977).

A *germ-line* marks the degree of reproductive specialization within a collective, e.g. in mammals like us only a small portion of cells can give rise to a new organism. Whereas somatic cells are diploid cells containing two sets of chromosomes, germ cells are responsible for the reproductive capabilities of an organism to produce offspring. In eusocial insects, such as bees, only certain bees reproduce, which suggests at least a certain level of reproductive specialization. ‘Germ-line’ refers to a special division of labour among cells in a multicellular organism that is specifically associated with reproduction. Any biological entity that exhibits a sharp distinction early on in its lifecycle to smaller scale entities, such as human germ cells, which give rise to new collectives, such as new humans, will satisfy this condition. This is a specialization of a certain sort—the third feature of Darwinian individuals below refers to a more general division of labour and specialization of parts. Godfrey-Smith argues that the existence of a germ-line is worth identifying separately from other divisions of labour because of its role in facilitating reproduction.

Integration is a feature of Darwinian individuals that includes a more general division of labour with a mutual dependence of the parts (2009, 93). These parts work together to sustain the whole system and maintain the boundary between the individual and what exists outside of it. The degree of integration places the entity on a gradient from loose aggregation, to intermediate levels of integration exhibited by colonies, to high levels of integration evident in multicellular organisms. How the parts are related to one another, as well as how they contribute to the whole system can vary at each stage. Piotrowska (2013) provides an illuminating way to think of this scale of integration: Loosely integrated parts ‘add’ together and are often individually

identifiable and each make contributions to the aggregative whole, such as in the case of eusocial insects. Intermediate levels of integration could involve components that retain a certain level of integrity and separation and the parts contribute through a linear relationship, such as the aphid-*Buchnera* symbiotic relationship I discuss in a moment. Finally, high levels of integration evident among the organs of mammals indicate a division of labour contributing to the whole system in a way that yields a strong mutual dependence of parts such that the parts are often not functionally independent and sometimes difficult to isolate.

The presence of a bottleneck with a high degree of division of labour—both in the reproductive sense and more general integrative sense, respectively—marks clearer cases of reproduction when compared to marginal cases of reproduction, e.g. marginal cases of reproduction are often less distinguishable from cases of growth as is the case with spatially contiguous ramets and genets of a plant, such as those in Aspen groves connected by large root systems. Collectives, like many organisms, have high values of germ-soma distinctions and integration, which distinguishes collective reproduction from simpler and scaffolding forms. Examples of paradigm Darwinian individuals are many multicellular organisms such as humans that score high values for all three parameters described above (2013, 22). Although each criterion, bottlenecks, germ-lines, and integration, is meant to stand on its own, Godfrey-Smith wants to leave open the possibility for entities that exhibit a combination with different values of each parameter. He thinks that marginal Darwinian populations often have individuals participating in marginal modes of reproduction (2009, 104). However, even by setting up a gradient model of Darwinian individuality, there are cases that Godfrey-Smith's view has difficulty accommodating.

Symbiotic relationships present problem cases for Godfrey-Smith's account. His model of individuality can handle entities with vertical transmission, such as aphid-*Buchnera* where the lineages run in tandem with one another, better than those entities which do not reproduce altogether in a linear fashion (see Ereshefsky and Pedroso 2013). Godfrey-Smith's view can accommodate aphid-*Buchnera* symbiotic relationships because the *Buchnera* bacteria are transmitted vertically creating a lineage that runs in tandem with that of the aphid (2013, 31). For Godfrey-Smith, different members in a multi-species collective must have parent-offspring lineages that develop alongside one another. However, squid-*Vibrio* consortia exhibit behaviour that appears to be evolutionarily advantageous for both the squid and the bacteria, as previously discussed. They just do not reproduce in a way that forms vertical lineages because the same strains of bacteria need not pair up with the same squids each night. In this case, there is a many-many relationship between both symbionts, which creates complicated parent-offspring networks when tracking transmission across generations. As such, a squid-*Vibrio* consortium cannot be accommodated as a Darwinian individual even in minimal and marginal senses of Darwinian individuality, despite appearing as an adaptive unit.²⁶ This is certainly a problem for Godfrey-Smith's view as most symbiotic associations are horizontally transmitted and symbiosis is found in all forms of life—it is everywhere (Nyholm and McFall-Ngai 2004, Paracer and Ahmadjian 2000). Given that is the case, our views of evolutionary individuality should be able to account for such diversity in the biological domain rather than marginalize it. Regardless, Godfrey-Smith's view does provide insight concerning how organisms are not necessarily individuals in selection.

²⁶ Godfrey-Smith argues that symbiotic consortia can be adaptive units without selection acting on the unit as a whole—they merely co-evolve (2011, 507).

2.6.3 Godfrey-Smith's Account of Organisms

Godfrey-Smith's account yields a gradient from metabolic organisms as non-Darwinian individuals to Darwinian individuals. However, on his view, organisms prove to be an intriguing case. Although organisms were once thought to be the paradigm individual, Godfrey-Smith argues that many organisms are *not* Darwinian individuals, e.g. sterile castes of social insects sometimes referred to as "super-organisms," and other sterile animals. These organisms metabolize, but are unable to reproduce, thus metabolism is not seen as essential for individuals in selection. "Organisms are systems comprised of diverse parts which work together to maintain the system's structure, despite turnover of material, by making use of sources of energy and other resources from their environment" (2013, 25). Organisms are essentially persisters: they "use energy to resist the forces of decay" and need not reproduce (ibid). However, in order for Darwinian populations to evolve, the individuals that comprise them must engage in the sort of reproduction that includes germ-line specialization and reproductive bottlenecks. On this picture, the sterile mule is *not* considered a Darwinian individual because it does not have reproductive capabilities.

At this point, the conceptual departure from preliminary work on individuals and organisms is clear. Recall that Leo Buss (1987) used 'organism' and 'individual' synonymously. Hull (1978) even discussed organisms as the paradigm case of individuals in selection, at least for the interactor type. However, for Godfrey-Smith, Organismality is a different ontological category that includes some overlap with Darwinian Individuality. Importantly, Godfrey-Smith's view of individuals in selection does not begin with the organization of organisms. Instead he draws from the role constituents of a Darwinian population must play in order for that population to undergo evolutionary change. This is a methodological choice—Godfrey-Smith

begins with our best formulation of TENS in order to draw conclusions about the nature of individuals involved in that theory. However, as we'll see in the next section, Pradeu (2010, 2012) approaches the problem of evolutionary individuality from a different angle. He thinks that although organisms are not *always* individuals in selection, it is necessary to begin with the heterogeneous organism to determine what those individuals are: "It is necessary to examine the physiological processes produced in the organism to arrive at a precise definition of what, in each case, counts as an evolutionary individual" (2012, 260). And while Godfrey-Smith highlights features that are involved in the making of a new individual, Pradeu offers an account which focuses on the maintenance of an individual over time.

2.7 Pradeu's Immunological Individuals

In his 1992 paper entitled "Individual," Hull noted that if physiology were theoretically-developed enough it would be useful for determining individuals, and Pradeu (2010, 2012) takes up this challenge. Pradeu maintains that the study of physiological processes gives insight into Hull's criterion of functional integration as a significant feature of individuals. So, while Godfrey-Smith proposes that TENS via reproduction is one of the definitive and necessary features of evolutionary individuality, Pradeu is concerned that evolutionary biology alone is not enough for a comprehensive account of individuals in selection. Although Pradeu (2012) offers a precise theory of physiology by appeal to a view of immune system function, this section focuses primarily on his claim that the physiological field of immunology can offer insightful contributions to the individuality debate. First, I introduce the feature of immunogenicity and its role in delineating individuals. Then I explain Pradeu's conjecture that physiology can inform questions of evolutionary individuality. Here I also propose what I see as an advantage, as well as the disadvantages, for his immunological conception of individuality.

2.7.1 Immunogenicity

Traditionally, immunity was thought to be a reaction of immune system components to foreign material alone (see Burnet 1960). Recently, however, Pradeu proposes a view of the immune system, which includes immune reaction to both endogenous and exogenous material.²⁷ In both cases though, immune system responses to antigens mark the boundaries of an organism. The triggering of an immune reaction—or immunogenicity—is not due to foreign antigenic material alone, according to Pradeu. It can, however, be caused by non-foreign antigenic activity (e.g. some cancerous tumours). Specifically, immunogenicity occurs in the presence of strong changes in antigenic patterns. Antigens are any exogenous or endogenous material that challenges the identity of an organism. And so, immunogenicity occurs when the patterns of activity by molecules (or ligands) that the immune system receptors continuously interact with exhibit strong, discontinuous changes when compared with previous interactions (2012, 131).²⁸

Notably, immunology results in a particular focus on organisms as the most individuated case (228-9). Organisms have highly-differentiated physiological boundaries which precisely individuate organisms in comparison to other biological entities. Rather than just one individual among others, the organism resides atop the hierarchy of individuality; a hierarchy which runs as a gradient from least to most differentiated cases. Organismality occupies the latter (229). An entity or collective of entities location in this continuum will be determined by the degree to which the entity's boundaries are sharply maintained against internal and external forces through

²⁷ Pradeu's Discontinuity Theory of Immunity is a departure from F. M. Burnet's traditional Self-Non-Self Theory of how the immune system functions. For Burnet, the immune system rejected non-self entities only, and so faced issues with cases such as the tolerance of symbiotic bacteria and the intolerance of 'self'-originating tumors.

²⁸ For more information regarding Pradeu's theory of immunology, see Pradeu (2012) and McConwell (2015b).

immunogenicity, or something with analogous function to an immune system.²⁹ Immune receptors survey the borders and maintain the integrity of individual organisms. The organism is then a set of “interconnected heterogeneous constituents, interacting with immune receptors” (2010, 256). And so, it makes sense for an evolutionary individual to be made up different constituents from different origins that are unified by common interactions with immune receptors” (259). The immune system by its surveillance activity defines what will be accepted and what will be rejected by the organism and can accommodate heterogeneity—entities from various origins. Immunogenicity is the criterion of inclusion for the organism and acts as the distinguishing factor of entities that stick together as constituents of the organism from entities that are excluded (Pradeu 2010, 253). Pradeu proposes that physiology, a non-evolutionary branch of biology, informs questions of individuality. The precision of his account concerning boundary delineation is certainly an advantage, but it is not clear how this concerns individuals in selection specifically.

2.7.2 Physiology and Evolutionary Individuality: Advantages and Disadvantages

Pradeu argues that physiology, a non-evolutionary branch of biology, informs questions of individuality. If functional integration is an integral component of individuals in the biological domain, Pradeu does well in answering Hull’s challenge by articulating a physiological criterion more precise than the vague functional integration criterion traditionally associated with physiology.³⁰ One major selling feature is that the physiological field of immunology can

²⁹ Throughout his book, Pradeu touches on the idea of plants having systemic responses analogous to that of an organism’s immune system.

³⁰ Specifically, Pradeu thinks that physiology can inform questions of biological *identity*, and what constitutes an entity’s identity is both individuality and uniqueness. In other words, a biological entity’s identity is determined by its ability to be individuated by identifying its boundaries, as well as its unique qualities that distinguish it from other individuated entities. And so, individuality is merely one aspect of biological identity.

successfully identify organismal individuality (2012, 264). In other words, immunology makes sense of why organisms are often seen as paradigm individuals. For Pradeu, the organism is the most well-defined individual (220). The understanding of immunological function helps one to identify the spatial boundaries of an entity, and how those boundaries are maintained over time (4, 8). Finally, it also informs how inclusion and exclusion occurs in an otherwise heterogeneous array of potential constituents. This helps in the basic individuation or carving that concerns the biological domain more generally. That is certainly an advantage, but does this tell us anything about *evolutionary* individuality?

Pradeu proposes that the Theory of Physiology by Immunology (TPI) plays a significant and necessary role in determining evolutionary individuality. This does not necessarily mean that his non-evolutionary, physiological approach is sufficient for the task. We learn from Lewontin (1970) that at minimum individuals in selection need some way to pass on traits for populations to evolve by selection. And so, more than physiology alone is needed to determine the nature of the sorts of individuals relevant to evolutionary theory. If correct, this renders Pradeu's immunological approach to individuality as complementary. It provides a resource for explaining how even evolutionary individuals maintain boundaries and functional integration. That is, any view of evolutionary individuality that cites a "bounded-integration" criterion will benefit from the precise formulation of immunology that is found in Pradeu's work. That said, Pradeu's account is certainly not sufficient to determine the nature of evolutionary individuality.

There may be two identifiable concerns with an immunological account of individuals in selection. First, notice that an account of the emergence of new individuals is available for Hull's replicator-interactor theory of individuality, as well as for Godfrey-Smith's Darwinian individuality. On the one hand, new replicators and interactors can emerge when the appropriate

replicating processes take place. On the other hand, new Darwinian individuals can emerge when lower level selection is suppressed, which yields a new integrative unit. In both cases, new token individuals are identified when the life cycle begins anew. However, Pradeu points out that the immune system plays a role in the control and suppression of emerging variants within an individual organism (261). This *prevents* the proliferation of lower level competition, such as particular cells replicating without control, etc. Pradeu can account for the *maintenance* of individuals, but says nothing about how new individuals come into existence. This is important in order to satisfy Lewontin's general constraint of heritability—offspring must be produced that inherit traits from their ancestors. Immunogenicity merely prevents the breakdown of an individual, but does not necessarily create a new one (McConwell 2015b). This suggests that although TPI provides insight into the feature of functional integration associated with biological individuality generally, it may not be enough for evolutionary individuality in particular.

The above objection is related to a second and more general concern. That is, Pradeu's theory appears to delineate individuals, but no clear role for individuals *in selection* is identified—why does selection act on only immunological individuals? The problem of evolutionary individuality is about the nature of individuals in selection. But purely physiological accounts of individuality say nothing about why certain sorts of individuals are in the purview of selection. They might individuate token individuals from one another, but there is no explanation for why selection acts on those individuals. And so, we understand *how* evolutionary individuals as immunological individuals are delineated, but not *why* they are visible to selection. Pradeu certainly anticipates this issue, which is likely why his main message is that a physio-immunological criterion *coupled with* TENS is better for delineating individuals in selection than TENS alone (see Pradeu 2012, 256). He maintains that there is an explicit

connection between immunology and evolutionary biology in terms of individuals, but such a connection needs further development (2012, 259-60, 268).

A lot of ground has been covered up to this point so a recap is in order before moving to the next section. Recall that Lewontin and Buss laid the groundwork for contemporary views of evolutionary individuality. Lewontin identifies that selection acts on individuals: variation, differential fitness, and heritability are integral features of individuals in selection. While Hull identifies two individuals required for selection—replicators and interactors, Godfrey-Smith thinks that a certain sort of reproduction is essential to satisfying Lewontin's condition of heritability. Pradeu's view, although informative, is merely complementary as it cannot identify the means for the emergence of new individuals that inherit the traits of previous generations of individuals. The next section of this chapter addresses an account of individuality that reflects on the views of Godfrey-Smith and Hull in addition to providing a new view of evolutionary individuality.

2.8 Ereshefsky and Pedroso: Biofilms as a Test for Hull and Godfrey-Smith

Ereshefsky and Pedroso (2013, 2015, 2016) use a case study of biofilms to test Hull's and Godfrey-Smith's accounts of individuals in selection. Ultimately, they demonstrate that biofilms make good candidates for individuals in selection despite violating Godfrey-Smith's specific criteria for Darwinian individuality. Inspired by Hull, their interactor theory of evolutionary individuality can accommodate biofilms as individuals in addition to other tough cases such as the symbiotic relationships noted throughout this chapter. In what follows, I will outline Ereshefsky and Pedroso's test case of biofilms used to assess the individuality accounts of Hull and Godfrey-Smith. Thereafter, I will discuss their positive view of individuality.

Biofilms are singular or multispecies communities of microorganisms set in an extracellular polymeric substance that holds the cells together (E&P 2013, 331-2). Biofilms range from plaque attached to teeth surfaces to free floating collectives of bacterial cells in rivers and streams. Cells gather together and through this co-aggregation, which sometimes occurs in a sequential process, biofilms are able to live in places that the individual cells could not survive in alone (333). The extracellular substance facilitates both communication and the exchange of genetic material. Communication between cells is achieved through chemical signalling known as quorum sensing, and often through cellular interaction, such as how the actions of the different cells produce a beneficial environment for the entire biofilm. The exchange of genetic material occurs by lateral gene transfer (LGT): the bacterial cells can either take up free DNA from the environment, known as transformation, or LGT can take place through conjugation, which occurs via cell to cell bridges that move genetic material (2013, 334). Ereshefsky and Pedroso maintain that biofilms are good candidates for individuals.

2.8.1 Biofilms Violate Godfrey-Smith's Account of Individuality, but satisfy Hull's

Notably, biofilms do not have clearly delineated parent-offspring relationships (2013, 331).³¹ Recall that Godfrey-Smith's account of evolutionary individuality begins with Lewontin's (1970, 1983) recipe for natural selection: In order for a population to evolve, individuals of that population must exhibit various phenotypes that result in differential fitness, and in turn, those traits are inherited by subsequent generations. Godfrey-Smith identifies a very specific sort of reproduction as required by the mechanism for such inheritance. That is,

³¹ Originally, Ereshefsky and Pedroso proposed that biofilms do not have reproductive bottlenecks in addition to lacking distinct parent offspring lineages and significant reproductive division of labour (2013, 331). However, upon further review, they concede that biofilms may be considered to have bottlenecks, such as when a small piece of a biofilm breaks off to form its own biofilm (2015, 10129).

individuals in selection must exhibit a significant reproductive division of labour (e.g. germ line cells) and ultimately reproduce in a way that includes the existence of reproductive bottlenecks and the formation of linear parent-offspring lineages. Furthermore, Godfrey-Smith's account accommodates multi-species individuals only if the reproductive lineages of the composite species run in tandem with one another, such as aphid-*Buchnera* symbiosis. However, biofilms do not fulfill that condition—their parent-offspring lineages resemble a complicated network in which one cell can have multiple parents, rather than a vertical, traceable lineage. But how do biofilms fare on Hull's replicator-interactor view?

According to Hull, generally individuals must be spatio-temporally restricted, but selection requires two types of individuals—replicators and interactors. Hull's account does not require the specific sort of reproduction emphasized by Godfrey-Smith. Replicators pass on their structure largely intact from generation to generation, such as genes. Interactors are entities that act as a cohesive whole with their environment, such as organisms, and they often contain replicators. The question is whether biofilms satisfy these requirements. Biofilms have life cycles which begin and end, so they are spatio-temporally located (E&P 2013, 342). Although biofilms are internally integrated and delineated from the environment, not all strains of bacterial species make it into every instance of a biofilm, so they are not replicators (343). But are biofilms interactors? Interactors are needed to change the distribution of replicators through selection—they ensure that replication is differential (343-44). Interactors are cohesive wholes, whose interaction with the environment has a unitary effect on its constituent replicators (ibid). Ereshefsky and Pedroso point out that “if ‘unitary effect’ means that the failure or success of a biofilm affects the survivalship of its constituent cells (replicators) in a uniform way, the

biofilms meet this condition” by providing defense against antimicrobial agents (344).³² The ambiguity of ‘unitary effect’ is one example of how the interactor account needs more precision, but nevertheless biofilms appear to satisfy Hull’s account of interactors.

Ereshefsky and Pedroso provide five additional supportive points for the consideration of biofilms as interactors (2015). Biofilms exhibit many characteristics associated with evolutionary individuality. First, they are internally integrated and delineated from the environment: cells of biofilms bond through aggregation, they are bounded by the extracellular matrix and they communicate via quorum sensing, there is an exchange of genetic material through LGT, and finally, they exhibit cooperative measures. Second, there is also division of labour and coordination among parts since different colonizers perform different functions. Third, there is cooperation among the parts, such as the production of public goods, as well as cheater control (2015, 10127). Biofilms also appear to be the bearer of adaptations, which exist at the level of the biofilm, such as resistance to antimicrobial agents and metabolic interactions like the digestion of nutrients that benefit the entire biofilm (ibid). Finally, there is a transmission of traits between generations of individual biofilms: biofilm level adaptations are passed on from generation to generation, such as quorum sensing systems, aggregation patterns, cooperative behaviour and more (2015, 10128).

The upshot of the list above is that if biofilms are indeed good candidates for evolutionary individuality, then this suggests that reproduction, at least as defined by Godfrey-Smith, is not necessary for evolutionary individuality. “Evolutionary individuality is achieved

³² The extracellular polymeric substance of biofilms contains molecules which prevent antimicrobial agents from entering the biofilm, and the biofilm itself provides shelter for the bacterial cells in environments such as rivers (E&P 2013, 344-45).

through other means than often-cited reproductive processes” (2015, 10128). And if biofilms are evolutionary individuals, then the genetic homogeneity requirement implied by Godfrey-Smit’s view should be dropped too. Multi-species consortia are often entertained as possible individuals in selection, but typically with constraints placed upon them, such as the requirement that the different reproductive lineages run in tandem. Or they are marginalized as quasi-individuals on some spectrum or scale. But if we consider biofilms as individuals, then parent-offspring lineages of individuals allow for the sort of complicated networks of lineages we see in those cases (2015, 10128).³³

By making the case for biofilms as evolutionary individuals, Ereshefsky and Pedroso articulate a strong critique of Godfrey-Smith’s requirements for individuals in selection. They also highlight virtues of Hull’s view. As such, they use Hull’s account of evolutionary individuality as a starting point to develop a more precise interactor theory of individuality. There are three parts to their positive view: First they unpack the notions of cohesion and unitary effect. This is followed by an assessment of the mechanisms for trait transmission and suggestions for accounts of evolutionary individuality more generally.

2.8.2 Ereshefsky and Pedroso’s Interactor Theory of Evolutionary Individuality

The imprecision of Hull’s interactor view is evident with regards to his notion of cohesion as a requirement of individuals, who as interactors work as a cohesive whole in contact with the environment. Does this cohesiveness mean the causal interaction among the parts of individuals? Or do the parts just happen to act in a unitary fashion (2013, 341)? Ereshefsky and Pedroso argue that biofilms are more than just mere groups; the causal interaction among their

³³ Ereshefsky and Pedroso address the objection that biofilms are ecological communities. Biofilms are not ecological communities because they exchange genetic content—they facilitate defense against threats, digest nutrients and communicate, and so they are more highly organized than ecological units (2016, 108).

parts renders biofilms functionally organized systems (344). Co-aggregation and communication through quorum sensing facilitate the cohesiveness of the whole biofilm, which yields a level of interaction that surpasses mere ecological groups (345).³⁴ The outcomes, such as defense against anti-microbial agents, are due to cells causally interacting and not mere aggregative effects.

The second condition for an entity to be an interactor individual is that its interaction must have a unitary effect on the interactor's constituent replicators. As mentioned above, 'unitary effect' is a vague notion. As Ereshefsky and Pedroso maintain, if 'unitary effect' means that biofilm survival means that all constituent cells survive, then biofilms satisfy the condition (2013, 344). They introduce the idea that interaction could be due to external forces (2016, 114). For example, the variation of cheater cells and non-cheater cells is caused by environmental forces—biofilms with more cheater cells produce less public goods, which fares worse for the entire biofilm (115). Biofilms have the features of evolutionary individuals; they contain replicators (genes and cells) and the biofilms interaction with the environment has a unitary effect on those replicators (2013, 332). With both replicators and interactors available, selection can occur.

Lewontin's conditions for selection include heritability, so there must be some way for a new individual to inherit phenotypic traits from ancestral individuals. Trait transmission fidelity is essential for evolutionary individuality, but the particular mechanism that transmits traits is not. Modes of trait transmission are themselves products of evolution (2015, 10129). Reproduction is cited as the mechanism of transmission, but narrow accounts of reproduction that exclude multiple consortia from proper trait transmission that evolutionary individuals

³⁴ Biofilm interactions are also more numerous than symbiotic interactions (ibid, 113).

engage in are suspect. This is especially because biofilms appear to have varying heritable traits that make a difference to their fitness (2016, 117). They exhibit a number of adaptive traits across biofilm generations such as quorum sensing and mutualistic interaction (ibid). There are mechanisms that regulate how biofilms aggregate and which cells are transmitted—this is what causes variation and fitness differentials among biofilms (ibid).³⁵ LGT is the biofilm mechanism for inheritance. They cite Griesemer (2000) as having a viable account of reproduction due to the emphasis on material overlap that confers the capacity to develop. This means that the reproduced entities must have the capacity to develop life cycles in addition to maintaining a genealogical relationship between parents and offspring (E&P 2015, 10129).

An important lesson noted by Ereshefsky and Pedroso is that the existence of highly integrated multi-species consortia, such as biofilms, aphid-*Buchnera*, squid-*Vibrio*, etc. suggests that a more inclusive account of individuality is needed (2015, 10130). They also call for an account of individuality that is sufficiently open-ended enough to capture the contingent nature of individuality. Making sense of what the contingent nature of individuality means will be the point of focus in Chapters 3 and 4. Again, since modes of trait transmission are evolutionary outcomes, they are still likely to evolve. Ereshefsky and Pedroso suggest that individuals in selection may be nested—they may be both contained in and comprised of more or less inclusive individuals, respectively (2015, 10131). A difference between Hull and Ereshefsky and Pedroso's view is that while Hull utilizes a replicator-interactor framework for selection, Ereshefsky and Pedroso focus on further developing interactor theory alone. Ereshefsky and Pedroso, however, are not the only ones sympathetic to Hull's account.

³⁵ Is aggregation a form of reproduction? Ereshefsky and Pedroso leave the question open.

Turning to our next account of evolutionary individuality, Dupré and O'Malley (2009) also find Hull's account favourable. They discuss individuals in selection within the greater context of a definition for life. The aim is to find a highly diverse version of individuality that does not succumb to the issues of, for example, focusing on narrow criteria such as Godfrey-Smith's version of reproduction. As we move forward to the few final sections of this literary landscape chapter, the proposed criteria of individuality cast an even wider net to capture the diversity in evolutionary individuality.

2.9 Dupré and O'Malley on Individuality: Metabolism Matters

Dupré and O'Malley (2009) take a broader approach to individuality by starting their inquiry with what it takes to consider matter as living. They approach the issue from a microbial perspective and do not focus on larger animal or plant life (2009, 3). To achieve a broad definition of life the definition itself must be minimal to include all living entities. From there one can then extrapolate a conception of individuality—in the sense of both general biological individuals and those individuals relevant to selection. The following tracks their progression from thinking about life to thinking about individuality.

Dupré and O'Malley aim to rectify a tension between reproduction and metabolism that is evident in thinking about life (2009, 2). That is, life is typically viewed as either the capacity to form lineages by replication or the ability to exist as a metabolically self-sustained whole (ibid). The former classifies viruses as alive, while the latter does not. They propose that matter is alive when the entities forming reproductive lineages are involved in metabolic processes. Often reproduction is associated with an entity's capacity to initiate and complete its own reproduction—a sort of "genetic autonomy" (2009, 10). But Dupré and O'Malley point out that other means of an entity reproducing itself, such as cell division or replication by external means

(re: Godfrey-Smith's scaffolding reproducers), reveal that the nature of reproduction is far from clear (10, 5-6). They broadly define reproduction as "the capacity of entities to make more of themselves" and as one of the things that most living entities fundamentally do (12). Alternatively, "metabolism" is a basic characteristic of living systems... [and it is] typically a collaborative activity" (13). Metabolism refers to the "transformative biochemical reactions that sustain life processes" or energy transformation (2, 12). In their account, metabolism as an internal activity can be engaged in autonomously or collaboratively through interactions with other entities (3, 12). They see metabolism as a generally collaborative enterprise.

2.9.1 The Feature of Collaboration as a Marker of New Individuality

Before delving into what collaboration entails, I must point out that one central aim of the work by Dupré and O'Malley concerning individuality is to understand the nature of entities formed by what are usually conceived of as separate individuals. This process is the emergence of a new individual. The emergence of new individuals is an important issue for biological individuality, which is why I have dedicated chapter 5 to that very topic. Often the issue of biological individuation is addressed by investigating how new individuals come to be. To understand the formation of a new individual is thought to unveil markers of individuality more generally. The motivation is that if we can understand how a new individual begins, then we will likely better understand the nature of individuals. According to Dupré and O'Malley, the emergence of a new individual is due to the collaboration of less inclusive entities.

Collaboration is viewed as a point in a continuum between cooperation and competition (or selfishness). As mentioned, they view metabolism as a "collaborative affair," but they also see the notion of selfish entities in competition with one another as overemphasized in evolutionary theory (2009, 2). Traditionally conceived, biological individuals are systems

elaborated around unique genomes, but we have seen how the case of multi-species consortia challenge the individuality criterion of genetic homogeneity. Dupré and O'Malley argue that this criterion cannot account for the collaborative and evolutionarily advantageous behaviour of symbionts, such as the mutual benefits evident in ant-*Acacia* consortium (Clement et al. 2008).³⁶ They argue that discussions of life and organization must take into account that symbiotic relationships are everywhere (2009, 12). Such mutualistic collaboration between biological entities blur the distinction between individual organisms and groups of individuals (ibid).

Specifically, Dupré and O'Malley define collaboration as the “interactions between components of a system that lead to different degrees of stability, maintenance, or transformation of that system” (2). It includes both cooperative and competitive activities. Functional wholeness is a characteristic of collaborative interactions involving diverse entities that comprise an individual (11). As an example, they briefly discuss the case of biofilms as they have “well-defined cell organization and a functional division of labour” (ibid). This includes metabolic coordination, and as previously mentioned, biofilm-level defense efforts in addition to coordination of movement, growth and reproduction. Moreover, there is cheater control, which suppresses a cheater cell's autonomy and competition among cells (ibid). Dupré and O'Malley comment on the interactor account outlined in Hull's and Ereshefsky and Pedroso's view previously discussed; interactors can include complex systems involving collaboration of many highly diverse lineage-forming entities. This emphasizes the importance of symbioses in selection (ibid, 13).

³⁶ The ant-*Acacia* mutualism is a symbiotic relationship that is not transmitted vertically—the interaction between ants and *Acacia* is re-established with every generation (Clement, *et al.* 2008, 954). *P. ferrugineus* ants defend *Acacia* trees from other harmful insects and the trees provide food sources.

2.9.2 Individuals in Selection

Dupré and O'Malley propose that individuals in selection are collaborations of many different lineage-forming entities (2009, 14). This form of interactor, they propose, is the most fundamental unit of selection. The parts of interactor individuals organize and collaborate with one another to achieve metabolic and reproductive success together. Collaboration has been largely ignored and this is a consequence of focusing solely on models of evolution that emphasize competition. "Microbial or microbe-like entities...[are] a very diverse group of things [that] both reproduce and participate in metabolic systems" (3). The diverse biological entities that collaborate in the way just described above, yield boundaries that are flexible and unfixed (14). At the very minimum, a biological individual will be both metabolic in nature and part of a reproductive lineage of metabolic individuals.

2.9.3 A Microbial Point of View

O'Malley in *Philosophy of Microbiology* (2014) further develops the collaborative-metabolic view of individuality. Her claim is that philosophers ought to start with the microbial world when analyzing biological individuality (2014, 131). In this world one finds collaborative interactions that yield the functional wholeness so characteristic of metabolic individuality, such as the case of biofilms. Metabolism as an important attribute of individuals is a more common and widespread biological phenomenon compared to, for example, the reproduction of large eukaryotic metazoa. The metabolic view of individuality is "an ecological point of view" that emphasizes the interactions between entities that comprise an individual (116). O'Malley is critical of Godfrey-Smith's view because most collectives barely meet his criteria for Darwinian individuals and, therefore, may not be selected upon (ibid). She points out that Godfrey-Smith starts his analysis with features (e.g. germ-soma distinction, reproductive bottleneck) that are

distinctive of humans and other biological entities found in the macrobial world (160). This is problematic given the ubiquity of microbial life.³⁷

One upshot is that we cannot assume traditional organisms (eukaryotic metazoa) as the only biological individuals in selection (2009, 2). The criteria of metabolically collaborative interactions and the reproduction of this interactive unit, reaches much further than members of Metazoa as the only individuals in selection. At first blush, one noticeable issue is that interactors, at least in the way discussed so far, are more than just parts that interact with one another. Interactors must *as a whole unit* interact with their environment and this interaction with the environment should have a unitary effect on the interactor's constituents. However, there are likely multiple means by which microbes obtain the energy they need from environmental nutrients.

Up to this point, Hull, Ereshefsky and Pedroso, as well as Dupré and O'Malley, all highlight the promise of interactor theory for evolutionary individuality. It appropriately accommodates complex symbiotic relationships that are often used as counterexamples to criteria for evolutionary individuality. Mutualisms that are not transmitted vertically, such as the squid-*Vibrio*, are problematic for accounts of individuality that require the reproductive lineages of participating entities to run in tandem. Interactor theories do not fall prey to the same objections. Huneman (2014a, b), the final account of individuality for this landscape chapter, focuses precisely on the concept of interaction. He criticizes the focus on *evolutionary* individuality and calls for a more general account of non-evolutionary biological individuality.

³⁷ Notably, Dupré (2014) distinguishes his later view from O'Malley in a more radically pluralist and processual view of individuality. This will be discussed in the final section of this chapter.

So far, I have outlined numerous views of evolutionary individuality though, so before turning to Huneman I must address a view that aims to reconcile the previous accounts.

2.10 Clarke's Multiple-realizability: Policing and Demarcation Mechanisms

Ellen Clarke in “The Multiple Realizability of Individuals” is also concerned with delineating the biological units that participate in evolutionary processes (Clarke 2013, 413). She acknowledges that there are different criteria for individuals such that each “generate non-coextensive classes of biological individuals,” which is demonstrated by some of the accounts described above (415). For example, recall that Godfrey-Smith's criteria of reproductive bottle necks and germ-line separation do not classify the sterile mule as an evolutionary individual, whereas an immunological account like Pradeu's can. Clarke seeks to reconcile different views and argues for the possibility of a “unification of existing definitions” (418, 429). Essentially, Clarke proposes that existing definitions should be reformulated so that they are treated as describing possible mechanisms that fulfill necessary functional roles—policing and demarcation (428). She contends that the functions of policing and demarcating can be realized through multiple mediums. I will briefly discuss each in turn.

Policing views of individuality emphasize what is required for suppression of lower-level selection without giving a particular account of the mechanism that does this (421). They limit the capacity for that object to undergo what Clarke calls “within-object” selection (428). For example, a specialized germ-line mediates internal conflict and reduces competition and therefore the capacity for that collective's ability to undergo selection. One worry is that the notion of policing can only be understood within the context of collective organisms because it entails the prevention of selection at the lower level. But one could also think of it as acting on collections of living parts (433).

Alternatively, demarcating mechanisms function differently. Demarcation mechanisms emphasize physio-spatial boundaries, such as cell walls or immunogenic responses. A demarcation mechanism is any mechanism that increases or maintains the capacity of a biological entity to undergo what Clarke calls “between-object” selection (424). Demarcated boundaries are important because they protect an individual’s capacity to undergo selection (426). The idea here is that when external entities compromise the integrity of an individual, that individual’s delineation from what is normally “outside” of it becomes blurred.

Individuating mechanisms can be either policing or demarcating, but individuals in selection must possess mechanisms which fulfill both functional roles (427). And so, Clarke thinks that the competing accounts of individuation can be construed as different mechanisms which are functionally equivalent—they serve to identify the levels at which selection is possible and support the idea that individuation can be achieved multiple ways. For Clarke, individuality plays a functional role as a theoretical object within evolutionary theory. However, as inclusive as her view appears, according to Huneman (2014a, 2014b) it is not general enough. Clarke states that “a biological individual must have a positive capacity to undergo natural selection at its own level” (2013, 423). But this is exactly what Huneman disagrees with. He concedes that the notion of individuality is a theory dependent notion, but he is critical of the attention to individuals in evolutionary theory alone (2014b, 374).

In the next and final account of individuality, we see how Huneman highlights the relevance of interaction for a concept of individuality more broadly construed. This goes beyond the Hullean-inspired interactor-type theories developed by Ereshefsky and Pedroso, as well as Dupré and O’Malley. In devising a more general account of biological individuality in terms of interaction Huneman articulates a critique of the evolutionary endeavour.

2.11 Huneman's Critique from Ecology: Weak and Strong Individuality

Huneman (2014a, 2014b) thinks that the evolutionary concept of individuality is too strong because many other biological individuals do not fall under that category. This is a problem if we want a concept of individuality for non-evolutionary theories, such as ecology. Huneman proposes that ecological communities are not arbitrary sets of things; the interactions within the community are stronger than interactions between that community and the external environment. What is of particular interest for the purposes of a dissertation focused on evolutionary individuality is Huneman's critique of evolutionary individuality, as well as his notion of interaction.

Huneman takes issue with extrapolating a general notion of biological individuality from more localized accounts of individuals in selection. He criticizes Hullean theories of individuality because they imply that a collective is an individual, only if it is a unit of selection. Because higher level selection of communities and ecosystems is problematic, extending the individuality concept beyond evolutionary biology proves to be a difficult task (2014a, 364). He thinks that interaction as a feature of individuality can explain the differences between individuals in selection and other individuals. Huneman develops what he refers to as strong and weak concepts of individuality. The difference between those concepts is the degree of interaction between entities within a collective being greater than their interactions with entities outside of the collective (2014b, 378). The strong concept of biological individuality includes individuals in selection, whereas a weaker concept can account for ecological communities because it does not require selection (*ibid*). Both concepts are defined in terms of degrees of interaction.

2.11.1 Huneman's Notion of Interaction

For Huneman, interactions are important because “within a theoretical domain [they allow] us to partition the assemblies into ‘individuals’ and ‘non-individuals’” (2014a, 361). Strong and weak individuality are differentiated by the strength and weakness of interactions between entities. And so, these interactions exist within a set of parameters formally defined in terms of how likely those interactions are to occur. There are different kinds of interactions. An example of mutualistic interactions is the ant-*Acacia* consortium,³⁸ whereas antagonistic interactions tend to be seen in situations of predation and competition. There can be highly intimate mutualisms, such as aphid-*Buchnera*, and mutualisms with lower intimacy (2014a 370, 2014b 379). Finally, ecosystem-engineering interactions involve a larger number of organisms from many species over a lengthy timescale through generations. The point here is that mutualistic interactions can function in different ways.

Although the final discussions of Clarke (2013) and Huneman (2014a, b) are brief in comparison to the previous sections, I introduce them as interesting ways in which one might approach and critique the problem of evolutionary individuality. The relationship between the claims I make in Chapters 3 with Clarke's view, as well as some objections inspired by her work, will be addressed in Chapter 4. Additionally, given that interaction is frequently discussed as a component of evolutionary individuality, Huneman's account demonstrates the reach of interaction as a criterion for non-evolutionary biological individuals. Certainly, this is an avenue for inquiry, but for my purposes the identification of non-evolutionary biological individuals provides a nice contrast for the task at hand: A focus on individuals in selection.

³⁸ See footnote on page 51.

2.12 A Brief Summary and Comparison of Evolutionary Individuality Accounts

A lot of ground has been covered. Here is a one-stop look at the history of individuality as discussed in this chapter:

Buss: Provides a model of the biological world and places individuals on various levels in the nested hierarchy of life.

Lewontin: Constrains the boundaries of the evolutionary concept by providing a recipe for evolution by natural selection, namely, variation, differential fitness, and heredity. Individuals in an evolving population must exhibit these features. Selection acts on individuals.

Hull: Proposes that two types of individuals are required for selection to occur: replicators and interactors. Replicators pass on their structure from generation to generation largely intact. Interactors cohesively interact with the environment in a way that has a unitary effect on their constituent replicators.

Godfrey-Smith: Distinguishes between metabolic organisms and reproducing Darwinian individuals: the former need not be individuals in selection. Darwinian individuals engage in the sort of reproduction that includes reproductive bottlenecks, germ lines, and integration via labour specialization.

Pradeu: Thinks that evolutionary biology is not enough to account for individuals. Physiology by immunology helps to delineate boundaries of individuals. Boundaries are identified by immunogenic responses to entities that disrupt the usual continuity of interactions within and without the collective unit.

Ereshefsky and Pedroso: Provide a critique of Godfrey-Smith's view with the case of biofilms: reproduction as defined by Godfrey-Smith is not required for individuality. Alternatively, they articulate a more precise Hullean-inspired interactor theory by formulating the notions of unitary

effect and cohesion as survivability of constituents and causal interaction, respectively. They point out that there may be other trait transmission mechanisms besides narrow views of reproduction that satisfy the heredity requirement for individuals in selection.

Dupré and O'Malley: Begin by framing the problem of individuality within the context of life. They aim to reconcile the tension between reproductive and metabolic views of both life and individuality. Evolutionary individuality involves the metabolic collaboration of many different lineage forming entities.

Clarke: Attempts to unify different views concerning evolutionary individuality, and proposes that evolutionary individuals are due to both policing (i.e. suppression of lower level selection) and demarcation (i.e. boundary delineation) mechanisms that can be realized multiple ways. Evolutionary individuality is a theoretical object within evolutionary theory that plays a functional role.

Huneman: Provides a critique from ecology about the evolutionary individuality concept and thinks that we need to discuss the notion of biological individuality more generally. Evolutionary individuals and other biological individuals (i.e. communities) can be accounted for in terms of the strength of interaction within the collective being greater than the interaction of that collective with the environment.

There are some striking comparisons to be made concerning the above views of evolutionary individuality. For example, there are instances of cross-classification when different views pick out different entities as individuals in selection. Whereas the sterile mule is an evolutionary individual for Pradeu's immunological view, that organism is not an individual in selection for Godfrey-Smith because it cannot reproduce. Additionally, both Huneman and Godfrey-Smith see individuality within a single set of parameters and place individuals on a

continuum that varies by degrees. Although arguably for Huneman, as well as for Pradeu, individual organisms will be the most well-developed and organized evolutionary individuals, according to Godfrey-Smith organisms need not be individuals in selection. Moreover, while Pradeu's immunological perspective of individuality focuses on boundary delineation, Godfrey-Smith's reproductive view highlights how new individuals emerge (i.e. through reproduction and de-Darwinization). And finally, whereas Clarke seeks a unification schema, Ereshefsky and Pedroso, as well as Dupré and O'Malley, call for a more pluralistic stance concerning the sorts of individuals in selection. Although the foregoing highlights some very important similarities and differences between contemporary accounts of evolutionary individuality, I will not further develop all contrasts here. However, there is one pertinent issue, which speaks to all the accounts, that requires attention.

2.13 A First Glance at Individuality Pluralism

The plurality of individuality definitions is often seen as a problem in need of reconciliation, as exemplified by Clarke's (2013) unification schema. Clarke aims at "a monistic account of [individuality] by identifying a functional commonality which underlies the existing plurality of views" (2013, 429). The question I intend to press in this dissertation, however, is whether a monistic view of evolutionary individuality ought to be the default position. Although there tends to be agreement that there are different types of biological individuals, there is disagreement over whether we should be pluralists about evolutionary individuality specifically. The question here is whether there is only one type of evolutionary individuality or multiple types. If the latter is true, then currently proposed solutions to the individuality problem are misguided. Rather than finding *the* nature of evolutionary individuality, the possibility of multiple types of evolutionary individuals suggests a shift in focus and will affect the way we

think about evolution itself. The following provides examples from section 2.5 through 2.11 relevant to the monism-pluralism debate.

As mentioned, one commonality between the views of Huneman and Godfrey-Smith is that individuality comes in degrees within a particular set of parameters, despite their different focuses on interaction and reproduction, respectively. Individuality on a continuum is supposed to allow for degrees of blurriness between boundaries of different individuals. However, it is not clear whether these views exemplify a pluralism about evolutionary individuality. In order for biological entities to count as individuals, they must fall within the set of parameters given to confine the spectrums in either case. In each case, although there may be varying degrees of evolutionary individuality in terms of interaction or reproduction, there is still only one type of individual in selection for Huneman and Godfrey-Smith.

Additionally, recall that for Dupré and O'Malley, there are diverse biological entities that collaborate metabolically, which yields boundaries that are flexible and unfixed (2009, 14). However, Dupré in "Animalism and the Persistence of Human Organisms"(2014) takes this further and introduces the notion of a processual view of individuals with an anti-realist flavour. He says, "distinguishing individuals within functioning biological systems composed of multiple intertwined lineages from cells is far from trivial, and may be done in different ways" (11). He identifies how the interdependence between cells forming different lineages causes the difficulty of discerning boundaries of individuals (ibid). Dupré argues that the best way to understand these multiply-intertwined cellular lineages is through a hierarchy of processes (12). From the notion of layered biological complexity, he argues the following is a natural conclusion: To distinguish individuals is *not* to track a natural category in nature, rather it is to satisfy practical or theoretical purposes (14). Instead of things, individuals are defined by, and sustained with,

processes such as metabolic processes (16). And so, individuality can be determined by a plurality of methodologies and theories. Dupré infers from the flexible and unfixed boundaries of individuals the following: The delineation of individuals is not to track natural individuations, rather the notion of individuality is merely a theoretical or practical notion. I think this goes slightly too far: It does not follow that individuation is a trivial human concoction from the acknowledgment of changing patterns in nature. Those patterns could still be *real patterns*, at least for some length of time (see Dennett's 1991 'Real Patterns'). Regardless, in following chapters, I make the case for evolutionary individuality pluralism. But first I begin to scratch the surface of exactly what that involves.

2.13.1 A Motivation for Achieving Individuality Pluralism

One might wonder what motivates the multiplicity of definitions for evolutionary individuality. The intrinsic heterogeneity of individuals in biology may be partly responsible (Wilson and Barker 2017).³⁹ As mentioned, despite some hesitation to accept the idea of many viable definitions for one kind of individual, there *does* seem to be a general acceptance of pluralism about individuals in biology in the sense that there are many kinds of biological individuals. For example, Godfrey-Smith thinks there may be no fundamental or “most-real” individuals in biology and that the biological individual may just be an object that some part of biology recognizes as worth describing (2013, 19). Additionally, Ereshefsky and Pedroso maintain that not only are there different sorts of individuals, such as chemical and physical, but

³⁹ A good contrast for the heterogeneity of and within individuals in biology is how quantum individuals are treated in physics. There is a metaphysical issue with distinguishing between members of a certain kind of quantum individual, such as the electron. Individuating particles that all belong in the electron category is a difficult task because they are so similar to one another. Alternatively, biological individuals are intrinsically heterogeneous and have many possible individuating features so it becomes difficult to delineate which biological individuals belong in a certain category.

also that there are different sorts of biological individuals (2013). These could be individuals in natural selection, in systematics, as well as metabolic individuals, immunological individuals, reproductive individuals, etc. This sortal view of individuality inspired by Wiggins (2001) suggests there are multiple theories to determine multiple kinds of biological individuals (Ereshefsky and Pedroso 2016, 104).⁴⁰ For example, while individuals in selection require processes that allow variation to be passed on, individuals in systematics require processes that cause them to be distinct lineages. So, we have multiple types of biological individuals, but what about pluralism for evolutionary individuality specifically?

2.13.2 Can We Be Pluralists About Evolutionary Individuality?

A dedication to finding *the* (rather than *a*) set of conditions for evolutionary individuality does not necessarily involve an acceptance of multiple, mostly incompatible, definitions. To be a monist concerning evolutionary individuality concerns only one type of evolutionary individual with only one corresponding account of individuality that identifies which entities are tokens of that type. But to be a pluralist about evolutionary individuality need not involve the acceptance of numerous incompatible accounts, rather a plurality of evolutionary individuality types warrants multiple accounts to capture that natural plurality.

Hull states that “there turns out to be no such thing as *the* scientific conception of *the* individual. Instead there are several different conceptions, depending on current theories” (1992, 180).⁴¹ Recall that he identifies two different types of individuals in selection: replicators and interactors. In developing a more precise account of interactor theory, Ereshefsky and Pedroso

⁴⁰ One exception is Pradeu (2010, 2012) who thinks that anything acted on by natural selection is a biological individual, which suggests that he thinks *all* biological individuals are just evolutionary ones, or perhaps more precisely evolutionary-immunological ones (2012, 255).

⁴¹ My emphasis on ‘*the*’ with italics.

push the notion of individuality pluralism further and claim that interactor theory can handle the various types of evolutionary individuality produced by evolution. They claim,

[Interactor theory] is sufficiently open-ended to capture the contingent nature of evolutionary individuality...we believe that the need for such an approach stems from the ongoing and open-ended nature of evolution, not from conceptual imprecision (2015, 10131).

This is an important point. Outcomes of evolution should inform what we take individuality to be. The production of evolutionary outcomes, however, often tells a story about how evolution unfolds. Given that my focus concerns *evolutionary* individuality, it makes sense to draw from a view about evolution itself. In the next chapter I introduce the Evolutionary Contingency Thesis. What the contingent nature of evolution means for evolutionary individuality is a central thesis of this dissertation. That is, I argue that the diversity of outcomes caused by evolutionary contingency yields a plurality of evolutionary individuality types. In the following chapters, I unpack that claim.

“Rarity has but one happy aspect—given enough time, it gets converted to fair frequency.”
—*Stephen J. Gould, Wonderful Life 1989, p. 62*

Chapter Three: The Evolutionary Contingency Thesis and Individuality Pluralism

In the previous chapter, I summarized the philosophical landscape of views concerning evolutionary individuality (Godfrey-Smith 2009, 2013, Dupré and O’Malley 2009, Ereshefsky and Pedroso 2013, 2015, Pradeu 2010, 2012, Clarke 2013, Huneman 2014a, b). Rather than argue for any particular account, I explore how evolutionary individuality is informed by a view about the nature of evolution itself. In this chapter I defend the view that individuality evolves contingently, and I identify two types of individuals in selection. The Evolutionary Contingency Thesis (ECT) is a view that emphasizes the role of contingency or dependency relations and chance as the hallmarks of evolution (Gould 1989, Beatty 2006a, b, Desjardins 2011a, b, Turner 2011a, b). If one accepts the contingent nature of evolution, then I argue that individuality pluralism makes sense. Not only does it make sense, but I also submit the bolder claim that evolutionary contingency yields ontological pluralism in the case of individuals. Section 3.1 outlines the notion of evolutionary contingency. Section 3.2 is an interlude—it provides a transition to thinking about individuality within the contingency framework. In Section 3.3, I apply ECT to evolutionary individuality. In this chapter, I end up with more than one type of evolutionary individuality, so the following chapter 4 investigates that pluralism further.

3.1 Evolutionary Contingency

Characterizing the structure of evolution and its contingent nature is a significant research programme, so I focus only on those features relevant to evolutionary individuality (Gould 1989, Beatty 2006a, b, Desjardin 2011a, b, Turner 2011a, b). John Beatty argued that evolution’s contingent nature makes sense of the non-lawlike status of biological generalizations, as well as

the plurality of mechanisms and theories biologists propose (1982, 1997). I argue that something analogous occurs for evolutionary individuality. With the aim to better understand the notion of evolutionary contingency, in this section I start with a famous disagreement between Gould (1989) and Conway Morris (2003) over the role of contingency in evolution. This is followed by a discussion of evolutionary contingency more recently, as well as Beatty's specific treatment of contingency within the context of laws and its relevance for evolutionary individuality.

3.1.1 The Famous Contingency Disagreement: Gould vs. Conway-Morris

It is best to start with a view Gould argued against.⁴² Simon Conway Morris, like Gould, studied the fossils of the Burgess Shale—a quarry located in the Canadian Rockies of British Columbia. It houses some of the earliest fossils from the Cambrian period around 570 million years ago. The fauna located in this quarry are of special interest because of the exceptional preservation of soft-part imprints that are otherwise usually obsolete. As Gould says, “the rare soft-bodied faunas of the fossil record are precious windows into the true range and diversity of ancient life” (1989, 24). But unlike Gould, Conway Morris (2003) argues that due to the nature of evolution, the existence of complex social and intelligent creatures like humans is inevitable.

The nature of evolution, according to Conway Morris, is convergent. He states, “convergence often reflects limited engineering solutions to particular problems” (2006, 826). Conway Morris is well known for accumulating numerous examples of evolutionary convergence.⁴³ Wings emerged for flight in birds, bats and insects. Fish and dolphins have both developed fins adaptable to swimming. Both the human eye and the octopus eye resemble the

⁴² Arguably, Gould used contingency to challenge evolutionary inevitability, in addition to panslectionism (see Beatty 2006, as well as the general structure of Gould's 2002 book). That is, Gould disliked emphasis on the exclusive role of natural selection in evolutionary change.

⁴³ Other publications by Conway Morris include “Creation and Evolutionary Convergence” (2012) and “Evolution: like any other science it is predictable” (2010).

function of a camera in important ways, yet humans and octopi have obvious differences because they belong to different phyla, chordates and mollusks, respectively. Convergence is important because it shows that adaptation is real. That is, evolution by selection will solve the same problem in similar ways across drastically different branches that diverged from a common ancestor, even as old as over 500 million years (ibid, 827). And when similar ways of adapting to environmental challenges occur over and over again, it seems as though the course of evolution is predictable; evolutionary outcomes will arise as long as the same conditions are met. Progress towards complexity is often associated with Conway Morris's view. Evolutionary history will not always matter because often traits that are selected for are evolutionary outcomes that converge—they can be analogously described in a way that highlights their functional similarities.⁴⁴ And so, the past makes no difference to these outcomes. Gould, however, did not agree with Conway Morris.

Gould (1989, 2002) argues that contingency, and not convergence, is the hallmark of evolution.⁴⁵ In studying the Burgess Shale, Gould noted that it contains fossils of more than 20 *Baupläne* designs. These are body plans or assemblages of morphological features that he took to distinguish different phyla. In his most popular book *Wonderful Life*, he notes that only four of the basic body plans survived (1989, 106). *Pikaia*, an ancient vertebrate found in the Burgess Shale, is potentially an ancient ancestor of humans—Gould argues that had *Pikaia* not survived,

⁴⁴ This is a criticism raised by Sterelny (2003): outcomes of evolution appear convergent depended on the description of that outcome being coarse or fine-grained. So perhaps the idea is that the more fine-grained the description, the less convergent the outcomes appear. Also see Currie (2012, 2013).

⁴⁵ Conway Morris does not think that contingency and convergence are necessarily opposing views as both are important in the history of life (2006, 826). He claims that the issue is how much more significant or frequent contingency is compared to convergence and vice versa. And Beatty (1997) argues in favour of theoretical pluralism in biology and illustrates how relative significance of theories is the issue and not necessarily which one theory best captures the entire domain. Arguably, the contingency vs. convergence debate is construed as one of relative significance—contingent outcomes are more significant (i.e. more frequent or common) than convergent ones.

along with a whole host of other events taking place in between the *Pikaia* and humans, humans would not have evolved. The existence of humans is *contingent* upon a very particular and sensitive trajectory of evolutionary history. Not only does human existence depend on this history, but coupled with chance-based factors, e.g. environmental disasters and the influences of stochastic processes such as mutation, human existence is a highly unlikely evolutionary outcome. To illustrate this point, Gould challenges his readers to consider the metaphor of replaying life's tape.

Rewind the tape of evolutionary history and let the tape run again to see if it looks anything like the original (1989, 48). If ten survivors of the Burgess Shale are superior in terms of their anatomy, then for convergentists, such as Conway Morris, those ten survivors will win every time because they have features that better able them to survive and overcome challenges. But if those survivors are “protégés of Lady Luck or fortunate beneficiaries of odd historical contingencies, then each replay of the tape will yield a different set of survivors and a radically different history” (1989, 50).⁴⁶ Gould thought that predicting the progress of humans would have been difficult to establish at the outset of evolution (233). Life does not unfold along predictable pathways of progress and increasing diversity (276). In summary, human existence was not inevitable.

Gould also appealed to the notion of evolutionary contingency to challenge the significance of natural selection for evolutionary change (Gould and Lewontin 1979). This is worth a brief digression. Gould and Lewontin were highly critical of the adaptationist programme, that is,

⁴⁶ For Gould, the history of life was not a continuum of development, but a record of punctuated genealogical instances of mass extinction and subsequent diversification, some of which could become so frequent that they would be perceived as evolutionary norm (1989, 54).

they did not agree that natural selection was the most dominant agent of evolutionary change.⁴⁷ They thought that many traits are just like the chin—by-products of evolution that have not evolved for any particular adaptive reason. Gould brought this complaint against panselctionism to the macroevolutionary scale and argued that appeal to evolution by selection is insufficient to capture the patterns found over large spans of time (2002). Although my focus is on the nature of individuals in selection, as we'll see, attention to stochastic processes like mutation plays a central role in the contingency of evolutionary individuality.

Against all cases—evolutionary convergence, human inevitability, and the significance of natural selection—is an appeal to evolutionary history as riddled with contingency. The presence of an “unpredictable sequence of antecedent states, where any major change in any step of the sequence would have altered the final result” calls those cases into question (1989, 283). Gould says, “Replay the tape a million times from a Burgess beginning, and I doubt that anything like *Homo sapiens* would ever evolve again. It is, indeed, a wonderful life” (289).

3.1.2 Two Senses of Contingency: Beatty, Desjardin, and Turner

While the previous section introduces evolutionary contingency in opposition to certain claims made by Conway Morris, I now turn to then notion of evolutionary contingency itself.⁴⁸ More recently, Beatty (2006a, b), Desjardins (2011a, b), and Turner (2011a, b, 2015) further develop Gould's framework. Beatty distinguishes between two senses of ‘contingency’ used by Gould in *Wonderful Life*: Contingent *upon* and contingent *per se*. Desjardin and Turner further

⁴⁷ Panselctionism, or the view that selection is the most important agent of evolutionary change, is often referred to as ‘the hardening of the modern synthesis.’ The modern synthesis refers to the combination of Mendel and Darwin's ideas. The notion of inheritance was further refined by T.H. Morgan and his graduate students who used Mendel's view as a platform in the early 1900s.

⁴⁸ Conway Morris champions the cases of evolutionary convergence and human inevitability, whereas Gould criticized the privileging of natural selection as *the* driver of evolution, which took place in the second half of the Modern Synthesis (2002, 520ff).

explore these two senses of evolutionary contingency. In what follows, I explain contemporary conceptions of evolutionary contingency, which sets up the framework used to address individuality thereafter.

3.1.2.1 Contingent Upon

According to the first sense of contingency, outcomes of evolution causally depend on prior evolutionary states, events, processes, and so on. This is often referred to as the historical sense of contingency, contingent *upon*, or contingency-as-causal-dependence. For y to be contingent upon x, y depends on x and x is necessary for y. This is a standard notion of contingency that many philosophers will be familiar with. When a particular outcome depends on the state(s) that precedes it, that outcome is contingent upon that prior state(s) (Beatty 2006a, 339). The relationship between the outcome y and the prior state x signifies one of *causal dependence* (ibid). Gould asks his readers to imagine rewinding the evolutionary tape—as in a cassette tape—back to the Burgess 540 mya ago and replay the tape from various starting conditions (WL 1989, 227, 289). He argues that life would look very different because every subsequent state of evolution depends on that which took place before it. The upshot here is evolutionary history is constrained by the variation available, and prior selected variations will shape future evolutionary possibilities (Beatty 2006a, 348). For instance, mammals now cannot evolve six limbs because previous structural traits would have needed to occur previously in order to make that a possibility.⁴⁹

The causal dependence sense of contingency implies that evolutionary history constrains future possibilities—the direction of evolution is shaped by the trajectories of prior evolutionary

⁴⁹ Also see ‘generative entrenchment’. Wimsatt and Schank (2004) discuss entrenchment and evolution.

pathways (Desjardin 2011b, 734). Desjardin distinguishes between an evolutionary outcome's causal dependence in terms of its sensitivity to initial conditions and in terms of its path dependence. The former emphasizes the degree to which certain starting conditions matter to an outcome. The latter emphasizes the particular order and sequence of events that took place before. Desjardin works out a representation scheme to capture that picture and explores the notion of historicity (*ibid*). That is, he explores cases where history matters to an outcome in contrast to cases where it does not. Consider the following example.

If I release a marble from the edge of a bowl, it will eventually stabilize at the bottom. This outcome occurs no matter where on the edge that marble is released from. Moreover, someone who has only found the marble at the bottom of the bowl cannot infer where the marble started nor the path it took to get there, such as which sides it likely rolled up and down before reaching an equilibrium (727). But not only is this process “information destroying,” the starting conditions and the path the marble took do not make a difference to where the marble ends up (729). In all cases, the marble reaches the same place—history does not matter. In cases where history matters, one gets multiple outcomes by tweaking initial conditions, but divergent outcomes can also result from tweaking the order of events in cases of path dependence, even if the initial conditions stay the same (*ibid*).

Both cases of initial conditions and path dependence constitute the historical sense of contingency, which can be summarized in the following way. What may have been likely to evolve in the past becomes unlikely as time moves forward and the raw materials available to selection have been modified such that some optional evolutionary pathways are no longer optional (*ibid*).

3.1.2.2 Contingent Per Se

The second sense of contingency tends to be forward-looking—the occurrence of a particular prior state is *insufficient* to bring about a future outcome (Beatty 2006a, 339).⁵⁰ Gould asks his readers to rewind the tape and hold everything fixed, that is, imagine there are indistinguishable ancestors in indistinguishable environments (1989, 278). On this second reply, one would still end up with different evolutionary outcomes. As mentioned, the survival of the primitive vertebrate *Pikaia* after the Cambrian explosion was potentially necessary, but alone provided no guarantee, for the existence of humans. This is because many other factors affected the sequence of evolutionary events that took place between *Pikaia* and *Homo sapiens*. And those factors likely included the role of stochastic processes, such as mutation, mutational order, and drift. Stochasticity involves random variables in the sense that such processes yield outcomes not determined by environmental conditions. This is what underwrites a lack of guarantee—even if conditions are held constant the influence of stochastic processes makes the prediction of human existence from *Pikaia* alone impossible. However, according to Turner (2011a), contingency as *causal insufficiency*, rather than as *unpredictability*, is the best way to interpret this second sense of contingency. This is because a particular prior state did not cause the outcome alone—many other events took place between the Cambrian explosion over 500 mya and current day (67). And so, nothing about any particular point in past necessitates an outcome of evolution.

⁵⁰ Turner refers to this notion of contingency as ‘causal insufficiency.’ He thinks that contingency as unpredictability is infelicitous. Turner argues that Beatty means to define this version of contingency as prior conditions that do not guarantee the outcome, which is not about our ability as humans to predict future events (2011a, 67).

But why is there a lack of necessity? Random mutation and mutational order are sources of this sort of contingency (Beatty 2006a, 348). These processes contribute to the sense of chanciness found here, which is important for the purposes of individuality. I maintain that sources of contingency can be any of the following: random mutation, mutational ordering, as well as other stochastic processes such as random drift, and even external disturbances such as mass extinctions, floods and other natural disasters.⁵¹ For simplicity, however, I will focus on the role of mutation insofar as it generates variation. Variation is an important for evolution by selection to occur, and so it is relevant for individuals insofar as they are objects of selection. Each of the processes on that list contributes to patterns of evolutionary change in ways that are unbiased, but nevertheless have significant influence concerning downstream effects.

In summary, this section's focus was to outline the landscape of contingency. I started with a brief overview concerning how evolutionary contingency is used to argue against convergence and inevitability through Gould and Conway Morris's dispute. Throughout one finds a recurring theme concerning the role of other processes besides selection in evolutionary change. And finally, Beatty distinguishes between two senses of contingency, contingent *upon* and contingent *per se*, which are further articulated by Desjardin and Turner.

In the next section, I mostly draw from the latter chancy-sense of contingency specifically concerning its mutational source to inform contingent individuality. In later chapters I outline what I take to be its generative aspect. Beatty further expands the reach of the Evolutionary

⁵¹ There is a dispute over the sources of contingency. Whereas Beatty thinks that mutation and ordering are sources of contingency, Turner (2011a, 66) argues that contingency is unbiased species sorting at the macrolevel. For example, Travisano et al. (1995) run an evolutionary experiment to test the significance of contingency in evolution. Beatty is critical of how they include random drift in addition to mutation (2006, 353), while Turner is concerned that they exclude species sorting at the macrolevel. I have argued elsewhere that a source-based approach to contingency clarifies this debate (McConwell and Currie 2016). The sources of contingency will be whatever causes a pattern of evolutionary change that natural selection, or other biased processes, cannot alone be responsible for.

Contingency Thesis (ECT) when he examines the implications for laws in biology (1980). What is of particular importance for developing a contingent notion of individuality is the method Beatty uses to address biological generalizations within the contingency framework. This is because something analogous happens in the case of individuality. And so, to finish this section, I introduce Beatty's expansion of ECT with a special focus on his example from Mendelian genetics.

3.1.3 Expanding the Notion of Contingency: ECT and Biological "Laws"

First I discuss how Beatty makes sense of why biological generalizations lack necessity—a common requirement for a generalization to be considered a scientific law. He then draws from a particular example, Mendelian meiosis. As we shall see, this example is relevant for contingent individuality.

Beatty (1980, 1995) argues that the contingency of evolutionary history implies there are no biological laws insofar as "law" is construed in the Hempelian tradition. Turner (2011b) describes Beatty's endeavour clearly:

[Beatty] has argued that the contingency of evolutionary history means that there are no strict empirical laws in biology. [He] reasons that if there were any distinctively biological laws, they would have to be generalizations about the outcomes of highly contingent evolutionary processes, and hence would lack the kind of necessity that we expect genuine laws of nature to have (161).

According to Beatty (1980), evolutionary contingency explains the inapplicability of traditional conceptions of scientific laws in the biological domain. Hempel argued that universal and exceptionless laws are needed for the deduction involved in scientific explanation. Analogously, philosophers often cite necessary criteria for all evolutionary individuals. For example, a particular form of reproduction may be *required* of *all* individuals in selection. I will return to

this later. Biological theories were considered problematic for citing laws of nature that do not meet those standards (Hempel and Oppenheim 1948). Laws of nature are supposed to be universal statements with empirically determined truth-values. Consider one of the conservation laws in physics. It states that *the total mass-energy of a closed system remains constant*. This law is true necessarily because any exception would be considered physically impossible (Beatty 1980, 398).

Recall that Hempel actually has two accounts of explanation. One involves universal laws, such as ‘All x are y’, and the other includes probabilistic laws such that ‘n% of x are y’ or the probability of being a y is n%. However, probabilistic scientific laws are still necessary because the percentage cannot change (Hempel 1965). Necessity is the feature that makes laws of nature, in either account of explanation, different from mere generalizations. Biological generalizations, however, admit of exceptions. Beatty argued that biological generalizations describe evolutionary outcomes—the exceptions one sees to biological “laws” is symptomatic of the biological domain. He draws from the case of meiosis.⁵² In section 3.3, evidence that the meiotic mechanism evolves will also be relevant for individuality.

3.1.4 Mendelian Inheritance and Mutational Change: Nondisjunction as a Meiotic Mutation

Meiosis is a process of cellular division that leads to the formation of gametes or germ line cells in sexually reproducing organisms. Mendel’s Law of Segregation states that two alleles in a chromosome pair segregate into different gametes during gamete formation. But there is an exception to this “normal” meiosis: Nondisjunction occurs when a homologous

⁵² Mendelian genetics and classical genetics are importantly different despite the fact that classical geneticists use the same, or very close, formulations of main principles from Mendel. Mendel did not fully articulate the notion of genes and chromosomes. T.H. Morgan and his graduate students proposed that inheritance patterns can be explained by postulating the existence of genes (Waters 1990, 127). Beatty is discussing the Mendelian principles used in Classical genetics as discussed by Morgan and his students.

chromosome pair fail to separate into different gametes during meiosis (Egel 2008). At first glance, “nondisjunction may seem to imply a process in which partner chromosomes that should have segregated failed to disjoin” (Janicke et al. 2007, 1645). However, this usually occurs when the chromosomes disconnect prematurely and cannot properly orient themselves to separate poles. Little is known about the mechanisms of nondisjunction and how such malorientation of the chromatids occurs (Hassold and Hunt 2001, Janicke, et al. 2007, 1645). Nondisjunction or the failure of homologue separation in either the first or second stage of meiosis results in one gamete that receives two of the same type of chromosome, while the other gamete receives no copy. Gametes without chromosomes, except for sex chromosomes, produce embryos that are not viable (ibid, 1645). Alternatively, Down syndrome is a common example of a gamete with an extra chromosome that participated in fertilization (ibid).

Meiotic mutants, such as nondisjunction, are not just exceptions to Mendel’s Law of Segregation. Biological generalizations describe contingent outcomes of evolution. The agents of evolutionary change, such as directed and random mutation, natural and sexual selection, random drift, etc., all have “rule-making and rule-breaking” capabilities (Beatty 2006b, 218). Generalizations emerge as certain traits are selected for (219). And “what the agents of evolution render general, they may later render rare” (222). Mutations like nondisjunction demonstrate that Mendelian meiosis has a genetic basis, which is itself subject to change. This is no mere philosophical conjecture. Marcy Uyenoyama proposed that the process of genetic transmission itself evolves by natural selection (1987, 21), and Bell (1982) discussed non-Mendelian inheritance. Even Crow (1979) questioned the ubiquity of Mendelian inheritance. More recently, Van Leeuwen et al. investigates how inheritance in mitochondria is non-Mendelian because there is not recombination through meiosis (2008, 5980). Non-Mendelian

inheritance is not only theoretically possible; it has been identified. Abnormal meiotic behaviour can be viewed as a mutant inheritance mechanism and evidence of evolutionary change. But what does any of this have to do with individuality?

I follow similar reasoning to Beatty, although my target is not scientific laws. Beatty argues that generalizations in biology describe contingent outcomes, so we should not think of those generalizations as lawlike in the sense that includes universality and necessity. I explore how individuals are contingent outcomes of evolution and what that means for accounts of individuality that specify necessary criteria. Furthermore, in other work Beatty uses contingency and evolutionary change to make sense of relative significance debates in biology. Biologists don't argue about *one* correct mechanism or *the* theory, and instead debate over how much of the biological domain mechanisms or theories can explain, that is, which mechanisms or theories are more significant (see Beatty 1997). Beatty's general project suggests that there are *many* (rather than one) viable mechanisms or theories that can do the job. Analogously, I defend the view that there are many types of individuality, and accounts of individuality should be judged on their scope and applicability. My treatment of evolutionary individuality draws from these aspects of Beatty's research.

3.2 Individuality Mechanisms as Evolutionary Outcomes

This section concerns not only a transition to thinking about individuality under ECT, but also a motivation for why the application of ECT to evolutionary individuality is warranted. I canvas candidates for mechanisms responsible for individuality and search for evidence of contingency in those mechanisms. Ultimately, I explore individuality in a way that is compatible with evolutionary change. Here we end up with more than one type of evolutionary individuality. Making sense of that plurality is the topic of Chapter 4.

3.2.1 A Transition: Individuals are Outcomes of Evolution

Recall from Chapter 2 that Lewontin's recipe for evolution by selection is a general constraint for evolutionary individuality. Individuals in selection exhibit varying, heritable traits that make a difference to their fitness. Currently there is dispute over how evolutionary individuals transmit traits (Godfrey-Smith 2009, Ereshefsky and Pedroso 2015). However, under Lewontin's framework there is room for a plurality of evolutionary individuality types. This is the case even if types of individuals in selection share common overarching features that distinguish them from other types of biological individuals.⁵³ I propose that as outcomes of evolution, different types of evolutionary individuals evolve to satisfy Lewontin's constraints.

It is often the case that similar environmental problems are adaptively addressed in different ways, such as the wings of bats, birds, and insects that all yield the ability to fly.⁵⁴ Similarly, there are different ways to satisfy the constraint of trait transmission. One may worry that this merely amounts to one type (rather than many types) of individuality realized in multiple ways. But as we shall see, we can distinguish between types of evolutionary individuality because different approaches will not classify biological entities in the same way. For example, one type of individuality might exclude biofilms, whereas another type of individuality includes them. The different types of evolutionary individuality are caused by different trait transmission mechanisms—the types are distinguished by the causal roles in which ancestors and their descendants are related to one another. Types of evolutionary individuality

⁵³ Examples of other types of biological individuals besides evolutionary individuals are metabolic, immunological, etc. This means that I do not define all biological individuals as strictly evolutionary.

⁵⁴ Although cases of convergence are often used as counterexamples to contingency (Conway Morris 2003), we should look towards the source of the convergence to make that assessment (McConwell and Currie 2016, Powell and Mariscal 2015).

are outcomes of evolution because the mechanisms that cause them are. Those mechanisms are what I turn to next.

3.2.2 Candidates for Individuality Mechanisms: Trait Transmission

Inheritance mechanisms matter for individuals in selection because they facilitate a pattern of ancestor-descendant relationships. This suggests that there are lineages of particular individuals (or tokens) that one can classify into different types. Analogous to how descendant organisms of a particular ancestor can be classified into different species, types of individuals will also branch off or merge creating a new type of individual. How and when an ‘individuality event’ occurs will of course be up for debate.

One example of a new type of individuality caused by the *merging* of branches (rather than *diverging*) is the transition to multicellularity, if indeed that transition occurred via endosymbiosis as characterized by Szathmáry and Maynard-Smith (1995). This will be the topic of Chapter 5. Major transitions in evolution are often construed as transitions or changes in individuality, such as the transition from unicellularity to multicellularity. There is rich literature concerning major transitions without concrete knowledge about the mechanisms of change (see Calcott and Sterelny 2011). Nevertheless, there is attempt to pin down the phenomena responsible for transitions to multicellularity specifically, such as aggregation, mother-daughter cell adhesion after division, and even endosymbiosis (Ratcliff et al. 2012). Godfrey-Smith says, “transitions in individuality...are events in which evolution produces new kinds of biological individuals” (2015, 10122). Previously, others have interpreted the transitions—originally construed by Szathmáry and Maynard-Smith (1995)—as transitions in individuality (R. Michod and Roze 1999). If we see the transition to multicellularity as a change in individuality, then this transition also marks the emergence of a new type of individual, namely, multicellular

individuals. I will return to this in Chapter 5. I cite this case now to hopefully mitigate any concerns about vagueness when discussing what individuality mechanisms are all about. The mechanisms of change in the transitions debate are not clearly identified either, but this does not hinder the research programme. Regardless, the merging of individuality types is facilitated through the merging of individuality “branches.” These branches are lineages of token individuals related by parent-offspring relationships, which are in turn facilitated by mechanisms of trait transmission.

Assuming that philosophers of biology are tracking mechanisms of individuality, there is groundwork for thinking about ways to pass on heritable material. One way to transmit traits is through reproduction. Godfrey-Smith (2009) focuses on the sort of reproduction that includes the formation of bottlenecks and germ-soma distinctions, whereas Dupré and O’Malley (2009) think any mode of reproduction will do. Ereshefsky and Pedroso (2015) call for other trait transmission mechanisms besides narrow views of reproduction. Heritability as a condition for evolution by selection points to the ongoing parent-offspring relationships of individuals. Trait transmission to offspring can occur vertically, such as through reproduction, division, and replication. It can also occur horizontally in aggregative entities through lateral gene transfer, such as in biofilms (Ereshefsky and Pedroso 2015). In each case, inheritance is caused by different trait transmission mechanisms, and so it is plausible that two types of individuality have been identified. In order to establish contingent individuality though, we should find evidence that the trait transmission mechanisms responsible for these two individuality types evolve contingently. This is the goal of Section 3.3. Although my focus is on trait transmission, it seems necessary to at least touch on boundary maintenance mechanisms responsible for the sort of functional integration of individuals found in the biological domain.

3.2.3 Candidates for Individuality Mechanisms: Boundary Maintenance

In addition to inheritance mechanisms, a second individuality mechanism is often cited: Individuals in selection are maintained by variations of boundary delineation mechanisms and integrative mechanisms (that can contribute to boundary delineation as well). Pradeu (2012) thinks that immunogenic response delineates the boundaries of individuals.⁵⁵ Ereshefsky and Pedroso (2015) discuss the cohesive causal interaction among the parts of interactor individuals in selection in addition to trait transmission. Huneman (2014a, b) also worries about the mechanisms by which strong interactions among an individual's parts occur such that the strength of that interaction delineates individuals. And finally, Clarke (2013) emphasizes boundary delineation and maintenance of boundaries by her focus on policing and demarcation mechanisms. Boundary delineation mechanisms are important because they spatially carve up entities into basic units. They also control emerging variants, which is an integral feature to sustaining and preventing the breakdown of an individual over time (Pradeu 2012, 261). Integrative mechanisms that yield physiological unity can in part help to delineate those boundaries by facilitating strong relationships among parts of the individual when compared to other entities in that individual's environment. However, I do have a concern with boundary maintenance as the sole criterion for individuals in selection.

If we are concerned with individuals in selection specifically, then it is unclear how accounts that focus *only* on boundary maintenance satisfy general constraints for evolution by selection (such as Clarke 2013, Pradeu 2010, Gilbert et al. 2012). They focus on boundary sustaining mechanisms, such as immunogenic response, strength of interaction, and other

⁵⁵ Gilbert et al. (2012) also propose that the immune system acts as a boundary delineating system in order to account for multigenomic associations they treat with group selection measures. However, they do not account for the formation of lineages of these individuals. I think they will be subject to the same criticism I am about to raise.

policing and demarcation mechanisms that work to sharpen the boundaries of individuals. However, the emergence of new individuals is important for lineage formation, which constitutes populations of individuals that evolve. Modes of inheritance are significant for individuals *in selection* because evolution by selection needs ways to transmit traits. This does not mean that immunological individuals don't exist or that ecology cannot inform individuality in some respect. These are different types of biological individuals, albeit non-evolutionary types of individuals. Views about boundary maintenance mechanisms are silent on how new types of individuals, as well as tokens of those types, emerge in evolution. This does not preclude immunological or ecological individuals from being individuals in selection. However, without a story of *evolutionary* change, boundary delineation views are supplementary at best.

In summary, out of two candidates for evolutionary individuality mechanisms, trait transmission is required for evolutionary individuality. Section 3.3 is devoted to finding evidence of contingency and evolutionary change in different modes of trait transmission. These different modes of trait transmission are what distinguish different types of individuals in selection. Before introducing some markers of contingency, I motivate why evolutionary change is important for individuality.

3.2.4 A Motivation for Contingent Evolutionary Change and Individuality

One common theme is the call for accounts of individuals in selection that are consistent with the idea that populations of individuals undergo evolutionary change. For example, Haber (2013, 213) calls for a notion of individuality that includes how individuals are expressed, maintained, and continuing to *evolve*. Godfrey-Smith's view sets up a degree of individuality, though dynamic, is confined to a particular set of parameters ranging from marginal to paradigm individuals (see Chapter 2 for his specific individuality criteria). Ultimately he argues that

evolutionary individuals are reproductive units forming lineages which “*evolve* by natural selection” (2015, 10124, my italics). Huneman (2014a, 367) proposes a gradient of individuality to capture how individuality can change throughout the course of evolution and thinks individuality *evolves* through time: individuals become and cease to be units of selection. And finally, Ereshefsky and Pedroso (2015) develop a pluralistic and open-ended account of individuality that can properly capture the vast array of heterogeneous entities, including multispecies consortia, such as biofilms. My goal is to provide a contingency framework for thinking about the evolution of individuals in selection. In this framework, we find that evolution yields many types of evolutionary individuals. The last section of this chapter explores the role of stochastic processes for evolutionary individuality, such as mutation, in addition to trait transmission mechanisms. Together the different ways to generate variation and the different ways to transmit traits all satisfy Lewontin’s general constraints for individuals in selection, yet each distinguish different types of evolutionary individuals.

3.3 Contingent Individuality

Individuals are outcomes of evolution because the biological mechanisms responsible for them are products of evolutionary processes. Some examples of evolutionary *processes* are natural selection, mutation, and random drift. Examples of evolutionary *products* are the Krebs cycle for metabolism, Mendelian meiosis, and even modes of reproduction, such as sexual reproduction, which will be addressed later (Beatty 1995, Turner 2011b, 164). Evolutionary individuals are products of evolution, which are influenced by processes that affect their likelihood as evolutionary outcomes. In this section, I argue that evolutionary individuals are products of evolution, which are influenced by processes that affect their likelihood as evolutionary outcomes. I identify two ways to generate variation with their corresponding means

of passing on those traits, and look for evidence that these variation and trait transmission mechanisms evolve contingently. My argument, then, looks something like this:

- (1) Different variation and trait transmission mechanisms underpin different types of evolutionary individuality
- (2) There is evidence that these variation and trait transmission mechanisms, as evolutionary outcomes, evolve contingently
- (3) Therefore, evolutionary individuals evolve contingently

While trait transmission mechanisms are important for distinguishing types of individuals in selection, we must not forget the role of random mutation in evolutionary change. Random mutation often provides the variation needed for selection to occur and it is a source of evolutionary contingency. On this picture, selection opportunistically draws from what is available (Jacob 1977). Furthermore, mutation influences the direction of evolutionary trajectories. Although mutations might be rare, if selected for they can eventually become the norm.⁵⁶ Before exploring the contingent evolution of variation generation and trait transmission, I introduce two markers of contingency within the context of individuality: (1) a lack of necessity and (2) impermanence due to evolutionary change. This grounds a more concrete analysis of two cases from biology to follow.

3.3.1 Two Markers of Contingency

First, nothing necessitates the existence of evolutionary individuality types. This is because biological mechanisms responsible for individuals are outcomes of evolution, dependent upon a complicated sequence of evolutionary events and processes. Their existence is due to many

⁵⁶ Those available variations, and whether they are passed on to later generations, will also be affected by other stochastic processes, such as random drift, or environmental disturbances (Turner 2011a, b). For simplicity, because Beatty focuses on meiotic mutation in his treatment of laws in biology, I will focus on mutation as a source of contingency.

chance-contributing factors that affect the likelihood of their existence. The relevant mutation or order of mutations may or may not occur, for instance. As products of stochastic processes individuals have complicated evolutionary pathways riddled with contingency. It would have been very difficult to predict the existence of a particular type of individuality at the outset of evolution.

Second, types of evolutionary individuals are impermanent and undergo evolutionary change. And so long as the products of evolution remain the objects of processes that drive evolution, they potentially continue to evolve. The sources of contingency are evolutionary processes that help to drive evolutionary change. For instance, mutations arise and are selected for that may or may not be passed to uncertain future generations of individuals. The ever-changing nature of evolution underwrites the lack of necessity—exceptions to the rule are not physically impossible, in fact one could argue that they are what needs to be explained (Beatty 1980, 405).

In summary, accounts of individuality describe outcomes of evolution, which are likely to be significantly affected by stochastic processes. Sets of universal and necessary conditions are, therefore, inapplicable. We can, however, identify criteria for individuality when certain traits responsible for individuals are selected for and become more significant. In other words, specific conditions for evolutionary individuality will emerge as genetically-based individuality mechanisms, e.g. trait transmission mechanisms, are selected for. And an adaptive need can often be met in a variety of different ways. However, there is more to evolution than just natural selection alone. Mutation and other evolutionary processes are also responsible for evolutionary change. And what was at one time “normal” may later become rare and vice versa. This means one cannot preclude what initially appear as exceptions to the rule from eventually becoming the

norm. Thus, a single account picking out one type of individual in selection does not quite capture this picture of contingency and change.

That a rare evolutionary occurrence can become standard will often trick us: From our limited perspective whatever is the norm is often seen as if it *must* be that way all the time and exceptions to that norm are viewed as mistakes or mere anomalies. For example, meiosis and sexual reproduction comprise one way of mixing up genes and passing on heritable material. This is a familiar form of trait transmission to animals like us. Many paradigm collective reproducers on Godfrey-Smith's account reproduce new individuals through these means (2009). However, Ereshefsky and Pedroso (2015) argue that some multispecies biofilms can mix up genes and transfer heritable traits. And this form of trait transmission found among microbes is not rare because microbial life vastly outnumbers other life forms (O'Malley 2014). However, on Godfrey-Smith's view biofilms, and most multispecies consortia, are marginal individuals at best. Regardless, as discussed later, there is a different type of evolutionary individuality that better accounts for the individuality of biofilms. With this general understanding of individuality within the framework of evolutionary contingency, it's time to move to more concrete examples. In the following I search for evidence of contingency and evolutionary change in two cases from biology:

- (1) Meiosis and lateral gene transfer (LGT) as different ways to generate variation
- (2) Bottleneck versus aggregate means of transmitting traits in the formation of new individuals.

3.3.2 Mixing Up Genes: Meiosis and Lateral Gene Transfer

There are different ways to mix genes into new combinations, thus creating the variation that selection works with. So, meiosis and LGT are ways to facilitate the variation needed for biological entities to be visible to selection.

Meiosis is a precursor to the successful passing-on of genetic traits to offspring. After germ cells are generated, it is through sexual reproduction that those traits are transmitted to later generations. Meiosis is one way to facilitate variation; new combinations of genes are generated by the disjoining of chromosome pairs into different gametes during gamete formation. However, consider how Rattray et al. (2015) study the mutation rate during meiosis in *Saccharomyces cerevisiae*. While germ-line mutations and meiotic sorting of parent alleles contribute to evolution, the process itself is “inherently mutagenic.” It increases the mutational load when compared to usual rates of mutations (2015, 11). This change in mutation-rate-allowance contributes to variation generally. I already discussed mutations of the meiotic mechanism, such as non-disjunction, in Section 3.1.

We know there are other ways of mixing genetic material besides the “normal” mechanisms of reproduction (i.e. meiosis, sexual reproduction). Consider LGT exhibited by prokaryotes and some eukaryotes. For example, in biofilms two mechanisms are responsible for LGT: Transformation allows a bacterium in the biofilm to take in extracellular DNA released from other cells. Conjugation transfers genes through bridges between bacteria (Ereshefsky and Pedroso 2015, 10127). LGT is a way for prokaryotes to express new combinations of traits. It is a way to mix up genes in microbes for new traits and to swap out the bad genes. Ragan and Beiko state that through this process various types of genetic material are exchanged in addition to whole genes (2009, 2243). This includes stretches of non-coding DNA, portions of genes,

intact genes, multi-gene clusters, operons, plasmids and more. They wonder if whole gene transfer would be “selectively most advantageous.” In doing so, they recognize that the mechanisms of LGT could exchange genetic material differently and in ways that might be better than transferring only segments of genetic material. As a viable mechanism for genetic exchange, they also note that “there is a broad consensus that LGT has contributed to genome evolution in prokaryotes” (ibid).

And so, evolution by selection can find different ways to achieve the same goal: “unlike engineers, tinkerers who tackle the same problem are likely to end up with different solutions” (Jacob 1977, 1164). There are different mechanisms by which variation is achieved through mixing of genetic material. This includes both meiosis and lateral gene transfer. Different types of individuals in selection will exhibit varying genotypes and corresponding phenotypes. Although well documented in prokaryotes and some eukaryotes, it is not known whether the considerable lack of LGT in some individuals is due to physical constraints, i.e. “protection of the germ line from intracellular bacteria” or regulatory constraints, such as problems integrating into that complex regulatory network (Ragan and Beiko 2009, 2245). Ku et al. (2015) suggest that eukaryotes evolved sex to complete this task as meiosis and LGT function as facilitators for variation and provide a platform for mutational change. These identified types of variation generation will lack necessity insofar as they are evolutionary outcomes sourced and affected by processes responsible for evolutionary contingency, i.e. random mutation. For example, there might not have been meiosis if prokaryotes never evolved, that is, if features of meiosis were indeed present in prokaryotic ancestors of eukaryotes. Different causal mechanisms that facilitate variation in populations of individuals are *in part* responsible for the individuation of different types of individuality. Trait transmission does the rest.

3.3.3 Reproducing New Individuals: Bottlenecks and Aggregation

The sexual reproduction of individuals, such as many of the paradigm collective reproducers in Godfrey-Smith's account (2009), is one way to create a new token individual that inherits the traits of its ancestor. This creates a lineage of a certain type of individual, which passes on heritable material vertically in parent-offspring fashion. Alternatively, horizontal modes of trait transmission create complicated parent-offspring networks. But if those individuals transmit heritable traits to new token individuals, then there are grounds for identifying another type of evolutionary individuality. I will consider each in turn.

Mendelian meiosis is an integral part of sexual reproduction because it creates variable genotypes that are later reproduced. Standard sexual reproduction is one way that trait transmission can occur. This is a type of evolutionary individuality such that token individuals reproduce when two conspecific gametes fuse to create a single embryo. We can identify the point that a new individual emerges because of the narrowing between generations. This is called a 'reproductive bottleneck' because the narrowing distinguishes the emergence of a new individual from mere growth of the parent. The parent-offspring relationships of individuals form reproductive lineages in the way that Godfrey-Smith is concerned with. But there is evidence that this type of evolutionary individuality is evolving.

Evolution of sexual reproduction is currently under study (Zimmer and Riffell 2011, 13204). Zimmer and Riffell investigate changes in reproductive development and argue that gametes undergo selection for mechanisms that increase sperm-egg contact, such as changes in morphology, physiological size, etc. It is reasonable to assume, then, that particular mutations in these mechanisms are selected for (or not) depending on how advantageous they are. That is, those mutations are available to selection. For example, odd gamete shape and methods of fusing

to conspecific gametes can arise as reproductive mutants just as nondisjunction is a meiotic mutant. I have also discussed the plausibility that meiotic mechanisms—those that facilitate variation prior to the occurrence of sexual reproduction—evolve. And so, if odd gamete shape and fusion are not advantageous, they will not be selected for. However, each opportunity still remains as one (though unlikely) possible pathway in the evolutionary history of that mechanism. Zimmer and Riffell give reason to believe that evolutionary change in reproduction, as a mode of trait transmission, is underway.

In vertical forms of reproduction, genetic traits are usually dispersed to new germ cells and through sexual reproduction those traits are inherited by the offspring. However, we know that many prokaryotic cells exchange and mix up genetic material via LGT. But are there parent-offspring lineages through which genotypic and phenotypic traits are transmitted? At minimum, to be another type of evolutionary individuality, there must be a new token individual emerging through a different process by which it inherits traits from its predecessor. Ereshefsky and Pedroso make the case that biofilms exemplify another type of evolutionary individuality because biofilm-level traits are transmitted to new biofilms (2015, 10128). New biofilms can be formed by cells that may have broken off from another biofilm. Through LGT those preliminary colonizers will transfer traits throughout the new biofilm as later colonizers attach. By way of aggregation we have a new individual; cells that contain genetic material previously exchanged through a lateral process among the cells of the ancestor biofilm. Recall that a reproductive bottleneck to a single-celled embryo in sexual reproduction marks the emergence of a new token individual. Analogously, new aggregative individuals also start with a small number of cells

when compared to the previous biofilm they departed from. And so, a new token individual emerges that inherits material from a predecessor biofilm.⁵⁷

If we accept aggregative means of forming new individuals as another way in which trait transmission can occur, one might worry that this is simply a form of “bottlenecking” that falls short of the standard reproductive bottlenecks. The objection goes something like this: new individuals through aggregation are not as clearly delineated because the bottleneck that marks the difference is not as narrow. One might further object that they’re the same type of individual insofar as cell bottlenecks mark the next generation. And so, the worry is that I have failed to distinguish between two types of individuals in selection because bottlenecking distinguishes new token individuals in both cases. However, recall that in order to distinguish between two types of individuals, I need to identify two different *causal* means of forming parent-offspring lineages through modes of trait transmission. We use the term ‘bottleneck’ to mark the narrowing between generations—bottlenecks are descriptions of the phenomena witnessed from a multicellular entity to a single cell when the process starts anew. They are not causal mechanisms in their own right. Bottlenecks are mere by-products of inheritance mechanisms in the production of new token individuals. It is, then, no surprise that in two different cases of trait transmission to new individuals, we have a narrowing that resembles something like a bottleneck in each case. The different types of individuality map onto different modes of inheritance that

⁵⁷ Clarke (2016) argues that biofilm-level trait adaptation and transmission is contentious. She appeals to the difficulty of identifying biofilm-level adaptations (2016, 14). However, that difficulty is present in many adaptationist stories (see Gould and Lewontin 1979). Furthermore, she says that LGT in biofilms “will not bring about the sort of across-trait relatedness that occurs as a consequence of common descent” and it is not clear how it serves to suppress competition in order for selection to occur at the level of the biofilm, rather than at the individual cells (17). On the contrary, however, one might point out that Clarke is using standard forms of trait transmission, such as sexual reproduction, as a measure for the individuality of biofilms, which begs the question whether biofilms are individuals in selection. I return to the challenges raised by Clarke in Chapter 4.

form ancestor-descendant relationships in different ways. The fact that they both happen to yield what looks like bottlenecks to us does not collapse the distinction between individuality types because bottlenecks are not causal, but are instead side effects of trait transmission processes.

And so, we are left with at least two types of evolutionary individuals that generally satisfy Lewontin's constraints of variation and heritability. First, if the nature of sexual reproduction evolves as discussed above (Zimmer and Riffell 2011), and if meiosis evolves (Beatty 1995 Uyenoyama 1987, Bell 1982, Crow 1979, Van Leeuwen, et al. 2008), then the type of evolutionary individuality relying on that machinery evolve. Second, we find another type of individuality that generates variation through LGT and transmits those traits through aggregative means. Here we also find evidence of contingent evolutionary change.

The point I am driving at is this: if we take the Evolutionary Contingency Thesis (ECT) seriously, the history of these mechanisms will be riddled with contingency and sourced by stochastic processes, such as the generation of random mutations and mutational order. Natural selection is not the only evolutionary process that drives change (Gould 1989, 2002, Beatty 1994, 36). The individuals studied in evolutionary theory should be grounded by how evolution works, which includes more than just the process of natural selection. And if the evolutionary histories of trait transmission mechanisms relevant for individuality types are affected by stochastic processes, then those types of processes do not yield outcomes that exist necessarily. Types of individuals, in selection or otherwise, are created and maintained by mechanisms subject to stochastic processes that chisel the structure of evolutionary pathways from a background of alternative possibilities. However, evidence pointing to the contingent evolution of individuality mechanisms implies the following: any identified types of individuals in selection will not necessarily remain the way they look to us now. Recall that the processes

driving evolution have both rule-making and rule-breaking capacities (Beatty 2006a, b, Gould 2002). What may appear as counterexamples to a view of individuality may just be new types of evolutionary individuals emerging, instead of quasi-evolutionary individuals that only minimally satisfy particular conditions. At this point I have defended contingent individuality and argued that there are at least two types of individuals in selection undergoing evolutionary change. In the next chapter, I make sense of this individuality pluralism and discuss how evolutionary contingency causes a plurality of evolutionary individuality types that emerge, evolve, and disappear through the course of evolution.

“A proponent of theoretical pluralism with respect to a particular domain believes that the domain is essentially heterogeneous, in the sense that a plurality of theories or mechanisms is required to account for it, *different items in the domain requiring explanations in terms of different theories or mechanisms.*”—John Beatty, 2006b, p. 229

Chapter Four: A Plurality of Evolutionary Individuality Types

In chapter 2, I discussed different accounts of individuality. There are several types of biological individuals, such as immunological, metabolic, ecological, and so on. Although nothing precludes those types of biological individuals from being individuals in selection, we established the importance of trait transmission mechanisms for evolutionary types of biological individuals. Chapter 3 included a search for evidence of contingent individuality. That is, evolutionary individuals are contingent when they are underpinned by biological mechanisms that (1) lack necessity due to a dependence upon stochastic processes, and (2) those mechanisms undergo evolutionary change. We discovered that trait transmission mechanisms are integral for biological entities to be evolutionary individuals—there must be some means of generating new token individuals that inherit traits from their ancestors. I identified evidence of evolutionary change and dependence on mutation, a stochastic process, for two different modes of trait transmission (through sexual reproduction and aggregative means) along with two corresponding ways of generating variation among heritable traits (through meiosis and lateral gene transfer). In doing so, arguably, I have identified at least two types of evolutionary individuals. That is, there are *at least* two types of evolutionary individuality underpinned by different causal mechanisms, which generate varying traits transmitted to offspring. That certainly helps a pluralist aim, but more is needed to show how individuality pluralism follows from evolutionary contingency. How we make sense of more than one type of individual in selection is the topic of this current chapter, which is organized in the following manner.

Section 4.1 is a menu of pluralism. I discuss different pluralistic and pseudo-pluralistic views to illustrate the sort of pluralism I am after. Section 4.2 is primarily motivational; I illustrate why individuality pluralism makes sense within a greater contingency framework. Thereafter, in section 4.3 I argue for the stronger claim, namely, that evolutionary contingency causes a plurality of evolutionary individuality types. Section 4.4 provides responses to anticipated objections. Finally, section 4.5 sketches a picture of individuality pluralism over evolutionary time; a diachronicity and synchronicity of types.

4.1 A Taxonomy of Individuality Pluralisms and Pseudo-Pluralisms

The purpose of this section is to survey possible pluralisms in order to explain ‘individuality pluralism’ for this dissertation. In contrast, individuality monism will be any view that maintains only one set of necessary (and perhaps sufficient) conditions that identify individuals in selection. Many philosophers aim for a pluralistic account of individuality in one way or another (Godfrey-Smith 2009, Huneman 2014a, b, Clarke 2013, Ereshefsky and Pedroso 2013, 2015). I intend to support that general endeavour. However, the pluralism argued for here is distinctive because it concerns evolutionary individuality specifically, and not just a plurality of biological individuals. This section is generally divided into two parts: A taxonomy of individuality pluralisms followed by a closer look at metaphysical or ontological pluralism.

4.1.1 Heterogeneity is not Sufficient for Individuality Pluralism

There are at least two views that construe evolutionary individuality as heterogeneous. Not only can different token biological entities be units of selection, but different types of entities can as well. This means that what counts as evolutionary individuals includes a variety of entities,

such as organisms and viruses, for example.⁵⁸ Furthermore, over time these types of entities become and cease to be units of selection—a heterogeneous account of evolutionary individuality can also accommodate change concerning units of selection. And so, some accounts of individuality capture the variety of different entities that persist at one time and across time. However, if that heterogeneous account provides a single set of parameters by which all entities will either succeed or fail to be individuals in selection, then it is not the sort of pluralism relevant here. Variety and change are simply features of the biological domain; to be an individuality pluralist takes a step further.

The foregoing suggests that *heterogeneity is not sufficient for individuality pluralism*. The biological domain is strange—the vast differences found in the organic world cause trouble for individuality because we are not sifting through heaps of identical stuff.⁵⁹ However, the various biological entities, which accounts of individuality aim to capture, are worth discussing. To capture heterogeneity addresses the nature of the organic domain. However, any account of evolutionary individuality restrained by a single set of parameters is not pluralistic. At first glance these views might seem to be pluralistic, which is worth disambiguating in order to make ontological pluralism—the topic of this chapter—clearer in how it differs from other claims to pluralism. Consider the following.

⁵⁸ Dupré and O'Malley (2009) discuss whether viruses are individuals. According to their view, individuals are collaboratively metabolic entities that reproduce. Recall from chapter 2 that their notion of collaboration involves both competition and cooperation. Viruses replicate, but only when they collaborate with other entities. It's unclear whether Dupré and O'Malley think that viruses are themselves individuals at the point-of-collaboration or whether they are merely parts of a metabolic whole. Depending on one's view, then, viruses could be individuals. Pradeu (2010) thinks that organisms are the most well-defined evolutionary individuals, whereas Godfrey-Smith's view excludes some organisms from being individuals in selection.

⁵⁹ While heterogeneity causes trouble for individuality in the biological domain, arguably it is homogeneity or sameness that makes individuation difficult in the physical domain. See McKenzie (2013), French and McKenzie (2012) for discussion concerning types of quantum particles and instances of those types.

Recall the accounts of individuality by Godfrey-Smith, Huneman, and Pradeu from Chapter 2. First, Godfrey-Smith (2009) argues that individuals in selection reproduce in a way that yields reproductive bottlenecks, they exhibit reproductive division of labour, and are functionally integrated units. He recognizes degrees of individuality—entities can score high on these parameters yielding paradigm individuals versus marginal individuals that score low on all three. Booth (2014, 671) views the account as pluralistic because Godfrey-Smith identifies two types of biological entities—metabolic organisms and Darwinian individuals. Second, Huneman (2014a, b) proposes that strength of interaction marks the boundaries of biological individuals—he worries about accounting for ecological individuals. According to Huneman, a strong concept of individuality includes individuals in selection, thus evolutionary individuals exhibit the strongest level of interaction delineating the interactions of entities with one another from interactions with entities outside of that unit (2014b, 377). He thinks that increasing levels of interaction grounds what he sees as individuality pluralism (374). Because we get a nested individuality reflecting different levels of the biological hierarchy, Huneman claims his view is pluralistic (*ibid*). Finally, Pradeu (2010, 2012) argues that immunology offers a theory that makes biological individuation possible on physiological grounds. Individuals in physiology are marked by immunogenic response to antigens. Immunological individuals might be individuals in selection though if they can pass on adaptive traits at the level of the whole to future generations. In this case, we get a distinction between immunological individuals and immunological individuals that are also evolutionary—two different types of biological individuals.

In all cases above, ‘pluralism’ is used ambiguously: There is a plurality of biological entities in Godfrey-Smith’s case as Booth (2014, 671) refers to organisms and Darwinian individuals as different types of biological individuals. Then, according to Huneman, we have different

individuals insofar as they correspond to different levels of the biological hierarchy—organisms, species, ecosystems, and so on. Finally, Pradeu articulates a view with at least two biological individuals—evolutionary and immunological. He sees evolutionary individuals as essentially immunological—this physiological criterion is necessary to determine the boundaries of evolutionary individuals (2010, 262, 264). But this does not necessarily entail that all immunological individuals are by that fact evolutionary. At minimum, one can conclude that pluralism concerning individuality is a shared research aim. However, drawing ontological pluralism from the variety of entities within the biological domain, a variety which also might change over time, is not enough to motivate and explain *why* there is a plurality of individuals in the biological domain. Capturing heterogeneity is not enough for ontological pluralism concerning individuality. There must be a way to distinguish between types of individuals. And finally, a plurality of biological individuals is not necessarily a plurality of evolutionary individuality types. What one gains, however, is further clarification of options for individuality pluralism: There are different types of individuals in selection and there are different types of biological individuals. There are, then, two lessons from this section.

First, both Godfrey-Smith and Huneman's views identify degrees of individuality. This is supposed to capture the vast differences and varieties of biological entities. A continuum of individuality is also supposed to address the change of individuality over time in the sense that different entities can become and cease to be individuals, e.g. viruses, organisms, etc. Furthermore, a collective of these different types can become an individual in selection when it satisfies the criteria stated above. And so, new biological entities may become individuals. However, both Godfrey-Smith and Huneman identify a single set of parameters that constrain one type of evolutionary individuality—for Huneman it is strength of interaction to yield the

sharpest boundaries and for Godfrey-Smith it's a set of three necessary criteria that mark paradigm Darwinian individuals. Huneman and Godfrey-Smith each provide different concepts of evolutionary individuality and each propose one way to be an individual in selection. Therefore, in both cases there is only one type of *evolutionary* individuality. A main message of this chapter is that there is good reason to be pluralists about individuality concepts, including evolutionary individuality concepts, because there are different types of individuals both in selection and otherwise. Godfrey-Smith and Huneman capture heterogeneity at a time and over time, but this is not enough. Rather, heterogeneity within *and between* types of individuals is evolutionary individuality pluralism.

Second, Huneman and Pradeu articulate a pluralism about biological individuality more generally. Whereas Godfrey-Smith is concerned with individuals in selection, Huneman and Pradeu identify ecological and immunological ways to individuate the biological domain. Arguably, the latter are two types of non-evolutionary biological individuals. Although the main concern is pluralism with regards to evolutionary individuality, a pluralism about types of biological individuals is worth pausing for. Huneman and Pradeu's immunological and ecological concepts also nicely capture the heterogeneity of biological entities. That is, the boundaries of individuality do not rely on a homogeneous grouping of entities. Rather, their views encourage a multitude of different entities encapsulated by different boundary delineation mechanisms in both ecology and immunology. This also suggests that the topic of individuality is relevant to other areas of biology in addition to evolutionary biology.

And so, Huneman and Pradeu identify a plurality of types of biological individuals that each correspond to non-evolutionary fields of biology. More is needed, however, if ecological and immunological individuals are going to be units of selection though, such as a mode of trait

transmission. So, we get plurality of biological individuals, but still not a plurality of evolutionary individuals specifically. The case of biofilms is an important case to support the idea that there are different types of individuals in selection.

4.1.2 The Importance of the Biofilm Case: Another Type of Evolutionary Individuality

Chapter 3 outlined the case of biofilms as discussed by Ereshefsky and Pedroso (2013, 2015). If biofilms transmit biofilm-level adaptive traits to offspring, then we have an instance of another evolutionary individuality type. This is in contrast to the type of evolutionary individual that transmits traits through sexual reproduction. There are two important details to be supported: (1) that there are indeed biofilm level adaptive traits, and (2) those traits are transmitted to a new biofilm through some mechanism. Recall that Ereshefsky and Pedroso argue that adaptive traits are transmitted through a different means of forming a new token individual, namely, aggregation. If they are correct, biofilms exhibit a different sort of evolutionary individuality. The accuracy of their claim is important for individuality pluralism—identifying another type of individual in selection is positive evidence in support of a view concerning multiple types of evolutionary individuality.

Standard forms of reproduction, such as that discussed by Godfrey-Smith, are often cited as *the* mode of inheritance. However, as discussed in Chapter 3, not only do biofilms exhibit reproductive specialization, the emergence of a new biofilm can be distinguished from growth of the same biofilm. Dispersal cells colonize a new site and they contain genetic material from the ancestor biofilm. From this point, a new life cycle begins and the primary colonizers laterally

exchange genes with later colonizers that attach.⁶⁰ It seems reasonable then to assume we have emergence of a new token biofilm individual. But in order to be a unit of selection, biofilm adaptive-level traits must be transmitted to offspring biofilms with fidelity. Does this occur?

Clarke argues that the existence of biofilm-level adaptations is not verifiable (2016, 5, 12). For example, Ereshefsky and Pedroso discuss the possibility that antibiotic resistance is a biofilm level adaption (2015, 10127). That is, mechanisms that resist antibiotics are not found among the individual cells. If LGT promotes the sharing of antibiotic-resistant genes, then as long as dispersal cells carry those genes the new biofilm should benefit too. Clarke complains, however, that hypotheses about adaptations are “limited only by our imagination and often we will be wrong” (2016, 13). I find her treatment of biofilm traits unsatisfying. If adaptations are evidence of selection at work, and we’re concerned with individuals in selection, it makes sense to search for adaptive traits. The problem of ‘just so’ stories with respect to adaptations is a problem that extends far beyond the case study of biofilms (Gould and Lewontin, 1979). If this is a problem for multi-species consortia like biofilms, then it is also a problem for single species units too. This would be a mark against the entire investigation of the nature of evolutionary individuality—we assume that adaptations are evidence of selection at work. Adaptationist programme concerns reach far beyond this context so I see no reason to abandon the search for adaptations in this case.

Furthermore, Clarke thinks that to account for multispecies biofilm evolution requires notions of group selection (2015, 9). She notes that cheater microbes can cause problems at the

⁶⁰ Clarke (2016) claims that the notion of a life cycle is contentious and whether or not biofilms exhibit life cycles needs more empirical study.

expense of the entire biofilm.⁶¹ However, Ereshefsky and Pedroso discuss ways in which cheaters are kept in check (2015, 10127). To claim multispecies consortia require group selection presupposes that the collective is not an individual. This is problematic if the issue at hand is whether or not the collective actually is an individual. If it is an individual, then group selection concepts don't seem useful. Often the mechanisms of individuality—integration and boundary delineation mechanisms such as the immune system for example—do the work for us. These mechanisms already accommodate the kind of cheater control that group selection is called upon to deal with. This makes the request for group selection principles concerning multispecies consortia superfluous if the problem is addressed by other means. Finally, there is an additional worry concerning Clarke's discussion of biofilms.

In assessing whether Ereshefsky and Pedroso's claim about biofilms meets Lewontin's constraints, Clarke measures that success against Godfrey-Smith's (2009) account. This is not a convincing move. For example, she says "paradigm examples of evolutionary individuals—such as mammals...have very high individuality because their parts are completely co-selected" (2016, 8-9).⁶² This looks suspiciously like the paradigm individual in selection Godfrey-Smith both concerns himself with and measures potential cases of individuality against. However, Ereshefsky and Pedroso have stated numerous times in print that biofilms score poorly according to Godfrey-Smith's criteria for individuals in selection. If Lewontin's constraints allow room for

⁶¹ Gilbert et al. (2012) also discuss notions of group selection to make sense of multispecies consortia as individuals. I think this misses the point of thinking about holobiont complexes as individuals. This is discussed later.

⁶² 'Co-selected' refers to the idea that parts of mammals will not out compete one another. This is false. Autoimmune diseases and certain forms of breast cancer are cases in which parts of the unit outcompete the rest and such diseases are thought to be heritable. See Rioux and Abbas "Paths to understanding the genetic basis of autoimmune disease" (2005). Although the heritable nature of breast cancer is not completely understood, there is work on the genetic predisposition to develop the disease (Erkko et al. 2007).

a multiplicity of individuality types, then to measure one type against another type merely begs the question.

How Lewontin's constraints—variability, differential fitness, and heritability—feature in the individuality debate is worth some reflection. Philosophers such as Godfrey-Smith (2009) and Clarke (2016) discuss Lewontin's constraints, and Lewontin's recipe for evolution by selection is repeatedly returned to in the literature (e.g. Pradeu 2012, Booth 2014, Ereshefsky and Pedroso 2015). For example, Godfrey-Smith proposes particular criteria for individuals in selection against the larger Lewontin background concerning how selection operates. But what work is Lewontin's recipe actually doing here?

4.1.3 The Category of Evolutionary Individuality and a Question of Realism

Up to this point, I have argued that heterogeneous views of individuality are insufficient for pluralism. The lesson is this: more is needed to distinguish *types* such that we have a plurality of evolutionary individuality types. We have also seen why the biofilm case is so important. That is, if multispecies biofilms are individuals, there is evidence in support of individuality pluralism. But it's worthwhile to pause for a moment over the role of Lewontin's recipe. In what follows, I argue that Lewontin's framework encompasses the class of *all* types of evolutionary individuals. This is what I heretofore refer to as the *Evolutionary Individuality Category* or the 'EI Category'. Familiarity with the difference between the species category versus species concepts is useful conceptual machinery for what is to come. And so, I will very briefly introduce that debate.

Biological systematists study how organisms and taxa are related (Ereshefsky 2001, 50). Species taxa consist of organisms grouped together in a particular way. There are, at this point, numerous concepts that prescribe how to classify organisms into species. For instance, roughly the biological species concept defines a species taxon as a group of organisms that can interbreed

and produce fertile offspring (Mayr 1970). This is one way to characterize a species taxon. Another species concept is the ecological species concept, which groups organisms according to ecological forces (Van Valen 1976). The species category, however, is the class of all species taxa. And so, questions concerning species concepts are questions about how to define the species category.

Although questions concerning species concepts and the species category are distinct, they are related in some respects. To think that one concept accounts for all species or the entire species category is to be monistic. Species concepts often draw very different pictures of the organic world (see Mayr's 1970 version of the interbreeding concept compared to Van Valen's 1976 version of the ecological approach). Moreover, one might be concerned that to accept a plurality of species concepts—a plurality of ways to organize species taxa—is tantamount to antirealism concerning the category. This claim is contentious, however. Ereshefsky (2001, 147) argues that unification and realism do not necessarily go hand in hand. He says, "the species category seems to be a heterogeneous category of very different types of entities" (157). Nevertheless, Ereshefsky thinks that species taxa are real, but he is skeptical of the species category.⁶³ And so, here we gain some conceptual tools in the species debate that can be repurposed to inform individuality: first, the distinction between concepts and categories, and second, the issues concerning species monism and species pluralism.⁶⁴

⁶⁴ Issues concerning the ontological status of species do not translate to issues concerning individuals: the former is about species-as-individuals or species-as-kinds (Kripke 1972, Putnam 1975, Ghiselin 1974, Hull 1978), while individuals just are, ontologically speaking, individuals. A third option to inform the individuality debate is to draw from realism versus antirealism concerning the species category as just pointed out here. I briefly touch on this later.

The following is an ambiguity concerning the problem of evolutionary individuality that is well-informed by the distinction between concepts and categories. In Chapter 2 I discussed a variety of individuality *concepts*. We saw different ways to group biological entities into evolutionary individuals. Recall Godfrey-Smith's (2009) Darwinian individuality view. Individuals in selection will transmit traits to offspring individuals through a particular form of reproduction, which includes bottlenecks and germlines. Alternatively, Ereshefsky and Pedroso (2015) argue that adaptive traits can be transmitted through modes of trait transmission that do not require those criteria, such as aggregation. These are two types of individuals in selection captured by different evolutionary individuality *concepts*. These concepts denote different ways biological entities are organized within the evolutionary individuality *category*. Additionally, recall that there are different types of biological individuals, e.g. immunological, metabolic, evolutionary, and so on. While the biological individuality category is a heterogeneous category comprised of different types of biological individuals, the *evolutionary* individuality category is the class of all types of individuals in selection. I focus on the *Evolutionary Individuality Category* (EI Category).⁶⁵

The EI Category is appropriately captured by a view about evolution by selection, such as Lewontin's 1970 formulation.⁶⁶ And although evolutionary individuality concepts and the individuality category are distinct, there are general commonalities among all types of

⁶⁵ In addition to the EI Category, there is a biological individuality category. For example, perhaps Pradeu's (2012) view of the immune system (or immunogenic response to discontinuous patterns) informing individuality is just one type within that category, while evolutionary individuality is another type.

⁶⁶ There are slightly different accounts of the 'recipe', such as Okasha (2006), Brandon (1990), and Bouratt (2014, 2015). Hull's replicator-interactor account may be just an extension of the original Lewontin formulation. The Price equation might be as well. Okasha (2006) explores the link between Price's equation and Lewontin's account of evolution by selection. The Price equation tracks the combined effects of two or more levels of selection on evolutionary change (2006, 18ff). There could be dispute over the EI category, which includes all types of individuals in selection, if there were a dispute over how evolution by selection works. So far, we seem to just have variations consistent with the original Lewontin formulation.

evolutionary individuals that distinguish them from other types of non-evolutionary biological individuals. For example, given that Lewontin's formulation covers the class of all evolutionary individuals, then at minimum all types of evolutionary individuals must exhibit heritable variation in fitness. And so, individuality concepts should work within those constraints. Notably, different accounts of how evolution by selection works might yield different EI category constraints. But overall, the nature of the EI category—or class of all evolutionary individuals—will be informed by our theories of evolution by selection. This makes sense if our concern is with the objects of selection. And so, to accept multiple individuality concepts as legitimate, is to accept a plurality of evolutionary individuality types. Alternatively, an individuality monist will search for a single correct EI concept to define the EI category. Pluralists will reject that endeavour. But does a claim that the EI Category includes numerous types of individuals in selection challenge the status of that category as a *real* or *natural* category?

Similar to Ereshefsky's (2001) discussion of the species category, the EI category is a heterogeneous category of different types of entities. To accept individuality pluralism, however, does not entail the EI category is unnatural or wholly dependent on pragmatic considerations. Rather, *given* a particular theory of how evolution works, namely the Evolutionary Contingency Thesis, coupled with the role of natural selection, I argue in section 4.3 that ontological pluralism follows. Ontological pluralism is a commitment to what the world is like. This is metaphysical pluralism, rather than an epistemological pluralism due to our epistemic limitations (see Cartwright 1983).

Epistemic pluralism is a plurality of equally legitimate perspectives, and each perspective's usefulness will depend on the given context (see Kellert et al. 2006). Generally, epistemic

pluralists reject the idea of one single investigative aim or interest, and accept a “plurality of *particular* interests and [determine] to what extent the concepts, theories, and methods might serve those interests” (Waters 2006, 197-8). No extra step is made as to whether those perspectives accurately capture the way the world is. Here is one motivation to *not* take that extra step: we are cognitively limited such that we cannot hope to understand all the complexities of the world. Within the context of individuality then, epistemic pluralism might mean that one accepts a plurality of individuality concepts, the usefulness of which will depend on aims, evidence, practice, etc. Perhaps, then, an evolutionary individual is dependent on the aims of biologists in labs. As such, one might think that types of individuals are real only insofar as the concepts, which define them, are useful to the investigator.⁶⁷

For example, Waters (2006) explains the centrality of genes in biological investigation. He says, “[genes] provide handles for manipulating biological processes” (208). One need not take the further step to assume that genes are actually central causal agents in the process. Analogously, perhaps our concepts of different individuality types in selection are useful for understanding how evolution by selection works. The upshot though is that things could be different—individuals in selection are, on this picture, entities used as tools in scientific practice.⁶⁸

Metaphysical pluralism, however, is a claim about ontology. Ontology concerns the way the world is, or rather, one’s commitment to what the world is like. But need one be a *realist* about the entities on that list? Are types of individuals in selection natural or real in some sense? There are different ways to read this to understand individuality pluralism as an ontological

⁶⁷ Queller and Strassmann (2009) identify organism concepts as what is useful to biologists in the lab.

position. First, one might think that types of evolutionary individuals are real—the concepts which refer to them accurately depict the way the world is and carve nature at its joints. This is not the intended version in this dissertation. Even though sometimes ontological considerations sound realist, they need not be.

Rather, I intend a second option: I take evolutionary theory, as a scientific theory, on its own terms. Evolutionary individuality and other types of biological individuals are not “necessarily eternal ontological categories; they are foremost groupings picked out by our best scientific theories and classificatory programs” (Ereshefsky and Reydon 2015, 984). In arguing for ontological pluralism concerning types of individuals, I am not concerned with the realist or anti-realist status of those best theories nor the realist status of individuals as entities relevant for those theories. Lewontin’s recipe for how evolution by selection operates might be groundwork for the class of all EI, but given evolution’s contingency, there is still room for a rich plurality of individuality types. In other words, given the way evolution works *according to our best theories* ontological pluralism concerning evolutionary individuality follows.⁶⁹ That there are many types of individuals in selection is not due to a lack of information, rather as we shall see, the plurality of types falls out of the nature of evolutionary change and the processes that drive it.

In summary, claiming that one type of evolutionary individual is heterogeneous—such that different biological entities can become and cease to be individuals of that type—is not enough to be an individuality pluralist. Moreover, my pluralist agenda is ontological rather than epistemological in nature. In making an ontological claim that the EI category includes multiple

⁶⁹ Claiming that ontological pluralism concerning evolutionary individuality follows from our best theories is open to there being a plurality of theories that “represent an evolutionary situation truthfully” (Waters 2005, 312). This is a tentative realism following Quine: we are committed to what our best science tells us is real. Although Waters is referring to ways in which one might model evolution by selection at different levels, the general lesson holds here.

types of individuals, I remain agnostic about a commitment to realism or antirealism about that category or the types of individuals that comprise it. Rather, *our best theories about* the nature of evolution and evolution by selection suggest that we should be ontological pluralists about types of individuals in selection. In sections 4.2 and 4.3, I explain this in more depth. But first, a discussion of ontological pluralism within the context of individuality is in order.

4.1.4 Ontological Pluralism

Ontological pluralism is a metaphysical claim. And so, individuality pluralism is a commitment to what the world is like, given the way our best theories of evolution characterize how the organic world operates. Evolutionary forces individuate biological entities in numerous ways. For example, in Chapter 3 we saw that even the objects of selection are influenced by other evolutionary processes, such as mutation. This means that processes other than selection matter for evolutionary individuality. Different means of generating heritable variation underwrites the different types of individuals in selection. Some types of individuals may be more statistically significant than others—similar to how rare traits can become more frequent in a population, rare types of individuals in selection can become more prevalent in the biological domain. In other words, there may be more of one type than another at one evolutionary time-slice, but this does not mean that the more significant type is *the* proper type of evolutionary individuality. The more common type can become rare and new types can emerge. Ontological pluralism in this context defines different types of evolutionary individuals because the forces of evolution shape and yield novel mechanisms for the basic units of selection.

Whether a single biological entity (or collective) can belong to multiple types of evolutionary individuals is a worthwhile question. Evolutionary individuals are lineage-forming entities. So, types of individuals in selection are distinguished by the ways in which ancestor-

descendent relationships are formed. In other words, the causal mechanisms by which new token individuals emerge and receive traits from parent individuals distinguish types of evolutionary individuality. This means that to account for how new individuals emerge and inherit traits will be integral for any viable EI concept (insofar as Lewontin's formulation constrains the general category). Under this framework, cross-classification of biological entities across types of evolutionary individuality is possible. An example of this would be a particular entity that can transmit traits in at least two different ways.⁷⁰ Additionally, cross-classification of entities across types of *biological* individuality is possible, especially if evolutionary individuality is just one type of biological individuality. Consider the following example of the latter scenario.

The same entity (or collective of entities) may be both an immunological individual and an individual in selection. Perhaps this cross-classification is common, which might explain attempts to account for evolutionary individuality in terms of immunological features (Gilbert et al. 2012, Pradeu 2010, 2012). Gilbert et al. entertain the idea that holobiont complexes—close symbiotic associations between macro and microorganisms—are individuals in selection. They explain the unity of these multi-genomic complexes by appeal to immune system function. Immunogenic response not only acts to control cheaters it also defines the complex whole from non-self entities by surveying boundaries (2012, 332). However, in order for a holobiont to be a unit of selection, there must be adaptive traits at the level of the whole system that are transmitted to new individuals.⁷¹ Otherwise, the holobiont in question is an immunological

⁷⁰ For example, we see organisms that can reproduce both asexually and sexually essentially switching between the two modes. In the case of evolutionary individuality, the entity would transmit traits through sexual reproduction and aggregative means, which would result cross-classification.

⁷¹ Gilbert et al. claim that the aphid-*Buchnera* case satisfies criteria for group-selection. Alleles can spread throughout a population because of the benefits they bestow on groups, regardless of that allele's effect on the fitness of individual organisms within the group. They think group selection is required to accommodate multi-

individual at best. The evolutionary aspect requires that this token individual transmits heritable traits found at the level of the whole complex. Only then do we find a cross-classification of entities under two types of biological individuality—immunological and evolutionary.

More specifically, humans are part of a multispecies collective—they are the macro-organisms included in a holobiont complex with other species, such as *Clostridium difficile*. *C. difficile* is one of the few species of bacteria responsible for synthesizing a particular mammalian metabolite⁷² (see Li et al. 2008). If Gilbert et al. are correct, then the human-*difficile* holobiont complex has boundaries maintained by immunogenic activity. On this picture not only are humans evolutionary individuals, they are also part of a complex that includes *C. difficile*, a complex which is itself an immunological individual. However, the human-*difficile* holobiont will only be an evolutionary individual if holobiont-level traits (whatever those might be) are transmitted to offspring (somehow).

Notably, under this framework it seems odd to define evolutionary individuals in terms of immunology. The insufficiency of immunology suggests that immunological individuals *might* be evolutionary, but need not be. And so, a biological entity or collective can be both an immunological and evolutionary individual so long as it meets the requisite criteria. This brings us to the next section, which attempts to make sense of individuality pluralism and evolutionary contingency. Thereafter in Section 4.3 I argue how ontological pluralism follows from the evolutionary contingency thesis.

species complexes, but I think this misses the point. If the complex is a unit of selection, group selection is not needed, especially if cheater control is achieved by other means.

⁷² A metabolite is any substance produced during metabolism, or the product (small molecules) that remain after being metabolized.

4.2 Motivating Individuality Pluralism

In this section I discuss how individuality pluralism makes sense within the evolutionary contingency framework. I give reasons to be individuality pluralists and reasons to reject individuality monism. Generally, this section sets up some machinery for what follows.

There are good reasons to be individuality pluralists given the setting of evolutionary contingency. The Gouldian view of evolution as contingently structured means that even if convergent evolutionary outcomes exist, they need not: Contingency in evolution is far more significant and convergence is not inevitable.⁷³ Having diverse and contingent mechanisms that meet Lewontin's general constraints for evolutionary individuality amounts to different types of individuals in selection. I argue for this claim later in section 4.3. As we'll see, these mechanisms are not just instances of trait transmission, but are alternative ways to form parent-offspring relationships needed for selection to occur. The contingent evolution of such mechanisms means we cannot ignore the role of stochastic processes. However, there are also good reasons to reject individuality monism.

Evolutionary contingency motivates a rejection of monism concerning evolutionary individuality. This is because any monistic account of individuality—ones that cite a single set of necessary conditions that cover all cases of evolutionary individuals in the biological domain—do not make sense within the evolutionary contingency framework. There is either one type of individual in selection or many types. However, any monist account of evolutionary individuality is held hostage by the contingencies of history. New individuals will likely evolve that do not meet monist criteria. Therefore, it is reasonable to explore a plurality of evolutionary

⁷³ Evolutionary convergences only count against Gould's contingency thesis when they are not due to internal constraints (see Powell and Mariscal 2015, McConwell and Currie 2016).

individuality types when one is compelled to reject the other option. One might even say that the reason why pluralism makes sense here is because, ontologically speaking, there are many types of evolutionary individuals. Some types of evolutionary individuality may be more prevalent or statistically significant than others. The upshot, then, is perhaps we tend to notice evolutionary individuals that fit Godfrey-Smith's account of reproduction more than others, however, Ereshefsky and Pedroso (2015), make a good case for the relative significance of other types of individuals in selection from a microbial perspective. Mirroring the reasoning of (Beatty 1994, 41), one could say that individuality accounts should be judged by the extent of their applicability in the biological domain and not by their universality (or even correctness) *per se*.

Perhaps the *reason why* ECT makes sense of individuality pluralism is because evolution, as depicted by ECT, yields multiple types of individuals in selection. For example, one may concede that there are multiple types of evolutionary individuals by accepting that at least two types of individuals in selection have been identified in this dissertation. The case of biofilms only gives further credence to the idea that there can be different types of evolutionary individuality. Types of evolutionary individuals undergo change and the entities which comprise them are affected by various types of processes. If different types of evolutionary individuals emerge, evolve, and disappear analogous to speciation and extinction events, then we have different types of individuality that succeed one another through evolution diachronically. But these different types of individuals also exist during the same evolutionary time-slice, albeit some with more prevalence than others. To suggest otherwise—that a single (or set of) mechanism(s) is responsible for individuals in selection—is tantamount to viewing the outcomes of evolution as highly constrained and that evolved individuality mechanisms, such as the

aforementioned modes of trait transmission, are and will continue to be maintained.⁷⁴ I am building a case against that suggestion here. Rather, contingency causes a diversity of evolutionary outcomes. I argue that this diversity amounts to a plurality of evolutionary individuality types, which is the topic of the next section.

4.3 Contingency, Diversity, and Individuality Pluralism

Making sense of individuality pluralism within the context of evolution's contingency is one thing, but showing that individuality pluralism follows from the evolutionary contingency thesis is quite another. Here's an argument.

Contingent individuality pluralism concerning evolutionary individuals requires not only the Evolutionary Contingency Thesis, but also selection as a process that drives evolutionary change. In other words, although ECT emphasizes non-selective, unbiased factors, it does not fully exclude the role of selection (see Beatty 1994 on relative significance). This means that contingent individuality pluralism follows from *both* ECT and some account of selection, in this case Lewontin's recipe. Natural selection is a process biased to environmental conditions and is a (rather than *the*) source of change. If selection were *the* driver of evolution, unobstructed by other factors, then so long as similar conditions hold one should expect similar outcomes. However, evolutionary contingency involves unbiased processes that influence evolutionary outcomes, as well as internal capacities that render the availability of particular traits. The latter means that possible developmental trajectories of traits are previously constrained by evolution, which affect the strategies available to natural selection. The acceptance of contingency as the hallmark of evolution does not completely exclude the role of selection, it merely keeps the

⁷⁴ The argument against evolutionary outcomes as highly constrained is from Beatty (1994, 52). Here I have applied it to the case of individuality.

power of selection in check. This means that individuals in selection are caused and maintained by evolved mechanisms influenced by other processes too, such as mutation, as emphasized throughout this dissertation. Contingent evolution is associated with divergent outcomes—ones that are very different from one another and likely would have been different had we started the evolutionary tape again, even under the same conditions. Such diversity is revealed upon a finer-grain of description concerning a particular outcome at the very least. For example, both octopi and humans have eyes to see, however, there are important structural differences unveiled upon closer investigation. That is, to focus humans change the shape of their lens, whereas octopi move their lens closer and further away similar to the lens of a camera. Moreover, the cellular organizations of octopus eyes and human eyes are very different (Young 1962). Similarly, there are diverse and varying mechanisms for not only trait transmission, but also ways in which variation might be generated too. This diversity is due to natural selection not having a clear shot: the power of selection is confounded by the influence of stochastic processes and internal constraints concerning available strategies to cope with environmental challenges. We saw at least two different ways to generate variation and to transmit traits in the previous chapter—diversity is what one should expect if evolution is contingent. And so, in schematic form, my argument looks something like this:

- (1) The mechanisms of evolutionary individuality are outcomes of evolution, contingently construed.
- (2) Evolution's contingency causes diverse outcomes along with numerous possible evolutionary trajectories.
- (3) Therefore, the mechanisms of evolutionary individuality are diverse with numerous possible evolutionary trajectories.

That this diversity amounts to a plurality of types requires a further step though. One might object that there is only one type of evolutionary individuality realized in multiple ways, such that reproduction and aggregation are mere physical instantiations of trait transmission. How to distinguish between one type multiply-realized and multiple types of evolutionary individuality is the focus of the next section.

4.4 Objections and Responses Concerning a Plurality of Types

How do we established that the diversity resulting from evolution's contingency is a plurality of individuality *types*? There are three variations of this concern to contend with. I take each in turn.

4.4.1 Objection version 1: Convergences are problematic for contingency

One version might go something like this. Because all individuals in selection transmit traits to offspring, all evolutionary individuals in some sense perform that similar function. Perhaps the function similarity overrides the evident diversity in trait transmission and variation generating mechanisms. So, one might argue that there is only one type of individual in selection because there is a functional convergence—trait transmission as a product of evolution has evolved numerous times across different lineages. This means that evolutionary individuality as functionally-defined reveals only one type of individual in selection. This is problematic for two reasons: First, only one type of evolutionary individuality is tantamount to individuality monism—any view that cites a single (set of) criteria for evolutionary individuality. I will address monism later. To start I begin with a more general issue, namely, another reason that functional definitions of evolutionary individuality might cause problems for my view. Traditionally, evolutionary convergences were thought to cause problems for ECT (Conway Morris 2003, McGhee 2011). Evolutionary convergences are often functionally-defined. And

so, a functional definition of evolutionary individuality might be construed as an issue for evolutionary contingency if convergences are indeed counterexamples to the significance of contingent evolution. However, I will argue that converging on a particular function, such as trait transmission, can make sense within purview of evolutionary contingency. Let's take a closer look at why convergences might cause trouble for contingency.

Convergences are evolutionary outcomes that occur over and over again under similar conditions, and are often considered as marks against ECT.⁷⁵ Conway Morris offers a list of numerous evolutionary convergences, such as fins for swimming in whales and fish. When similarities in function cross vast boundaries of relatedness, they are construed as convergent evolution. Conway Morris's list of counterexamples is supposed to undermine the prevalence of evolutionary contingency as defended by Gould (1989, 2002). Because evolutionary outcomes are dependent upon a whole host of factors—internal constraints, evolutionary processes such as mutation and drift—evolution's contingency is more closely associated with *divergences* rather than convergences. This is because there is reduced likelihood of the same outcomes occurring even under the same initial and environmental conditions. That is, evolutionary outcomes are products of unique evolutionary histories that, in turn, shape unique future trajectories of evolution.

⁷⁵ Additionally, Convergences are also cited in support of evolutionary inevitability or predictability of outcomes (see Conway Morris 2003 and McGhee 2011).⁷⁵ That is, as Currie (2012, 584) describes convergences, if we find ourselves under similar selective pressures in similar environments, there should be similar forms. We do not see this with evolutionary individuals: biofilms and birds occupy very different environments with different success conditions. Whereas variability is important in fast-changing environments, finding ways to dampen variation and competition in more stable environments might increase the rate of fitness. With different environments, birds and biofilms face different selective pressures determining optimal adaptive fit. Since one can contest the degree of environmental and thus selective similarity, it's dubious that all evolutionary individuals are relevantly similar enough to be typed together in a non-trivial fashion.

ECT, then, was thought to be the opposite of strong selection pressures yielding extreme convergence (Beatty 1994, 52-53). So, what can we make of the alleged convergence, or in other words, the similarity in function among evolutionary individuals? If we concede that biofilms transmit traits, then both birds and biofilms transmit traits. Here we have different phylogenetically distant lineages converging on a particular outcome—both have adapted to transmit traits somehow. One might argue that this adaptation, as an integral function to evolution by selection, is important enough to override the relevancy of differences concerning how that function is structurally realized. If selective pressures were strong enough, at least in identical environmental conditions we should find outcomes that converge on similar functions to address the adaptive issue at hand. And so, finding cases of evolutionary convergence, as Conway Morris does, is supposed to count against the role of contingency. The frequency of convergence is supposed to demonstrate the power of selection pressure yielding the same adaptations for the same environmental demands.

Up to now I have emphasized the role of stochasticity, or processes such as mutation that are unbiased, rather than biased to environmental conditions. Stochasticity underwrites variety—although wings for flight have evolved numerous times, the morphological and phenotypic details of insect and bird wings vary on a finer grain of analysis. For example, insects do not have the same capacity as birds and bats to alter wing shape (Ray et al. 2016). The Ray et al. (2016) study suggests that *Drosophila* wing shape is not optimized for flight characteristics known to be important. Moreover, bats have more articulated wings with multiple joints that allow for maximal control compared to most birds. As such, birds, bats, and insects fly differently. Similarly, a finer-grained analysis reveals a diversity of mechanisms that generate variation and transmit traits. Chapter 3 discussed how genetic material can be shuffled through

meiosis or lateral gene transfer. Traits can be transmitted through different modes of trait transmission, such as sexual reproduction and other aggregative means. Sometimes what first appears as a convergence falls apart upon a closer look.

Gould was opposed to the prevalence of convergence; he argued that evolutionary history was significantly more contingent such that outcomes are unlikely and unpredictable rather than guaranteed under certain conditions (1989, 233). Recently, however, there has been much critique over the nature of convergences and when exactly they count against Gould's general project (Powell and Mariscal 2015, Powell 2009, McConwell and Currie 2016, Currie 2013, Ghiselin 2016). That types of evolutionary individuality exhibit a functional convergence on trait transmission can be addressed using similar machinery that I will not repeat here.⁷⁶ The main message is that evolutionary convergences are not necessarily inconsistent with ECT. Even if we have instances of evolutionary convergence, espousing ECT is not tantamount to a full rejection of natural selection; it merely defines selection's role modestly in relation to the prevalence of other processes. One might see trait transmission itself as a convergence—trait transmission mechanisms have evolved numerous times in separate lineages with significant phylogenetic distance. However, the point here is that their structural differences are salient enough to distinguish them. Moreover, given the very different environments of biofilms and

⁷⁶ Converging traits that evolve in separate lineages are morphologically distinct, but perform the same function. Some convergences (or so-called parallelisms), however, occur due to internal constraints, such as “molecular-developmental generators,” while others are due to external (i.e. selection) constraints (Powell and Mariscal 2015, 9). The former typically occur in to closely related species, while the latter occurs in distantly related lineages that evolve similar adaptations over long periods of time (Inkpen and Turner 2012, 15). Parallelisms can be construed as consistent with ECT—they are due to internal developmental constraints rather than external constraints, such as natural selection for environmental conditions. In other words, because ECT downplays the significance of selection compared to other processes, convergences-as-parallelisms are consistent within the purview of contingency. And so, some convergences on trait transmission might be parallelisms, though likely the paradigm cases of the two types of evolutionary individual I've identified here (i.e. humans and biofilms) are not parallelisms, which is why I emphasize their structural differences. But the point in this section is merely that convergences are not necessarily inconsistent with ECT.

humans, as exemplars of each individuality type, it's unlikely that external constraints are solely responsible for the existence of trait transmission mechanisms in both cases. That is, strategies available to natural selection are highly constrained.

4.4.2 Objection version 2: The more abstract you go, the less contingency matters

That individuals in selection all transmit traits may not on its own be problematic for the ECT.⁷⁷ Instead one might argue that trait transmission is itself important for evolutionary individuality, but *how* individuals transmit traits is irrelevant. That is, the more abstract you go, the less contingency matters.⁷⁸ Perhaps a functional classification concerning evolutionary individuals has “superior generality” and is valuable because it unites across lineages.⁷⁹ Functional identification of individuals in selection might be seen as necessary and prior to the identification of various mechanisms which function to transmit traits.⁸⁰ Not only does contingency matter less according to this concern, but identification of general function is indispensable when thinking about individuals in selection. On this view, evolutionary individuality is in itself a functionally-defined convergent outcome best captured by the effects of trait transmission, rather than extraneous finer details. This complaint acknowledges the diversity, but downgrades its importance, which undermines using that diversity to distinguish between types.

⁷⁷ Indeed, sometimes convergences can count *in favour* of contingency (McConwell and Currie 2016, Powell and Mariscal 2015). If there is a convergence evident between two types of individuality from similar developmental resources (or a parallelism), then the option is ‘open’ to tokens of that type—the trait in question is evolvable. The emphasis here is not on external conditions shaping what types of individuality arise, but instead on the internal developmental resources of the particular individuals. Our concern should be about what causes the convergence. The idea is that sometimes internal (rather than external selective) forces can cause evolutionary convergences.

⁷⁸ ‘The more abstract you go, the less contingency matters’ objection is from a conversation with Philippe Huneman at the Individuality Workshop in Gut Siggen, Germany in July 2015.

⁷⁹ Reference to superior generality and unity is Griffiths' (1994, 213-4) description of an argument in favour of functional kinds.

⁸⁰ Rosenberg and Neander (2009, 309) argue that selected-effect functions are used in prior identification of parts deemed to be homologous.

What follows is a response to the above concern.⁸¹ Convergences are sensitive to description and often finer-grained details are lost in functional accounts. Suppose Type₁ to include all evolutionary individuals that engage in meiosis and sexual reproduction as modes of variation generation and trait transmission, respectively. Type₂ includes all evolutionary individuals that generate variation through lateral gene transfer and transmit traits to new individuals through other means, such as by recruitment or aggregation. Humans as examples of Type₁ individuals and biofilms as examples of Type₂ individuals each have independent evolutionary histories riddled with the influence of stochastic processes such as mutation. Yet as token individuals of each corresponding type, they both transmit traits to offspring. The point pressed throughout this dissertation, however, is that the details of how this is done matters.

Whether two individuals count as belonging to the same type of evolutionary individuality will depend on how fine-grained the descriptions of those individuals are.⁸² A functional description of evolutionary individuality unites various mechanisms by appeal to their purposes or effects. These descriptions distinguish between types of individuality on a functional basis or by analogy, rather than their unique historical paths and common ancestry. However, defining evolutionary individuality based on function alone does not provide further information about the diverse ways in which those mechanisms actually transmit traits. It is, rather, a coarse-grained description: Although each type of individual may transmit traits differently, we learn nothing more about those mechanisms beyond what they generally do. Correspondingly, we do not learn much about evolutionary individuality. That is, if one

⁸¹ I am borrowing some investigative machinery from a wider debate. Namely, the dispute over classifying character traits according to functional convergence versus a common origin that includes different character states over time (Ereshefsky 2012, Griffiths 1994, Rosenberg and Neander 2009).

⁸² See Inkpen and Turner (2012) for discussion of convergences and coarse vs. fine-grained descriptions of evolutionary outcomes as a critique of Ben-Menahem's (1997) view of convergences.

analyzes evolutionary individuality on purely functional grounds, the finer details are lost at that level of analysis along with the distinguishing structural details. It's not clear, then, how useful functional accounts are when taken only by themselves. There's a cost to giving a functional analysis of individuality. We can, however, distinguish between types by grouping entities according to "their unique continuum starting at the origin of an evolutionary novelty" (Ereshefsky 2012, 384). Moreover, evolutionary individuality types are distinguished by the causal roles in which ancestor-descendent relationships are formed.

A finer-grained description picks up on how Type₁ and Type₂ generate variation and transmit traits. Those details are important. The evolutionary histories inform how trait transmission mechanisms evolve. Not only do finer-grained descriptions matter for uncovering salient differences, they can also be revealing. That is, types of evolutionary individuality converging on a general function of trait transmission actually bodes well with evolution's contingency. Convergence is only a problem for ECT when the finer details, such as the role of stochasticity and other processes unbiased to the environment, are ignored. In turn, ignoring those finer details glosses over the evolutionary histories of each trait transmission mechanism. Albeit the functionalist story can be useful—identifying commonalities between all types of evolutionary individuals helps to distinguish them from other types of non-evolutionary biological individuals. But alone functionalist stories are insufficient if we are interested in the phylogenetic relationships between different mechanisms important for individuals in selection, and the role of other processes besides natural selection concerning those individuals. It is historical, rather than function (or ahistorical) classification that allows us to explain the structural details. Structural methods of analysis allow us to understand how even though bats have more articulated wings than birds, birds outperform bats in terms of flight efficiency by the

finer morphological and ecological features (Mujires et al. 2012). We do not understand this only by knowing that birds and bats both fly. Ditto for trait transmission in both humans and biofilms: if our aim is to understand evolutionary individuality, then more attention to structural features satisfies that aim. And as it happens, we find more than one evolutionary individuality type. Simply put, the details matter.

4.4.3 Objection version 3: How does contingent individuality pluralism compare with Ellen Clarke's Monistic Multiple Realizability View?

Even if one is convinced that convergences are consistent with ECT, as well as that diversity in structural details matter because the fine-grained descriptions unveil a plurality, perhaps there is one final concern. It might be tempting to consider both Type₁ and Type₂ individuals as each having mechanisms that are mere instances of trait transmission. That is, there is really one type of evolutionary individuality defined by a function, which is realized through various physical instantiations—evolutionary individuality is *multiply realizable*. Again the diversity is acknowledged, but there is a denial of multiple EI types. According to Clarke (2013), there is only one functionally-defined type of individuals in selection that is realized by multiple biological mechanisms. There are three notable differences between her view and the one espoused in this dissertation.

First, although Clarke claims to be concerned with individuals in selection, she focuses only on boundary delineation mechanisms. She says,

The problem of biological individuality is a central conceptual issue in evolutionary biology, concerning our ability to delineate the biological units to which fitness can be properly attributed and which participate in the evolutionary process (2013, 413).

Yet her individuality criteria are only policing and demarcation mechanisms:

A policing mechanism is any mechanism that inhibits the capacity of an objection to undergo within-object selection...A demarcation mechanisms is any mechanism that increases or maintains the capacity of an objection to undergo between-object selection (421, 424).

Clarke identifies sexual reproduction as an example of a demarcation mechanism and the immune system as an example of a policing mechanism. No matter how these functions are realized, an individual must have both for selection.

My focus, however, has been on the structural details of trait transmission.⁸³ Evolutionary individuals as units of selection, and therefore integral components of the evolutionary process, must transmit traits somehow. I previously suggested that other types of non-evolutionary biological individuals need not transmit traits. The transmission of heritable traits is, according to Lewontin (1970), a necessary ingredient for evolution by selection. That trait transmission mechanisms distinguish between evolutionary individuals and other biological individuals that are non-evolutionary seems right. However, for Clarke an example of a demarcation mechanism is sexual reproduction—a mode of trait transmission (2013, 421, 424). This means that boundaries are somehow defined by trait transmission, though we learn not much more. Although boundary delineation and maintenance mechanisms may be necessary in some broader metaphysical respect (see Hull 1978, Pradeu 2012), they are insufficient for evolutionary individuality. Evolutionary individuality as a kind of biological individuality will share general properties with other types of biological individuals, such as boundary delineation, but inheritance matters for all types of evolutionary individuality. What exactly Clarke means by

⁸³ Clarke (2016) does discuss trait transmission and Lewontin's general constraints for evolutionary individuality in her assessment of Godfrey-Smith (2009, 2015) and Ereshefsky and Pedroso (2013, 2015). She does not discuss trait transmission directly in relation to her multiple realizability view put forth in her 2013 paper, however.

sexual reproduction delineating boundaries is unclear at best. Regardless, the case has been made for other ways to transmit traits besides sexual reproduction alone.

A second difference between Clarke's multiple realizability view of individuality and contingent individuality pluralism is the following. Clarke's view of individuality moves from the top-down: she defines individuals in terms of a common functional generality. Her view is monistic as she identifies only one functional type. However, I identified the details of specific mechanisms such as sexual reproduction and aggregation that transmit traits, including their morphological and genetic resources. Each trait transmission mechanism having their own unique evolutionary histories is a basis for distinguishing more than one type. Another basis is different causal relationships between generations in either case. Again, functional classifications, although perhaps compatible with classifications according to evolutionary history, are superficial (Griffiths 1994, 216). We can only explain the differences among ways to generate variation (meiosis and LGT) and the differences among the ways to transmit traits (sexual reproduction and aggregation) by emphasizing the details concerning how those activities came about. We gain no understanding of how traits are transmitted just by knowing *that* something transmits traits. Additionally, the causal roles in which relationships between parents and offspring are formed serve to distinguish different types. To promote such a brand of abstraction and unity glosses over the relevant differences between trait transmission mechanisms, which is what I turn to next.

A third difference is that functional accounts, such as Clarke's, or narrow views of trait transmission that privilege sexual reproduction, such as Godfrey-Smith's (2013), fail to acknowledge how different trait transmission mechanisms actually affect selection. If I am right, then there is yet another reason that a focus on structural diversity is worthwhile.

Clarke says that evolutionary individuality emphasizes a biological entity's capacity to respond to selection by evolving cumulative adaptations (2016, 8). She identifies the continuous shuffling that occurs due to horizontal variation generation mechanisms like LGT as eliminating the adaptive value of a novel trait. This is because traits are not passed on with fidelity in aggregative entities like biofilms (11). She argues that fitness-enhancing novelties will lose their fitness by aggregative modes of trait transmission.

Additionally, Godfrey-Smith maintains that the presence of a reproductive bottleneck "has a link to the production of evolutionary novelty" (2009, 91). Bottlenecks play a role in reducing evolutionary activity among the components of the individual because it ensures uniformity rather than competition and ensuing variability at that level. This allows for novel and fitness-enhancing traits that can be built upon to create complex adaptations. However, I argue that if evolution does not put exclusive weight on complexity, then the capacity to pass on heritable complex traits should not be *the* factor in determining evolutionary individuality.

Consider the following:

Basically, by breaking apart the gene combinations that have been favored by past generations of selection, sex and recombination tend to produce less fit offspring...[w]hy is sex so prevalent?...[G]enetic variation is the fuel of evolutionary change, and if sex increases genetic variation, the response to selection will be faster among sexually produced offspring..[but] while a single sexual individual can produce more variable offspring than a single asexual, a group of asexuals can be remarkably diverse, and altogether produce more variable offspring (Otto 2017, 260).

If groups of asexuals can be more diverse and produce more variable offspring, then almost certainly groups of biofilms are something of the same. Drawing from the passage above, if aggregative evolutionary individuals, such as biofilms, produce variable offspring, and because selection relies on variation, those individuals should be more fit than their standard eukaryotic,

sexually reproducing counterparts. In other words, the variability from non-sexual forms of reproduction produce more variable, and so more fit, offspring. While Otto looks to reconcile the prevalence of sex in light of the fact that sex and recombination tend to produce less fit offspring, she mentions nothing about that capacity to produce complex traits as contributing factor.

Notably, Clarke's (2016) critique of biofilms as individuals relies on a biofilm's inability to produce complex traits. Complex traits, due to their cumulative nature such as eyes, cannot evolve in entities like biofilms—the shuffling of genetic material potentially interrupts accumulation of the simpler traits that complex traits are comprised of. But what if evolution by selection does not put a value on complexity? According to the passage by Otto (2017) above, better fitness is evident in variability—something gained through assemblages of entities, which we see in aggregative means of forming new individuals. The relationship between complex traits and better fitness compared to fitness and variability is presumptuous. The upshot is that fitter individuals need not have heritable *complex* traits—this downplays that role variability plays in establishing fitness. If high variability yields fitter individuals, then aggregation as a mode of trait transmission affects selectability. And so, *individuals in* selection in part influence the process which defines them. This is not to say that variability in lieu of complexity is always better though.

Perhaps there are contexts in which assemblages with various simpler traits is a better strategy than the capacity to generate complex novel traits that accumulate over time. Clarke's functionalist account of evolutionary individuality (or any account that de-emphasizes diversity for that matter) does not capture the differences of selection in different environmental situations. One type of evolutionary individual may fair better in particular environments than other types, such that particular strategies work better than others in certain contexts. For example, generally

genomic shuffling is only advantageous “if the environment changes very rapidly overtime (changing direction every two to five generations) or over space is the mean fitness of offspring higher with genomic shuffling than without” (Otto 2017, 260). The evolutionary advantage of more or less shuffling will depend on the environment at hand. And so, a lack of complexity is only a problem in contexts that call for complex traits. If high variability is advantageous in volatile environments, we should not expect complex traits to arise in those situations. Therefore, that biofilms lack complex traits does not negatively affect their status as evolutionary individuals given the kind of environment they occupy.

4.4.4 So there’s a plurality of types, but does “anything go” when it comes to individuality?

A final worry might be whether we have an individuality pluralism that has ‘gone rogue,’ so to speak. Can just about anything be an individual in selection? What about other types of biological individuality? There needs to be some constraints to avoid a trivial collection of individuality types. One might think that types of individuals are just relative to whatever we think or want individuals to be. If so, then asserting that some biological entity is or is not an individual carries no weight. And it does not make sense to say an account of evolutionary individuality (or other types of biological individuality) is more accurate compared to others. The concern is this: identified types of individuals in selection are relative to the observer in a way that causes all sorts of trouble for the pluralist.⁸⁴ And so, there needs to be some means for assessing what counts as a type of evolutionary individuality and what counts another type of biological individuality.

⁸⁴ This description of the ‘anything goes’ objection tailored to individuality is a version borrowed from Ereshefsky (2001, 158-162) that he addresses concerning species pluralism.

To distinguish evolutionary individuals from other types of biological individuals, recall that I have argued individuality pluralism falls out of the evolutionary contingency thesis. For evolutionary individuality specifically, along with ECT and Lewontin's recipe for evolution by selection, a diverse set of evolutionary individuality types follows. I argued that this diversity amounts to a plurality of types. Distinguishing between those types was the focus of the above sections 4.1 to 4.3. I am working within a particular context concerning the nature of evolution and natural selection. All types of individuals in selection, according to Lewontin's framework, must transmit varying heritable traits that make a difference to fitness—these general constraints at minimum distinguish individuals in selection from other types. But how do we judge accounts of evolutionary individuality specifically? I mentioned previously that accounts of individuality types should be judged on their applicability. We then require guidelines for assessment of accounts concerning types of individuals in selection.

I cannot hope to give a full-fledged set of instructions here, but I can sketch what this might look like. First, the act of sorting biological entities into types of evolutionary individuals or other types of biological individuals should satisfy the motivation for sorting those entities—the aims of 'individuality-typing' should be captured to avoid arbitrariness.⁸⁵ This is a form of internal coherence—the specified type of individuality in an account, evolutionary or otherwise, should be consistent with the line of inquiry. Identified individuality types are not relative to the observer, there are guidelines to what makes an individuality type appropriate in a certain context. For example, that particular immunological individuals are not evolutionary, such as a

⁸⁵ These two guidelines for sorting and assessing accounts of individuality types are from Ereshefsky and Reydon (2015) and their discussion of normative naturalism in the classification of kinds. Ereshefsky and Reydon also identify progressiveness as a third criterion—classificatory programs must predict novel facts. So perhaps accounts of individuality types must tell us something new about evolutionary change driven by selection given that evolutionary individuals are units of selection.

sterile mule, does not matter to immunology. This is because immunology is not necessarily concerned with the capacity to transmit traits so much as it is concerned with the stability of particular entities in the presence of biological material that is extraneous (or even pathogenic) to the whole system in question. Questions in physiology, then, will guide what makes an individuality type appropriate in that context—immunological types are more obviously relevant to physiology, whereas evolutionary types might not be.

Second, given that accounts of individuality types must be applicable in the biological domain, their applicability should be empirically testable, at least in principle. We are, after all, making a claim about the nature of particular biological entities in accordance with general views about evolution. For example, claiming that an insect colony is an evolutionary individual at minimum says something about the nature of entities that comprise it—they are parts of a complex system that work together to sustain the function of the whole, for example. Whether a colony of a species of bees fits that bill is an empirical matter. Treating insect colonies as a type of evolutionary individual, for instance, can help to reconcile evolutionary change among different collectives of genetically identical entities. If biologists can learn something new about evolutionary change by treating some entity, or collective of entities, as individuals in selection, then this supports the empirical adequacy concerning their guiding view of individuality. To judge accounts of evolutionary individuality based on their applicability is to find a production of new discoveries relevant to the initial inquiry. If a plurality of individuality accounts does the same, then even better for the individuality pluralist. Notably, I began my inquiry with an aim to explore the reach of the evolutionary contingency thesis and found a plurality of evolutionary types. Not just ‘anything goes’ with individuality pluralism because views of evolutionary individuality must be consistent with, and constrained by, how evolution works and what our

best theories tell us about the world. This means that if “nature’s theme is diversity,” we should work to capture that feature (Gould 1989, 39, 42). Certainly, if the goal is to capture diversity, this renders functionalist or any generally unificationist accounts as supplementary at best.

4.5 A Picture of Individuality Pluralism: The Diachronicity and Synchronicity of Types

There are two versions of individuality pluralism one gains from an evolutionary picture of individuality. First, there are multiple types of individuals in selection over time—new types of individuals evolve through merging and branching events, and perhaps the same type can be distinguished over time analogous to sympatric speciation events. Sympatric speciation is when a new species evolves from a single ancestor without geographic isolation. Similarly, a new type of individual can evolve over time from another type of individual when enough change occurs without branching events that distinguish the types. The succession of multiple types of individuals in selection through evolution is a diachronic form of pluralism. Second, during any evolutionary time-slice in which more than one type of individual in selection exists, there is a synchronic form of pluralism.

Importantly, an aim of this last section is a transition to the next chapter. I illustrate diachronic and synchronic pluralism by using an example concerning the evolution of sexual reproduction. This sets up the next chapter, which focuses on a specific example concerning how new types of individuality emerge through evolution.

As discussed previously, lateral genetic transfer and sexual reproduction (including meiosis) are two ways to shuffle genomic material, which creates the variation that selection works with. There are current studies that explore the evolution of sex. That is, eukaryotic sexual reproduction probably appeared as a resulting outcome of the evolution of lateral genetic transfer (Markov 2014, 219). This is described as an evolutionary move from “lateral gene transfer to

reciprocal whole-genome exchange” (ibid, 231). That meiosis is dependent on eukaryotic cell biology suggests that the emergence of sex and the emergence of multicellular eukaryotes were “inseparable processes” (Gross and Bhattacharya 2010). There is a well-known hypothesis that eukaryotes are of endosymbiotic origin, namely, that mitochondria as organelles within eukaryotic cells originated by an archaeon engulfing a bacterium (Martin et al. 2015, O’Malley 2014, 19). If the emergence of sex is intertwined with eukaryogenesis, then we should expect that sex as a trait somehow evolved from horizontal modes of transfer found in prokaryotes. And we know that in prokaryotes, whole gene transfer is possible in addition to transfer of other genetic material such as non-coding DNA, portions of genes, and multigene clusters (Ragan and Beiko 2009, Markov 2014, 231). This provides grounds for an evolutionary relationship between horizontal and vertical modes of genetic shuffling and transmission. And so, it also provides grounds for an evolutionary relationship between the types of individuals in selection that rely on these mechanisms.

The evolutionary transition from single-celled prokaryotes to multicellular eukaryotes is addressed in the following chapter in greater detail. For now, the idea that sex potentially evolved from horizontal genetic transfer is enough to posit that types of evolutionary individuals, which rely on sexual reproduction, evolved from types of evolutionary individuals that rely on horizontal modes of transfer. This gives a basis to start thinking about a plurality of individuality types over time and at one time. In Chapter 3, I briefly discussed why inheritance mechanisms matter for evolutionary individuality—they create a pattern of ancestor-descendent relationships. This suggests that there are lineages of particular (token) individuals that can be classified into different types. As I said, analogous to how descendent organisms of a particular ancestor can be classified into different species, we may get a new type of evolutionary individual through

branching, or through the merging of two types, or even through significant evolutionary change over time within one type. If this happens, we get a plurality of types over time and at one time. Whereas Chapter 5 analyzes how these ‘individuality events’ might occur, it’s worth pausing briefly for a general picture of individuality pluralism.

A diachronic plurality is a multiplicity of evolutionary individuality types over time. One type of evolutionary individuality (i.e. sexually reproducing multicellular individuals) potentially evolved from another type of evolutionary individuality (i.e. single-celled horizontal trait transmitting individuals). How and when such an individuality event occurs may be up for debate. A type of individuality may change so much that eventually we want to distinguish it from the type it was previously classified as. This would be analogous to sympatric speciation when a new species evolves from a single ancestral species. Moreover, a new type of individuality may branch off perhaps due to isolation of a particular set of token individuals analogous to allopatric speciation. Finally, a new type of individuality might emerge through the merging of two types of individuals (as will be discussed in Chapter 5). However, similar to how a new organism does not make a new species because species are distinct populations that have succeeded for generations (Ereshefsky 2001, 35), a new token individual does not necessarily make a new type of individual. This is because types of evolutionary individuality are distinguished by differences in trait transmission mechanisms that have evolved over a significant amount of time. These inheritance mechanisms not only distinguish different types, but they also facilitate an individuality type’s continuous existence over time. The evolution of individuality mechanisms is contingent upon processes that contribute either towards the stabilization or towards the breakdown of the type in question, such as when the inheritance mechanisms become more prevalent or more obsolete.

In summary, multiple types of evolutionary individuals exist over time. Sexual reproduction and horizontal modes of trait transmission underpin two types of evolutionary individuality that potentially succeeded one another in evolutionary history. This is true if indeed sexual reproduction evolved from LGT. But given that we see both types now, we gain a synchronic plurality of different types existing at one time. But how exactly does a new type of individuality emerge? That is the topic of the next chapter.

“Nature’s theme is diversity”—*Stephen J. Gould, Wonderful Life 1989, pp. 39, 42*

Chapter Five: Individuality Emergence and Disunity in Major Transitions

The aim of this chapter is to investigate the emergence of new types of evolutionary individuality, as well as the role of contingency in major transitions in evolution. I focus on the transition to multicellularity as a case study, which is often considered a major transition in models of large scale evolution and construed as a change in individuality. I also argue that we should expect disunity—all major transitions in evolution do not share a common property because there are different kinds of transitions due to the diverse outcomes caused by evolutionary contingency.

5.1 Major Transitions in Evolution: Traditional Models

Philosophers and biologists offer models to capture the major transitions in evolution (Szathmáry and Maynard-Smith 1995, Calcott and Sterelny 2011, O’Malley 2014, Kirk 2005). Major transitions mark pivotal turning points in life’s history. These are events that yield significant downstream effects and changes in evolutionary processes. However, the identification of such events turns out to be a challenge. Different models of major transitions emphasize various criteria for what counts as a major event, which means different models pick out different events. Szathmáry and Maynard-Smith (1995, 228) give a well-known list of events that they take to be major transitions, which can help get us started with a general understanding. The properties of events that unify their model are contentious—because they do not share the same properties, it’s not clear that all the events on the following list are of the same kind:

- Replicating molecules to populations of molecules in compartments
- Unlinked replicators to chromosomes
- RNA as gene and enzyme to DNA and protein (genetic code)
- Prokaryotes to eukaryotes (to multicellularity)
- Asexual clones to sexual populations
- Protists to animals, plants, and fungi (cell differentiation)
- Solitary individuals to communities (non-reproductive castes)
- Primate societies to human societies (language)

What do the events on this list have in common?⁸⁶ Szathmáry and Maynard-Smith identify common features that occur in many (but not all) of the transitions listed above:

- (1) Entities that were capable of independent replication before the transition can only replicate as parts of a larger unit after the transition
- (2) The division of labour increases efficacy due to task specialization
- (3) Changes in information storage and transmission

These three features should be familiar—they represent a connection between evolutionary individuality and major transitions. In previous chapters, I discussed the nature of individuals in selection. For example, Hull (1992), as well as Ereshefsky and Pedroso (2015), discuss the role of interactors in evolution by selection. Interactors contain replicators—they act as vehicles for replicators and the success of constituent replicators is often dependent on the success of the

⁸⁶ There are historical figures, such as Huxley (1953) and Stebbins (1969), who also sought common properties among notable events in the history of life. In Huxley's 1953 book *Evolution in Action* he discusses the concepts of 'higher' and 'lower' in reference to the Great Chain of Being from microbes to humans. In order to ground a common thread concerning what increases when moving to 'higher' beings, such as humans, he entertained the idea of complexity as one factor among others, but concluded that control of and independence from the environment was the unifying factor in all transitions leading to humans. Stebbins developed the idea of increasing hierarchical structure or levels of organization evident in transitions, such as in the transition to multicelled life. Both authors attempt to motivate a progressive directionality resulting in humans—something the notion of a Great Chain of Being exemplifies. Directionality and progress are denied by Gould (1989, 2002) who argued for a greater role of chance and available trajectories in evolution. Alternatively, the work of Michod (1999) concerning evolutionary transitions in individuality is described as a large-scale search for directionality without a focus on humans (McShea and Simpson 2011, 31).

whole system. New levels of organization often include a collective of parts that interact with the environment, and so we have (1). Moreover, division of labour or task specialization for individuality is discussed as an integral feature of evolutionary individuals by Godfrey-Smith (2009), Clarke (2016), and Ereshefsky and Pedroso (2015), which satisfies (2). Finally, I have emphasized trait transmission for evolutionary individuality throughout this dissertation. In (3), Szathmáry and Maynard-Smith discuss changes in the transmission of information. This is described generally to include their last event on this list, namely, the transition to human language from primates. Regardless, they see changes in transmission as salient. And so, the three commonalities above that are supposed to unify the list of transitions are also thought to be important features for evolutionary individuality.

The connection between major transitions and individuality is not surprising since evolutionary events cited as major transitions typically involve changes to the objects of selection.⁸⁷ Bouchard and Huneman (2013) discuss the emergence of individuality characterized by the transition from a group of entities to members of that group as parts of an individual. The transition to multicelled life is the emergence of a new individuality type, and this matters for both major transitions literature and work on individuality. I do not mean to say that all major transitions are transitions in individuality. Rather, transitions in individuality provide a convenient platform to explore the role individuals play in that context.

I will discuss the transition to multicellularity in detail because it provides an example of how a new type of evolutionary individual emerges. But interestingly, just as how evolutionary contingency influences types of individuals in selection, I contend that contingency also matters

⁸⁷ I leave open the question of whether major transitions *should* (or should not) focus on changes in evolution by selection alone. O'Malley (2014) makes a good case for including other events such as the oxidation of the Earth.

for major transitions. There are numerous debates over the Major Transitions in Evolution (MTEs), such as concerns about the disunity of Szathmáry and Maynard-Smith's model (McShea and Simpson 2011, Michod 1999, Michod and Roze 1999, Queller 2000). I will discuss how evolutionary contingency and its emphasis on divergence and disparity challenges unificationist aims concerning MTEs in section 5.3.⁸⁸ As we shall see, investigating the major transitions through a contingency lens furthers two projects put forth in this dissertation: First, the transition to multicellularity includes an emergence of a new type of individual in selection. Second, analyzing both individuality and major transitions within the purview of evolution's contingency show that framework's scope as a general project concerning the nature of evolution. Before moving on, however, I must introduce the notion of an evolutionary transition in individuality or an *ETI* because the transition to multicellularity is often characterized by that description.

5.1.1 Major Transitions as Evolutionary Transitions in Individuality (ETIs)

Many of the events on Szathmáry and Maynard-Smith's list above, such as the transition to multicellular life, are characterized in terms of transitions in individuality (Michod 1999, Michod and Roze 1999, Michod and Herron 2006, Clarke 2014). That is, transitions are the “evolution of higher-level wholes from lower-level individuals, the emergence in evolution of new and higher levels of selection” (McShea and Simpson 2011, 28). Such a description demonstrates how major transitions are directly relevant to evolutionary individuality because they include the notion of a hierarchical organic domain: “lower level units group together...to form higher level units of organization” (Michod and Roze 1999, 1). Michod and Roze view transitions between levels in the hierarchy as the process of Darwinian properties, such as

⁸⁸ Other debates over models of major transitions not directly addressed are questions of hierarchy or scale, e.g. how the different levels exemplified in the list are related (Jablonski 2007), or the notion of hierarchy versus scale (Odenbaugh, n.d.), or life having a directional trend (see Conway Morris 2003, Vermeij 1987).

heritability and varying fitness, emerging at a new level “from the evolution of interaction in groups of lower level individuals” (ibid).

However, the characterization of *all* MTEs on Szathmáry and Maynard-Smith’s list as transitions in individuality is disputed (see McShea and Simpson 2011 on miscellaneous transitions⁸⁹ and O’Malley 2014).⁹⁰ A common complaint is one of disunity.⁹¹ Szathmáry and Maynard-Smith’s model of transitions is disunified if there is not a common thread—a shared property that unites all events on the list. As McShea and Simpson state, “a common thread will reveal something about the evolutionary process, about its robustness perhaps, its repeatability, or the nature of the forces guiding it” (2011, 22). Conversely, one theme of this chapter is that the *lack of* a common thread is also revealing. Specifically, the lack of a common thread reveals something about the fragility, diversity, and the nature of the forces besides natural selection driving evolutionary change. There are two ways one might approach the task of unifying transitions: One might start with some variable “predicted to increase by evolutionary theory...and ask what series of transitions (if any) it predicts” (ibid). Considering major events to be ETIs as Michod (1999) is an example of that approach. In this sense, properties associated with changes in individuality are identified first and used to pick out events that count as major. Alternatively, one might give a series of events identified as major transitions and investigate the commonalities between them as Szathmáry and Maynard-Smith (1995) have done. In both cases, to provide a unified model is the aim. The latter half of this chapter challenges that endeavour.

⁸⁹ Miscellaneous transitions are events that do not count as significant.

⁹⁰ Even though McShea and Simpson (2011) criticize the unity of MTE models, such as Huxley’s, Stebbin’s, and Szathmáry and Maynard-Smith, they still call for unified model to achieve ‘theoretical consistency’.

⁹¹ A related complaint to the disunity of major transition models is that conceiving of MTEs as ETIs leaves out events that shouldn’t be left out, such as the oxidation of the Earth. This is a concern about how to identify which event should be considered major events such that they count as transitions, rather than miscellaneous or ‘minor’ events.

The importance of the transition to multicelled life in Michod's framework concerning ETIs is twofold. On the one hand, it is an wonderful example of how a new type of individual in selection emerges, as well as how multiple evolutionary individuality types can exist at one time. On the other hand, Michod's view that all major transitions include changes in individuality gives necessary background for the alleged problem of disunity—the lack of common properties shared by all major transitions. However, under a contingency framework I will show why one should embrace disunity. I argue that the divergence and disparity found in ECT supports a disunified model of major transitions.

I have briefly introduced the major transitions debate and the idea that some of those events count as evolutionary transitions in individuality. This gives needed background for the case study of this chapter: the transition to multicellularity. The chapter takes the following structure: Section 5.2 explains how transitions to multicellularity can occur, which includes details of how unicellular life comes together to form a multicellular unit, such as through endosymbiosis or aggregation. The transition to multicellular life is often characterized as a transition in individuality—entities that were at one time discrete units of selection come together to form a new unit of selection. In Section 5.3, I move to a broader scope and discuss a problem concerning the quest for unity in major transitions literature. I address this problem by exploring the major transitions within the framework of evolution's contingency. Finally, evolution's contingency often yields exceptions to general rules concerning the operation of evolution. And so, Section 5.4 explores individuality “in reverse,” namely, whether cancer is a breakdown in individuality and a failure of the multicellularity transition.

5.2 The Transition to Multicellularity

Generally, this section aims to give a sense of how new individuals in selection emerge through transitions in individuality. Although the details are contentious, I first discuss how multicellular life occurs by exploring the transition to multicellularity through endosymbiotic and aggregative means. Second, I outline Queller's (2000) classification of ETIs into two kinds. His classificatory scheme draws from the relationship among entities that form a new multicellular individual.

5.2.1 Numerous Transitions to Multicelled Life

Referring to *the* (rather than *a*) transition to multicellular life is infelicitous: there have been numerous transitions to multicellularity (Bonner 1998, Wolpert and Szathmary 2002). "Plants, animals and fungi are the most spectacular and complex achievements of this kind" (Wolpert and Szathmary 2002, 745). Grosberg and Strathmann (2007, 622) claim that "multicellular organisms independently originated at least 25 times from unicellular ancestors...once for metazoa...multiple times (with secondary losses) in plants, fungi, and the Eubacteria." The first evidence of multicelled life is early in evolution dating back 3 to 3.5 billion years ago (Knoll et al. 2006). The "most ancient transitions occurred in the major lineages of large multicellular eukaryotes approximately 1,000 million years ago" (Rainey and Kerr 2010, 1). As I mentioned in previous chapters, basic morphological structure of metazoa saw increased diversification approximately 500 mya. This gives a sense of the timeline. There are at least two identified ways multicellularity can occur. First, by the merging of at least two or more different cells, such as in the endosymbiotic origin story concerning mitochondria in the cells of multicellular eukaryotes. And second, through aggregation. I take each in turn.

Endosymbiosis is a symbiotic relationship. Generally, symbiotic relationships occur between two or more organisms from different species in a way that often benefits both parties. These relationships are constituted by a variety of associations. There is endosymbiosis within cells, ectosymbiosis outside of cells, as well as mutualistic, commensal, and parasitic interactions (Moya et al. 2008, Moran 2006). I have already introduced symbiosis in chapters 2 and 3. Recall that one example of a symbiotic relationship is vertically transmitted symbionts that live in insects, such as the aphid-*Buchnera* symbiosis. *Buchnera aphidicola* “is the obligate symbiotic intracellular bacteria of aphids” (Charles et al. 2011). Other associations are more intermittent with horizontal modes of transfer, such as the squid-*Vibrio* association in which the bacterial symbiont *Vibrio fischeri* enters the light organ of its host the Hawaiian Bobtail Squid (Nishiguchi 2002). I have also discussed the holobiont complex—multicellular eukaryotes such as Metazoa like humans have complex relationships with “colonies of persistent symbionts” (Gilbert et al. 2012).

The above examples of symbiosis show that accounts of selection pressure concerning populations of same-species individuals are too simplistic (Bouchard and Huneman 2013, 5). How different views of evolutionary individuality address multispecies consortia was addressed in Chapter 2. For current purposes, cases of symbiosis represent potential instances of new types of evolutionary individuality emerging through the merging of multiple lineages. As mentioned, symbiosis can help us understand how a new individual emerges because it is one means of transitioning to multicellularity through the union of two types of cells. One well-known origin account of eukaryotes states that an archaeon engulfed a proteobacterium 1.5 billion years ago. That proteobacterium evolved into what we now know as mitochondria (O’Malley 2014, 19, Ku et al. 2015, Alvarez-Ponce et al. 2013). Mitochondria are eukaryotic organelles that have

“conserved their prokaryotic biochemistry, but their genomes are reduced” (Ku et. al. 2015). In this case, a new type of evolutionary individual emerges because at some point two individuals in selection joined forces. The emergence of a new type of individuality through endosymbiotic means might seem particularly compelling because of the “engulfing” component. Selection acts on the entire complex, which is physiologically contained one inside the other, rather than on the units which comprise it. However, as long as a similar amount of functional integration is achieved, it is not obvious that physical containment is necessary for all cases where two or more individuals merge to count as one unit in selection.

Another way to characterize the event is this. Darwinian properties are now found at the level of the whole such that the fitness of one constituent wholly depends on the success of the entire system. Godfrey-Smith (2009, 2013) refers to this as *de-Darwinization* when lower level competition decreases and selection is suppressed. Recall that Szathmáry and Maynard-Smith (1995) also discuss suppression of lower-level competition as a marker of major transitions.

A second way multicellular individuality can occur is through an aggregation of cells where the relationship among cells transitions into something new—these cells come together to form one multicellular individual (see Bouchard and Huneman 2013). The cells can be related as when daughter cells are glued together in *Pseudomonas fluorescens* (Hammerschmidt et al. 2014, 75), or when unrelated cells in biofilms aggregate (Doolittle 2013, Ereshefsky and Pedroso 2015). Often model organisms are used to investigate how this happens.

For instance, Hammerschmidt et al. (2014) discuss the role of cooperation, cheater suppression mechanisms, and controlled generation of cheater phenotypes using *Pseudomonas*

fluorescens as a model organism.⁹² Rainey and Kerr (2010) discuss the same case study but in reference to life cycles, collective reproduction, and again cheater control. Others claim that collectives of *Saccharomyces cerevisiae* form a multicellular collective in response to environmental stress that includes evidence of reproductive division of labour (Libby et al. 2014, Koschwanez et al. 2011). And finally, there are additional model organisms used to investigate the transition to multicellularity include unicellular and multicellular phases in life cycles, such as *Dictyostelium discoideum*—a slime mold or other social amoeba (Queller and Strassmann 2012). In studying the transition to multicellularity, these authors seek to understand how a new type of evolutionary individual emerges—Darwinian features, such as heritable varying fitness—emerge at a different level of organization out of entities that were each previously individuals in selection on their own.

There are different stories for how multicellularity arose whether it be aggregately or endosymbiotically. Each case shows how a new type of individual in selection emerges. Queller (2000) proposes that there are two kinds of transitions to multicellularity. If he is right, then not only do we learn how new evolutionary individuals emerge in transitions, we also gain general insight into transitions in individuality.

5.2.2 Two Kinds of Evolutionary Transitions in Individuality

At least two kinds of ETIs have been identified: fraternal (Queller 2000, Birch 2012) and egalitarian (Queller 2000, Kerr and Nahum 2011, Baptiste 2014). Fraternal transitions occur

⁹² Hammerschmidt et al. state that “cheats play a critical role in a simple multicellular life cycle where the central problem is not cheater suppression, but rather controlled generation of this phenotype” (2014, 75). This is an alternative to the view that evolution of mechanisms for cheater suppression is a critical step in the transition to multicellularity (ibid). Notably Godfrey-Smith’s notion of de-Darwinization and critiques of aggregatively-formed individuals, such as Clarke (2016), rely on the role of cheater suppression. Hammerschmidt et al. distinguish between cheater control and cheater suppression.

among entities that are closely related, such as the related daughter cells that glue together in *Pseudomonas fluorescens* mentioned above (Hammerschmidt et al. 2014, Rainey and Kerr 2010), as well as multicellular yeast, such as *Saccharomyces cerevisiae* (Libby et al. 2014, Koschwanez et al. 2011). Egalitarian transitions occur among entities that are not closely related, such as multispecies biofilms (Doolittle 2013, Ereshefsky and Pedroso 2015), as well as the endosymbiotic origin of eukaryotic mitochondria. Egalitarian transitions are particularly interesting. They make sense of the idea that multispecies individuals, such as biofilms, are evolutionary individuals and not merely marginal cases of individuality. Additionally, distinguishing between two types of transitions in individuality is a step towards a more pluralistic model of MTEs discussed in Section 5.3.

Queller (2000, 1648) describes egalitarian transitions as the assemblage of alliances forged between different entities. Egalitarian transitions are common in the microbial world and occur when “higher level units emerge from genealogically different components” (Baptiste 2014, 3). Having already discussed biofilms at length in previous chapters, another example is *Parakaryon myojinensis*, a microorganism discovered off the coast of Japan, which seems to have cellular features intermediate between prokaryotes and eukaryotes. This microbe is thought to establish a path between the two types of cells and support the origin story for mitochondria (Yamaguchi et al. 2012, 2014). If the endosymbiotic origin story of eukaryotic cells is accurate, then we have an instance of an egalitarian transition to a new type of evolutionary individual. Egalitarian

transitions show how functional differentiation can arise in previously unrelated units, which then comprise one heterogeneous individual system as an object of selection.⁹³

Whether egalitarian and fraternal transitions exhaust the categories for transitions might be up for debate. These are general ways to describe a change in organization such that a new level in the biological hierarchy includes objects of selection. The transition to multicelled life also sets a foundation for thinking about the different ways in which a new type of evolutionary individual can emerge, and especially how more than one type of evolutionary individuality can exist at one time. This brings us to the next section where I explore the transition to multicellularity within the framework of contingency.

5.2.3 A New Type of Evolutionary Individual Existing with Other Types

Recall from chapter 4 that a new type of evolutionary individual existing with other types at the same time is a synchronic plurality. Also, recall that evolution's contingency causes diverse outcomes along with numerous possible evolutionary trajectories. I argued that this diversity amounts to a plurality of evolutionary individuality types. Importantly, however, the transition to multicellularity not only illustrates the emergence of a new type of individuality, but it also suggests that other types of individuals in selection do not perish upon the emergence of a new type. In other words, some of these "individuality events" do not necessarily result in the extinction of individuality types whose tokens might have been involved in the event. If this is the case, we get different types of evolutionary individuals existing at the same time. The main focus of what follows illustrates how synchronicity of individuality types is viable.

⁹³ Notably, Queller (2000) states that through egalitarian transitions, parts are still able to sustain their own reproductive autonomy even with cooperation and cytodifferentiation. Since reproductive division of labour is evident in biofilms, that contention can be challenged. More recent work discusses the role reproductive specialization has in microbial egalitarian transitions (Kerr and Nahum 2011, Baptiste 2014).

Here is an example. There is good evidence that the endosymbiotic origin story of multicellularity—the engulfment of a proteobacterium by an archaeon resulting in the modern day eukaryotic organelle, the mitochondria—is perhaps one way in which a transition to multicellularity occurred. The emergence of the eukaryotic cell resulted from the merging of two different cells from two different domains of life. There are now, in effect, three domains of life: Bacteria, Eukarya (eukaryotes), and Archaea (Pace 2006). The joining of archaea and the proto-version of bacteria did not result in the eradication of the type of individuality that includes single-celled organisms, like bacteria and archaea, which pass on heritable traits mostly through binary fission.⁹⁴ If we think of multicellular individuality as one type of evolutionary individuality, other types, such as single-celled entities, still exist despite the transition to multicelled life.

Not only do we get a diversity of individuality types at one time, but the transition to multicellularity unveils diverse ways in which a new type of individual can emerge. This should be expected if evolution is contingent—evolution’s contingency causes diverse outcomes along with numerous possible evolutionary trajectories. These trajectories shape the possibility space for evolution that may or may not be fulfilled depending on what transpired previously. We have seen at least two ways that the transition to multicellularity occurred through symbiosis (e.g. the endosymbiotic origin story) and through the aggregation of unicellular microorganisms (e.g. biofilms). The different mechanisms that facilitate such changes are disputed, however. For example, there is disagreement over what counts as the primary conflict mediator in the

⁹⁴ Pace (2006) states that archaea and eukarya are more closely related to one another than either is to bacteria. Single-celled organisms will be a type of individual in selection insofar as they are selected—they have different mechanisms for passing on heritable traits. Prokaryotes reproduce mostly by binary fission and never experience mitosis, namely, the division of nucleated cells (O’Malley 2014, 51).

evolution of multicellularity (Grosberg and Strathman 2007, 18). Conflict mediation matters for the emergence of a new individuality type because conflict breeds differential selection—cheaters or defectors can outcompete other organisms by taking advantage of community-building altruistic behaviour for resources or defense. On the one hand, some philosophers and biologists discuss the role of the unicellular bottleneck and emphasize relatedness as a main factor in the transition to multicellularity (Keller and Surette 2006, Szathmáry and Maynard-Smith 1995, Queller 2000, Godfrey-Smith 2009). Increased relatedness decreases the variation selection needs to work with. On the other hand, there are others who omit the bottleneck entirely or acknowledge its significance as secondary (Buss 1987, Michod and Nedelcu 2003, Ereshefsky and Pedroso 2015). Instead, they emphasize features such as self-policing, apoptosis (or programmed cell death), the separation of the germline from other cells, and maternal control over cell fate, such as mitochondria DNA transmission through the maternal line in most animals. It is not clear that one method of conflict mediation is better than the other—bottlenecks might work better in contexts of relatedness or fraternal types of transitions, whereas a case with diverse phylogenies, such as in egalitarian transitions, can be managed by other means. Notably, in the latter case we find multiple ways to deal with conflict even under the same conditions from self-policing to maternal control over cell fate. In the final section of this chapter, I discuss how some of these methods of conflict mediation go awry in the case of cancer. To characterize discussions of conflict control as a dispute is misleading, if the different camps each emphasize a mechanism that can control conflict according to a particular context. To think that one size fits all, that is, to think that bottlenecks manage conflict equally well in all evolutionary situations, does not demonstrate an appreciation for the vast array of challenges individuals might face at any given time.

We know that multicellularity has evolved over twenty-five times in at least two different ways (Ratcliff et al. 2012, Yong 2012, Bonner 1998). This fact alone challenges the idea that there is only one method of conflict control—why should we be so conservative when evolution provides us with reasons not to be? Some strategies work better in particular contexts, which means that complaints of too much variation require contextualization. For example, bacteria and other prokaryotes have “limited morphological variation” (Bonner 2013, 3).⁹⁵ However, especially in multispecies biofilms, there is great genetic variation, at least when compared to standard metazoan multicelled life. I previously discuss in chapter 4 how individuals with increased genetic variation do best in rapidly changing environments—the sort of environments that microbes are suited to.⁹⁶ From this one draws a general lesson: some methods of conflict control might not include a decrease in variation *tout court* precisely because that type of variation—genetic, morphological, etc.—is advantageous in a certain environment. This undermines complaints about too much variation in microbial individuals formed through aggregation when variation is beneficial to that individual’s survival.

In summary, egalitarian transitions that involve the emergence of new evolutionary individuals from unrelated components provides an interesting platform for thinking about certain transitions to multicellularity. We have seen how this can occur through means of symbiosis or aggregation. But a new type of individual also requires a method of “staying

⁹⁵ I discussed Clarke’s (2016) complaint of too much genetic variation in microbial individuals formed through aggregation in chapter 4.

⁹⁶ Bonner (2004) discusses the role of size in evolution from a microbial perspective. Whether evolutionary transitions in individuality always signal an increase in complexity and the significance of complexity in evolution are both contentious. McShea and Simpson (2011) deny this and Bonner (2004) argues that an increase in size requires an increase in complexity. The main message is that the existence of complexity does not necessarily discount the importance of simplicity in evolution. In situations where an increase in size is called for, an increase in complexity merely suffices to get the job done.

together” through conflict control. I have argued that different strategies work better in different contexts, and as such, it is likely that one method of conflict control might fare better or worse depending on the nature of the relationship needing to be maintained. A project in favour of evolution’s contingency should oppose conservatism about evolutionary outcomes. That is, to suggest that views concerning methods of conflict control are necessarily in dispute with one another such that only one can be correct is not careful enough. There are different sorts of conflict control employed in different situations and sometimes even under the same conditions. We also should not expect all methods of conflict control to be exactly the same given the diversity of the biological domain.

In summary, a focus on the transition to multicellularity shows how types of individuals in selection can exist synchronically—the emergence of a new type of evolutionary individual does not entail the extinction of previous types. Additionally, accepting multiple conflict control strategies for transitions to multicelled life is consistent within a contingency framework. It captures the diversity associated with evolution’s contingency. And some modes of conflict control simply may not be available as strategies depending on the evolutionary history concerning how an egalitarian individual came to be. I now move to a problem concerning the major transitions that is broader in scope, namely, the problem of disunity. In the next section I discuss how the Evolutionary Contingency Thesis addresses that problem.

5.3 Contingency and Unity of Major Transitions Models

There are numerous debates over Major Transitions in Evolution (MTEs), such as concerns over which, if any, features are similar enough across transitions such that they unify the set of events specified by Szathmáry and Maynard-Smith (McShea and Simpson 2011, Michod 1999, Queller 2000, Calcott 2011). I argue that evolutionary contingency causes different kinds of

major transitions. That there are many kinds of transitions calls for a disunified model. That is, there is not one property, or a single set of properties, that all and only major transitions share. If there is a plurality of transition kinds, then the quest to unify a single model of all major transitions is far less compelling. There are, rather, multiple sets of major events.

First, I start with a selective historical introduction to the problem of unification. Thereafter I assess Calcott's (2011) pluralistic view as one possible solution and discuss my approach to the debate.

5.3.1 Background on the Problem of Unification

As mentioned, Szathmáry and Maynard-Smith's (1995) list of events draws attention to the following problem: Which events should be considered major transitions in evolution or *MTEs*? In other words, how does one identify events that significantly influenced the direction of evolution? To discover a shared property allegedly provides insight into life's history. This common property *unifies* disparate events. One possible shared quality among major events is a shift in biological organization, which has been characterized as a change in individuality. These shifts cause a more inclusive level of organization, such as transitions from unicelled to multicelled life, that selection acts on. I will further discuss the ETI model which identifies all major transitions as changes in individuality (Michod 1999 and Queller 2000), followed by two responses (McShea and Simpson 2011, O'Malley 2014). All parties aim to provide a unified model of major transitions. Together, their accounts will help both to shape the landscape of research on this topic and to situate the view I propose later.

Michod (1999) and Michod and Roze (1999) understand the transitions as the origin and maintenance of a biological hierarchy. This means that *MTEs* are events that affect the organization of different biological levels. Increase in hierarchy was thought to signal an

increase in complexity—significant events in life’s history result in a new level of organization for selection to act on. These were construed as the emergence of new individuals in selection or *ETIs*—Evolutionary Transition in Individuality. Michod and Roze primarily assess and develop views about the methods of cooperation and conflict control when groups form new higher level individuals. If all major transitions constitute an evolutionary change of the sort that yields new individuals in selection, then we have a unified model—each event shares a common feature that unites them as MTEs. Queller (2000) was influenced by the focus on transitions in individuality. As discussed in Section 5.2, Queller explores the role of cooperation and conflict control (Queller 2000, Queller and Strassmann 2009, 2012). He states that “many of the major transitions in evolution involved the coalescence of independent lower-level units into a higher organismal level” (2000, 1647). I have discussed the two ways in which he thinks this occurs in Section 5.2.2 of this chapter, namely, fraternal and egalitarian transitions. Michod, Roze, and Queller remedy the unity problem by narrowing major transitions to only the transitions that include changes in individuality.

So far, if the goal is to give a unified model, then identifying events in which a new evolutionary individual emerges is one way to meet that challenge. In other words, all major transitions are just transitions in individuality. But one might wonder whether this is too narrow. McShea and Simpson (2011) discuss miscellaneous transitions not included on Szathmáry and Maynard-Smith’s list, as well as the notion of minor transitions compared to what counts as ‘major.’ Their work embodies a turn against Michod’s focus on increased hierarchical complexity and higher levels of selection. McShea and Simpson note that Szathmáry and Maynard-Smith’s model is, as it currently stands, disunified. They are critical that all events on Szathmáry and Maynard-Smith’s list share a common thread (2011, 32). Michod’s focus on

transitions in evolutionary individuality does not necessarily capture the case of cultural transmission, for example, since that case does not obviously produce higher level selection (30). They call for a revision of the received model that doesn't focus on hierarchical complexity through the creation of new units of selection, as well as for the continued search for a common feature to unite that model (31). They claim that to relinquish unity yields to theoretical inconsistency. Specifically, the lack of a common thread results in an unprincipled analysis of major events. This can result in inconsistencies in our explanations, as well as an arbitrary collection of events or as they say, "just one damn thing after another" (22, 32).

O'Malley (2014) is also critical of the traditional model, but for a different reason. Not only is the original Szathmáry and Maynard-Smith model disunified, the attempts to unify that model often leave out significant events. O'Malley discusses the Great Oxidation Event facilitated by ancestral cyanobacteria around 2.4 billion years ago (6, 20, 198). She argues that this event qualifies as a major event because it was important for all life. However, the Great Oxidation Event is typically excluded from that set due to both a focus on multicellularity and attention to evolutionary transitions in individuality. She states that "half of the eight transitions are concerned with features of multicellularity (obligate sexuality, cellular differentiation, social groups and human communication)" (20). There is a eukaryotic bias that ignores much of microbial life and other events in Earth's history. O'Malley is concerned that too much attention has been paid to a macro, rather than a micro, perspective demonstrated by the focus of transitions that led to our existence as humans and metazoan life generally. O'Malley's concern is echoed by Szathmáry himself in later work when he says we should be "linking transitions to Earth's history" rather than only the history of life because the former is necessary for the latter (Szathmáry and Fernando 2011, 307-8). This characterizes The Great Oxidation Event as an

important event in Earth's history, as well as for the history of life itself. Overall, O'Malley criticizes any model that achieves unity through a bias towards larger life. In other words, we should *not* narrow our focus to achieve unity at the risk of overlooking significant events.⁹⁷

As illustrated above, attempts to explain the structure of evolution typically include the search for a common thread that unifies pivotal turning points in life's history. Identifying a shared property among transitions in evolution is supposed to reveal something about their nature. That is, the identification of a shared property unifies diverse events, and by that token explains them. The search is for a stable and robust pattern, which is supposed to help us understand why such changes occurred and how they affected not only the trajectories of evolution, but also the evolutionary processes themselves. As we shall see, Calcott (2011) offers an alternative way to understand life's history, however, the aim for unity remains the same.

5.3.2 Calcott's MTE Pluralism and Inheritance as One Possible Unifying Factor

Calcott (2011) thinks there can be multiple similarities among major transitions. First I discuss his view that inheritance is a potential unifying property of transitions—he is worried about the mechanisms that *cause* major transitions, rather than effects of transitions (i.e. effects such as increase in complexity or more inclusive hierarchy). Second I address his explanatory pluralism as a potential, yet problematic, solution to the problem of unity.

Calcott argues that the evolution of inheritance matters for transitions in individuality. We already know from previous discussions in this dissertation that inheritance mechanisms are integral to evolutionary individuals—they are what sustains populations of individuals in selection by the creation of new token individuals of a particular type. Especially the evolution

⁹⁷ For a review of O'Malley's 2014 *Philosophy of Microbiology*, see McConwell (2015a).

of multicellularity requires evolution of a “higher” unified entity with its own fitness and developmental cycle, which both require advances in mechanisms of inheritance.⁹⁸ Such transitions in inheritance “involve[e] innovations that expand the fidelity and bandwidth of inheritance” (Calcott and Sterelny 2011, 11). Calcott and Sterelny propose that high-fidelity inheritance is required for cumulative or complex traits such that development is structured for the next generation. If the mechanisms of evolutionary individuality are inheritance mechanisms, such as sexually reproducing multicelled life with bottlenecks to address conflict or precise dispersal and recruitment techniques, then it makes sense that changes in individuality correspond with changes in inheritance. Though I argued in Chapter 4 that complex adaptive traits are not necessarily required for evolutionary individuality, Calcott’s proposal of inheritance as a property of major events is important because it reveals new major events, such as the Cambrian explosion.

Calcott argues that the Cambrian explosion should be considered a major transition in evolution because of its innovations concerning inheritance. Over 500 million years ago “modern multicellular animals make their first uncontested appearance in the fossil record...[it] marks the advent (at least into direct evidence) of virtually all major groups of modern animals” (Gould WL 1989, 24). Calcott focuses on the mechanisms that *bring about the major transitions*, rather than their effects alone (e.g. increases in complexity, 2011, 35). The Cambrian explosion is also a major diversification event, which at first glance seems relevant to an account of transitions within the purview of the evolution’s contingency. Moreover, innovations in inheritance as features of MTEs not only picks out diversification events, but inheritance is also a

⁹⁸ Calcott and Sterelny (2011, 11) introduce Calcott’s entry in the edited volume as a view about alternative ways of seeing common features across the transitions.

feature of individuals in selection (Ereshefsky and Pedroso 2015, Godfrey-Smith 2009). And so, that major changes in individuality include changes in inheritance mechanisms should be no surprise.

Calcott, however, maintains that innovative inheritance is only one potential unifier of transitions. He thinks that there are multiple similarities among major transitions that unify the set. The exploration of multiple similarities yields a plurality of unifying explanations—he is a unificationist concerning major transitions in evolution. He states,

Claims of similarity across the transitions are best understood as explanatory generalizations. The properties that are similar pick out key factors that enabled particular transitions to occur, yet they do so in a way that remains abstract enough to apply across diverse events. In doing so, they both *explain and unify* the recurring pattern of transitions (2011, 35 my italics).

There are, then, multiple legitimate ways to identify unifying properties of major events. Calcott proposes that the identification of inheritance innovations is just one way to identify commonalities among the events on Szathmáry and Maynard-Smith’s list, in addition to the three originally proposed properties.⁹⁹ In what follows, I outline Calcott’s pluralist position to set up a contrast for my own view, which is informed by a particular way to think about evolution itself. Specifically, even as a pluralist Calcott aims for unity, whereas I think there are good reasons to doubt that aim.

Calcott maintains that “even when we identify a particular biological phenomenon, we can still go about explaining it in a number of ways” (2011, 35-6). There are different kinds of

⁹⁹ Recall that Maynard-Smith and Szathmáry identify three properties as commonalities among the transitions in their model: (1) entities capable of independent replication before the transition can only replicate as parts of a larger unit after the transition, (2) the division of labour increases efficacy due to task specialization, and (3) changes in information storage and transmission.

explanation in biology that can address the transition to multicellularity, for example. With cooperation as an integral component to the advent of multicellular life, there are several factors that stabilize cooperation, such as relatedness or conflict control mechanisms. He argues that something similar occurs for the set of all major transitions. Typically, generalizations about MTEs abstract away from the biological details to cover a whole range of different events (39). In his paper, Calcott uses different generalizations to explain the transition to multicellularity specifically. He then turns to all MTEs and applies the same reasoning at a larger scale: We can give different explanations for the major transitions by identifying broad explanatory generalizations, which each pick out key factors that enable transitions to occur. The broad generalizations are abstract enough such that they apply across a diverse set of events, in effect, unifying the set (2011, 35).

However, the explanations that rely on broad abstractions are not in conflict with one another because they vary in their focus of analysis. For instance, Calcott discusses how multicellularity can be explained by conflict mediation. He also discusses how the generation of benefit occurs such that individuals in groups will do better together than on their own (2011, 39). Finally, he proposes that one might give a historically-inclined explanation, which identifies the evolution of traits from unicelled to multicelled life. Each explanation—conflict mediation, benefit, or history—addresses the transition to multicellularity by appeal to different mechanisms, which I will discuss in a moment. In all three cases, there is an attempt to identify a difference maker, namely, something responsible for the occurrence of the transition. The three explanations are not incompatible with one another—they identify different patterns of evolutionary change that are together important for understanding multicellularity.

Even before discussion of the three mechanisms for multicellularity, at this point one might be suspicious of an ambiguity between (1) whether there are multiple mechanisms in the transition to multicellularity and only one is the difference maker, or (2) whether the same transition to multicellularity can be caused by different mechanisms, namely, a set of difference-makers. There is a passage from Calcott's chapter that might help to clear up the confusion:

Let's say we want to explain how a kangaroo jumps. A typical response might mention a number of factors: how the tail is used as a counterbalance, how the alignment of the enlarged fourth toes with the leg bone serves to drive the jump, and how the elastic tendons in the ankle store and release the energy to aid the jump. Given a *target of explanation* (how the kangaroo jumps), we respond with a set of *difference-makers* (the tail, the toe, and the tendons), and some generalizations about how these difference-makers affect the target of explanation (36, original italics).

We can, by the above passage, rule out option (1) because Calcott accepts that there are multiple mechanisms constituting a set of difference-makers. And so, if we want to explain how the transition to multicellularity occurs in *Volvox carteri*, a species of green algae, we might mention several factors: how conflict mediation occurs (e.g. through germline allocation), how benefit is generated for individual cells residing in a group (i.e. so more resources like phosphate can be stored), and how the pathway to multicellular *V. carteri* looks from a historical perspective (e.g. which mechanisms appear at each step towards multicellular *V. carteri*). Overall, different targets of explanation each call for difference makers—some causal intervention that an effect is counterfactually dependent on. In each explanation, the causal interventions are mechanisms responsible for the transition to multicellular *V. carteri*. The idea is that we can have a plurality

of explanations for one transition to multicellularity with each explanation distinguished by both its target and difference-making causal mechanism.¹⁰⁰

And so, according to Calcott, one explanation identifies one difference-maker, since the three difference-makers above correspond to three different explanations discussed in his article. Recall that he thinks explanations will not be in conflict so long as they have different explanatory targets. However, if that's the case, then how are these three explanations—conflict mediation, benefit, and history—not in competition with one another when the target of explanation is the same, namely, multicellularity? This is exactly what Calcott denies—the targets of the explanations are different upon careful investigation. For example, conflict mediation focuses on populations, whereas the generation of benefit focuses on the individual cells (43). To distinguish between targets of explanation, Calcott relies on a different grain of analysis—though conflict mediation and benefit generation are both relevant to the transition to multicellularity, they each target different aspects of that transition—populations versus individuals. And so, one particular transition to multicellularity can be explained in different ways. When used in conjunction with one another, Calcott proposes, multiple explanations can provide a richer understanding of the transition more generally (49). In this case, he argues, we find multiple ways to unify the set of all major events.

Understanding how Calcott's explanatory pluralism works in the transition to multicellularity is necessary to understand his treatment of major transitions generally. Calcott repurposes the same argument structure to identify patterns across all major transitions. Here's the main idea.

¹⁰⁰ Notably Calcott identifies mechanisms as the difference-makers so maybe he means something different than 'mechanism' as per a mechanistic account of causation, unless he thinks that mechanisms are just structures of difference-makers. Perhaps Calcott is just thinking counterfactually and calling it 'difference-making.'

There are different ways to unify the set of all major transitions because the mechanisms that cause major shifts in evolution, though diverse, share similarities. These different explanations identify similarities across a diverse set of events, thus unifying those events through those shared properties. It is precisely in how we find such similarities that Calcott's treatment of major transitions takes shape.

Calcott argues that to seek multiple explanations is an acceptable approach to modelling transitions, so long as those explanations pick out different targets. However, in the case of all major transitions, the explanations "need to be specified far more abstractly to be applicable across a greater domain" (45). Generalizations that pick out similarities abstract away from the physical details: "By ignoring detailed physical facts, the resulting explanation is one that could easily be generalized" to many organisms and levels of organization (46). For example, different organisms can possess similar features, namely, analogies, such as the body shapes and triangular fins in both sharks and dolphins (47). These features are good for swimming even though their bearers are so different; dolphins are mammals and sharks are fish. Analogies are supposed to be indicative of convergent evolution when two species face a similar environmental challenge. The traits tend to be described in terms of what they *function for* in order to draw out their similarities, despite evident structural differences between the body shape and dorsal fins of these animals. Similarly, despite a variety of mechanisms that cause major transitions, if we can find broad functional similarities across those mechanisms, then we discover common threads that act as our unification tools. In effect, if we adjust our focus and zoom out, we'll find not only one unifying feature, but many.

Now exactly what it means for major transitions to admit of a variety of causal mechanisms is up for debate. On the one hand, Calcott's view could be similar to Ruse (1969, 1987), who

thought that a plurality of species approaches—morphological, biological, etc.—picked out the same set of taxa. If Calcott advocates a similar pluralism, then the identification of different causes picks out the same set of events. Calcott says that “even when we identify a particular biological phenomenon, we can still go about explaining it in a number of different ways” (2011, 36). *We do this by using different types of explanations distinguished by their different targets.* These targets are distinct due to the level in focus and not due to difference in target-kind. We see this in his account of multicellularity in *V. carteri*: He appeals to how conflict mediation targets properties of populations instead of properties of individuals. On this picture, there is an array of similarities that each pick out the same set of events regardless of their various explanatory targets. Notably, the aim to unify all major events, even with various properties, remains the same under this description. In the next section I discuss why the quest for unity is not compelling.

On the other hand, one might wonder whether Calcott’s pluralism concerning different causal mechanisms suggests that there are multiple kinds of major transitions. This would be opposed to thinking that there is only *one kind* of major transitions in evolution whose membership is realized through the presence of multiple properties all token events of that kind share. That sort of monism seems more obviously suitable to proposals for a single common thread, as seen in section 1. However, in Calcott’s case, which includes many similarities across numerous causal mechanisms, his ontological commitments concerning kinds of transitions are not as clear.¹⁰¹ As we will see, a plurality of transition kinds is a viable alternative nonetheless.

¹⁰¹ One might think that Calcott is an ontological pluralist who thinks there are many kinds of transitions, but he adopts a unity aim for heuristic reasons to at least look for several unifying causes. In conversation with Calcott, he claims that there are numerous ways to unify the same set of transitions in the sense that there are alternative resources for completing that task. However, he clarifies that, “biology is messy, and unification is always going to

Up to this point, I have discussed the aim of theoretical unity: Major transitions are unified if all the events share a common property (or properties) that makes them what they are. Calcott maintains that there are many properties shared by major events each at different grains of analysis, which makes it worthwhile to investigate multiple unifying approaches. Specifically, he focuses “on similarities in the mechanisms responsible for bringing about the major transitions,” rather than just searching for a single common thread (2011, 35). He makes suggestions for how to identify “very general principles that may provide alternative ways of unifying the mechanisms underlying the major transitions” (49). According to Calcott, by abstracting away from the details, multiple unifying similarities of transition mechanisms will be found.

5.3.3 Contingency and Disunification

We have learned that Calcott is not only pluralistic about similarities across transitions, but perhaps also about the causal mechanisms responsible for them. Regardless, he still aims to find similarities general enough to range over diverse events—he is a unificationist. In what follows, I argue that contingency and its emphasis on divergence supports a disunity among transitions. Remember that explanatory unity concerning the major transitions is achieved if all the events share a common property, which makes them what they are. Calcott is an explanatory pluralist because he maintains that there are many properties that unite major events, which makes it worthwhile to investigate multiple approaches. However, it looks as though Calcott is an ontological monist concerning kinds of transitions—there is only one kind rather than many. If true, this makes sense of his quest to unify transitions, even if it is by appeal to numerous

be partial.” This still sounds like we only ever get a partial picture of one set of transitions rather than transitions of many kinds.

causes. Calcott's explanatory pluralism is different than an ontological pluralism concerning kinds of transitions.

To be an ontological pluralist about transition kinds is to think that transitions do not all share a common property (or properties). Rather a kind is distinguished by mechanisms peculiar to the events that constitute it, and events are classified according to their different properties. The quest for unity within that context does not seem nearly as compelling. Evolution's contingency and its emphasis on divergence supports a disunity among the transitions. In what follows I unpack a similar argument from chapter 4 within the context of major transitions:

- (1) The mechanisms that cause major transitions are outcomes of evolution, contingently construed.
- (2) Evolution's contingency causes diverse outcomes along with numerous possible evolutionary trajectories.
- (3) Therefore, the mechanisms of major transitions are diverse with numerous possible evolutionary trajectories.

That this diversity actually amounts to numerous kinds of transitions requires further argumentation, which I turn to after discussing the steps in the argument above. As we shall see, since a unified model requires a property (or properties) shared by all events, multiple kinds of transitions will yield a *disunified* model. That is, not all kinds of transitions share similar properties—their differences are what distinguish them. In turn, this implies they cannot be unified across the board, or at least not in a way that is substantively informative.

Premise 1. That the mechanisms responsible for major transitions are contingent outcomes of evolution requires elaboration. As outcomes of evolution they will be subject to change.

Consider the following. Cooperation has been cited as an integral mechanism causally responsible for transitions to multicellularity as discussed earlier in this chapter. It is reasonable to view such cooperative behaviour as itself evolving over time, but attempts to capture the nature of cooperation abstract away from such finer details. Cooperation between humans is a foundation of human society, for instance. However, we see cooperation among other entities too, such as cells. A general description for both cases—human societies and associations of cells—is possible.

For example, cooperative human social behavior, or social behaviour of other “higher” mammals generally, is often the explanatory target of game theory. Evolutionary game theory, though popular as an explanatory and predictive tool for human behaviour in societies, is also used to make sense of the different environmental situations and “strategies” of cells (see "Evolutionary Game Theory: Cells as Players" by Hummert et al. 2014). Game theory tracks patterns of cooperation and conflict by analyzing the costs and benefits for cheaters. The upshot is an understanding of cooperation regardless of what sorts of players are in the game. Additionally, there are also ecological explanations of interaction between an organism and its environment including conspecifics and members of other species, such as the use of predator-prey models (Sarka 2016). So at first glance, the dynamics of interaction are supposed to remain the same across different phenomena because the roles of the interactors remain stable. However, similar to how Mendelian laws admit of exceptions, the general game theoretic rules that characterize cooperation do not always hold for the same set of target entities.

Cooperative relationships are outcomes of evolution, and as outcomes of evolution they are subject to potential evolutionary change. Game theory attempts to capture the nature of cooperative relationships by identifying generalizations that hold among interactions between

different sorts of biological entities. This is analogous to the Mendelian generalizations that govern meiosis.¹⁰² In both meiosis and game theoretic accounts of cooperative interaction we find cases that are exceptions to the rule.¹⁰³ Meiosis and cooperation, as outcomes of evolution, are sensitive to not only the events leading up to their evolution, but they can also be influenced by stochastic processes and undergo change. Specifically, cooperative behaviour in mutualistic associations that benefit both parties can change. Here's an example.

There is work on the impact of drought on the extinction and breakdown of mutualisms, which can have cascading effects on biodiversity (Harrison 2000). When such droughts are due to weather events that cause temporary changes in the world climate, such as the El Niño, an increase in ocean temperature occurs due to complex interaction between wind and waves. In these cases, the very same entities no longer cooperate due to external disruption¹⁰⁴ and so any game theoretic rules that might have applied no longer do. This is, in effect, a story of evolutionary contingency because the evolution of cooperative mutualisms is dependent on both historical and stochastic processes relevant to geology, meteorology, and oceanography. However, through this example we only see the fragility or breakdown, rather than the robustness, of cooperative mutualisms under such disruptions. Instead, we need some sort of positive case for diversity in cooperation if indeed various cooperative instances are outcomes of evolution. I turn to this now.

¹⁰² Recall that Mendel's law of segregation—that two homologous chromosome pairs separate during gamete formation—admits of an exception, namely, non-disjunction when the pairs fail to separate into different gametes.

¹⁰³ Exceptions to meiosis are cases of nondisjunction, whereas exceptions to cooperative action could be cases of defectors who “cheat” for their own self-interest in a system that is otherwise set up to benefit them when they cooperate with others in the designated relationship.

¹⁰⁴ See Inkpen and Turner (2012) for their discussion of contingency and external disturbances.

Similar to how diverse mechanisms yield the possibility for novel traits by the generation of variation, such as through meiosis and lateral gene transfer (Godfrey-Smith 2009, Ragan and Beiko 2009, Ereshefsky and Pedroso 2015), there are diverse mechanisms for cooperation as well. Cooperation itself should be contextualized: cells might cooperate with one another exhibiting control over their own proliferation. They might also cooperate by sacrificing themselves through apoptosis or programmed cell death, or even through the transmission of resources to interior cells that are “resource limited,” such as in *Saccharomyces cerevisiae* (Ratcliff et al. 2012, 1597).¹⁰⁵ In studying *S. cerevisiae*, Ratcliff et al. observed the evolution of division of labour through programmed celled death, which is a cooperative activity and a key feature in transitions to multicellularity. Additionally, we find cases of cancer-like phenomena in *Volvox*, another multicellular individual formed through aggregation, due to anti-cooperative mutants (Aktipis et al. 2015, 8).¹⁰⁶ Generally, proliferating cells are susceptible to accumulating somatic mutations (10). This means that different mechanisms identified as facilitators of cooperation, such as proliferation inhibition, are influenced by stochastic processes like mutation. Stochasticity is integral for contingent evolution and mutational occurrence is often to the multicellular individual’s detriment. Importantly, there is diversity in cooperation—the mechanisms in cooperation are various and themselves outcomes of evolution. Therefore, insofar as cooperative mechanisms cause major transitions, those transitions will be contingent outcomes of evolution too. This brings us to the second premise of the argument.

¹⁰⁵ Aktipis et al. (2015) also discuss the different forms of cooperation cancer cells defect from.

¹⁰⁶ Recall that we considered nondisjunction as a meiotic mutant, as thus one possible pathway, of the meiotic mechanism.

Premise 2 and Conclusion. In Chapter 4.3 I explained how evolution's contingency causes diverse outcomes along with numerous possible evolutionary trajectories. Premise 2 follows directly from the nature of evolutionary contingency described earlier. Imagine how our conception of major transitions would change if we considered the causes of major transitions as something of the same—diverse with multiple possible future trajectories. To conclude that this diversity amounts to a plurality of transition kinds is worth exploring. And if there is a plurality of transition kinds, then the goal to give a unified model of transitions by some common explanatory feature(s) seems less compelling. Let me explain.

That a diversity of major events yields a plurality of types requires the following. To sort major transitions into different kinds, those kinds are distinguished by the mechanisms that cause them. For example, Queller (2000) makes a compelling case for two kinds of transitions in individuality: egalitarian transitions between unrelated entities, such as in multispecies biofilms formed through aggregation, and fraternal transitions between related entities. These changes in individuality are different due to the relationships between their different constituent entities and the causal mechanisms that bind those entities together into one multicellular organism. However, these different types of transitions in individuality share the properties of cooperation and conflict control, which according to Queller are key properties for the emergence of new individuals. Sharing such properties groups both egalitarian and fraternal transitions under one kind, namely, as transitions in individuality. This grouping occurs despite the differences that distinguish the two transitions as subcategories within one type.

Other kinds of major transitions may not involve cooperation or conflict control. For example, recall that O'Malley argues that the "Great Oxidation Event does not have any status in Maynard-Smith and Szathmáry's classic work" (2014, 21). This is the case despite that from an

ecological perspective, oxygenic photosynthesis “might well be regarded as the central event in the history of life” because it “liberated biology from hydrothermal vents and other environments” (Knoll 2003, 4-5). Szathmáry and Fernado propose to extend the original transitions model and link it to important events in Earth’s history, such as the oxygenation of the Earth (2011, 307). They view this event as a marked transition in metabolism, which makes it at least relevant to life (if we define life in metabolic terms).¹⁰⁷ However, one could argue that two kinds of major transitions have been identified—one concerning the history of life and the other concerning the history of the Earth. This is not to deny that there might be some overlap. Kinds of transitions can cross-classify events such that the Great Oxidation Event happens to be a major transition in Earth’s history in addition to the history of life. These two histories are complexly intertwined after all. In other words, some of the transitions in Earth’s history might also be major events for the history of life. Though the foregoing is rather general, I simply aim to give a sense of what different kinds of transitions might look like.

The main message is that evolution’s contingency yields diversity and one can argue that this diversity is a plurality of transitions kinds. If this is correct, then no wonder we have failed to find just one similarity (or set of similarities) to capture them all. The disparity is due to difference in kind, which implies that there is not *one* unifying property yet to be found.¹⁰⁸ One might object, however, and try to construe multiple kinds as a plurality of unities (akin to Hacking 1996), especially if kinds of transitions contain subtypes. For example, ETIs as a kind

¹⁰⁷ See Dupré and O’Malley (2009) for a discussion of the definition of life in terms of metabolism versus replication.

¹⁰⁸ Admittedly, I have not provided a specific account of natural kinds, i.e. how properties and the relations between them make something the kind that it is (see Boyd 1999, Ereshefsky 2001, Slater 2015, Franklin-Hall 2015). I am simply appealing to the general claim that difference in kind means that different kinds do not share the same properties. There are different causal mechanisms responsible for kinds of transitions such that the transitions do not share properties due to those differences.

of major transition contain egalitarian and fraternal subtypes unified by the fact that in both subtypes a new individual emerges (Queller 2000). But if all kinds of major transitions lack shared properties, then successfully finding *the* unified model amidst a plurality of transition kinds looks dismal. Rather, there is a disunity among the transitions—they are dissimilar. Such diversity underwrites many kinds of major events and perhaps, one might speculate, many kinds of major transitions relevant to life's history alone. However, a place of disunity is not necessarily a concerning place to be.

Recall that Calcott (2011, 36-7) gives an account of explanatory generalizations that abstract away from the biological details in order to capture a vast and various range of events. One might overcome a disunity among multiple kinds of transitions by seeking a very general quality in which they all share. They are, of course, all *major* transitions and as such they all share in being events whose occurrences cause the course of activity—evolutionary, ecologically, astronomically—to shift drastically with new trajectories that cascade down radically different channels. In contrast, minor transitions might exhibit less drastic organizational changes and have smaller downstream effects, whereas miscellaneous transitions have no effect on a specified trajectory at all (though they may affect others). So, one might say that *major* events mark major changes and this unifies all transitions in evolution and otherwise—they share in being major, rather than minor or miscellaneous events. At this stage, however, it appears that we do not learn much more. The definition of 'major' in this case is vague to say the least.

Simply put, my complaint is about the explanatory aim of unification in this context: Attempting to unify disparate events requires abstraction away from the finer details, as Calcott (2011) suggests. Attention to the detailed differences among major transitions lends itself to a

better understanding of how transitions occur, the nature of these events, and our ability to predict outcomes of transitions based on what we know about their causes. Tasks of unification work from the top-down, and by doing so the variation among different types of major events is lost. I propose a shift in focus: What if we work from the bottom-up? It is worth noting that until this point I have been discussing a form of *ontological* unity.¹⁰⁹ The debate has been about whether there are or (as I have argued) are not properties shared by all events that count as major. Epistemically, that all major events have a common property might be explanatorily useful—we have an explanation of these events by identifying abstract generalities about their nature and the relationship between them. This certainly seems to be a motivating reason behind Calcott’s account. However, even if we can identify broad generalizations, top-down abstractions should be scrutinized for their explanatory power. For example, we could say that all transitions in individuality are for the emergence of a new type of individual, just as dogs, birds, and lizards all have legs to run. One can characterize having legs as *for* a common general end, namely, to run. However, this tells us nothing about the diverse structural details of the legs themselves. Similarly, one can characterize transitions in individuality as *for* the emergence of new types of individuals. However, such a general account of transitions in individuality tells us nothing about the intricate variations of how these activities occur, which are revealed upon closer analysis. We have learned that some types of individuals emerge through mutualisms like symbiosis (O’Malley 2014, Ku et al. 2015, Alvarez-Ponce et al. 2013), while others emerge through aggregation (Bouchard and Huneman 2011, Hammerschmidt et al. 2014, Ereshefsky and

¹⁰⁹ See Cat (2017) “The Unity of Science” for the varieties of unities, such as epistemological and ontological. Ontological unity concerns the metaphysical aspects of entities and the relationships between them, such as the sharing of properties. Epistemological unity focuses on goals of explanation by drawing methodological connections, such as reductive strategies to a fundamental science in order to unify the structure of science in terms of that relationship. Arguably, ontological unity also has explanatory force.

Pedroso 2015). Such details are lost when one tries to paint all evolutionary transitions in individuality with a broad brush. Attention to structural detail is what distinguishes a plurality of individuality transition types and it embodies a suspicion of functionalist approaches, which unify by appeal to broad abstractions. However, one might argue that abstracting away from the details to provide explanatory generalizations is not the only way to unify a set of events.

I could imagine the development of reductive strategies in order to unify the structure of major transitions by identifying, for example, which major transitions are more fundamental than others in the sense that one is required to explain the workings of a more inclusive transition. In this sense, one could get a hierarchy of major events analogous to the hierarchy of sciences proposed by Oppenheim and Putnam (1958). Alternatively, one might aim to unify the events by identifying how the relationship dynamics operate between transitions analogous to the non-reductive, unifying strategy of Darden and Maull (1977) concerning the relationship between scientific fields. Perhaps major transitions depend on one another in some way, and one can investigate the nature of that relationship. However, this is something I will not pursue further at this point. I imagine that a repeat of the debate over scientific unity and anti-reductionism could replay within the context of major transitions, but only with properties of events rather than the contents of theories. To be completely transparent, I am skeptical that we ought to seek unity for unity's sake. It is not that the attempt to unify transitions, or more generally, the attempt to unify diverse biological entities, processes, etc. under one type, is necessarily wrongheaded. Rather, it can be complementary to a more detailed understanding of the phenomena in question. If unification is sought to gain explanatory power, yet we learn more through exploring the diverse nature of different transition kinds, then we should pursue the latter option. The aim of unity as

an epistemic virtue should not be taken as an obvious requirement when our research aims could be better realized through detailed investigations.

If the prospect of disunity within the context of major transitions seems unsettling, fear not. We are in good company. There are many well-established views that develop the meaning and (often favourable) impact of scientific disunity. See *The Disorder of Things* by Dupré (1993), as well as other members of the Stanford school who support an overall picture of disunity, such as Cartwright (1983,1999), Hacking (1996), and Suppes (1978).¹¹⁰ We are, then, on solid foundation to engage with the prospects of disunity among major transitions. Pluralism makes room for an informed disunity: accounting for multiple kinds of transitions could achieve explanatory sophistication by attention to structural detail. Inspired by evolution's contingency and its emphasis on diversity, I have merely offered a sketch of how shifting focus away from unificationist aims might be grounded in a view about how evolution works.

Finally, disunity is also revealing. Specifically, the lack of a common thread reveals something about the fragility and diversity evident in evolution, as well as about the nature of forces besides natural selection driving the evolutionary process. Why should we expect that one (or one set of) mechanism(s) are responsible for such drastic changes in evolutionary trajectories from deep evolutionary time to the present? We miss out on the positive, or generative, aspects of evolution's contingency, namely, its ability to open possibility space for the future direction of evolution at the larger scale. This positive or generative aspect is how we get plurality—even in identical environments evolution does not yield the same outcomes over and over, if indeed

¹¹⁰ Also see Cat (2017) for an excellent history of the unity of science debate.

selection lacks the power to override disparity in all cases.¹¹¹ Accepting disunified models of transitions does not impoverish our understanding of major transitions in evolution. Again, if it is true that “nature’s theme is diversity,” as Gould (1989, 39, 42) maintains, then abstracting away from and glossing over the finer details produces a superficial unity at the expense of a deeper understanding of the history of life.

5.3.4 A Short Interlude: Reflections on Contingency

At this point of the dissertation, before I move to its final section, I would like to reflect on the project as a whole. I have discussed how contingent mechanisms yield positive outcomes: Types of transitions and types of individuals in selection are caused by mechanisms dependent upon stochastic processes responsible for numerous possible evolutionary trajectories. Not only do we find a diversity significant enough to underwrite a plurality of types, but this diversity marks a vast possibility space for new types that might emerge and potentially continue to evolve. In other words, we identify salient diversity that warrants a pluralism of types for both individuality and transitions. We should also *expect* this diversity to continue based on a *de-emphasis* of selection’s power to override that disparity. We can get a handle on this plurality of evolutionary phenomena by understanding how new types of that phenomena can emerge. This is why I discussed how new types of individuality come to be, as with the case of multicellularity, which also happens to a major event in evolution. The transition to multicellularity is ‘major’ because it influenced how evolution operates and opened up new possibilities not necessarily available to unicellular life.

¹¹¹ I am thinking of Wimsatt’s notion of generative entrenchment.

Overall, the focus has been on more positive aspects associated with evolutionary contingency: new products of evolution often can (and do) emerge that warrant recognition of their diversity based on the variety of mechanisms that cause their existence. The positive or generative aspects of evolution's contingency, namely, the ability to open possibility space for the direction of evolution, is associated with the *evolvability* of individuals in selection.¹¹² That they are contingent upon stochastic processes, such as mutation, reveals potential future evolutionary pathways. At the finer scale, the evolution of variation-generating mechanisms such as meiosis and LGT each exhibit the potential options for change *within* their respective types of individuals. How much change yields a new type of evolutionary individual is of course up for debate. At the coarser scale, the variability evident *between* types of evolutionary individuals affects how long term evolution is channelled through different trajectories in phenotypic space (see Pigluicci 2008, 76 for the landscape of evolvability concepts). Perhaps, the broadest scope of individuality types is analogous to clades where there is capacity to overcome genetic and developmental constraints, which opens even more possibility space.¹¹³ We could run something similar to this over again for the mechanisms of major events in deep evolutionary time. This is all positive in that it emphasizes the ability of evolution to create something new, which is a generative aspect of evolutionary contingency I have utilized, rather than a focus on only historical constraints. The positive or generative aspect of contingency is how we get a plurality—even in identical environments, evolution does not yield the same things

¹¹² Sterelny (2007) defines 'evolvability' as the differing evolutionary potential of lineages. He thinks evolvability is not just due to the supply of variation, but also to the capacity for lineages to evolve complex adaptations. (Brown 2014, 550) defines 'evolvability' as an "abstract and robust dispositional property of populations whose physical basis is the many non-selection based features of populations (such as mutation rate, developmental constraint, and population structure)."

¹¹³ The brief and perhaps speculative discussion of evolvability and individuality is very much inspired by some insightful distinctions made by Pigluicci in "Is Evolvability Evolvable?" (2008).

over and over again if selection lacks the power to override disparity. By de-emphasizing selection, we are de-emphasizing the power of overly abstract adaptationist approaches that group traits, mechanisms, causes, and events according to their function in solving environmental challenges. One upshot is that trying to capture such a disparate picture under static and broad abstractions is a difficult task indeed. Variety, especially heterogeneous variety, causes trouble for generalizations that rely on functional similarities when those functions take a backseat to finer-grained analyses.

5.4 In Reverse: Cancer as an Exception to the Transitions and a Breakdown in Individuality

To round out a focus on the positive aspects of evolutions contingency, namely the diversity of outcomes and potential evolutionary trajectories, one might ask what happens when the effects are negative. Philosophical issues concerning cancer intersect with both the major transitions and individuality topics. Very briefly in the section concerning MTEs, I touched on a negative component of evolutionary contingency: its ability to break down products of evolution, such as the sensitivity of some mutualisms to environmental impact.¹¹⁴ Rather than generative, contingency can be destructive. That is the topic of this last chapter section: Does cancer count as a breakdown of individuality or as the emergence of a new individual? On the one hand, if we consider the transition to multicellularity as the emergence of a new type of individual, then the out-of-control proliferation of its parts signals a breakdown in the functions which sustain it. On the other hand, if cancer is an object of selection, then perhaps we should consider it an evolutionary individual itself in competition with other individuals instead of a manifestation of

¹¹⁴ The previously mentioned negative element of contingency was the impact of drought on the extinction and breakdown of mutualisms, which can have cascading effects on biodiversity (Harrison 2000).

individuality failure. Another way of putting the question is whether the progression of cancer counts as a positive transition in individuality or a negative “failed” transition—is it the emergence of a new individual or do cancer cases amount to breakdown instances of a current type?

5.4.1 Philosophical Aspects of Cancer: A Product of Selection, a By-Product of Novel Adaptions, or a By-Product of Other Evolutionary Processes?

There is current work on whether cancer is a by-product of novel adaptations or whether cancer is a unit of selection in its own right. I will briefly discuss each option and articulate the relationship to evolutionary individuality and transitions among individuals.

5.4.1.1 Cancer as a by-product of novel adaptations

Graham (1992) argued in *Cancer Selection* that changes in morphology and life-history can increase the risk of cancer. The main idea was that “changes in the design of a product often result in a transient decline in its quality” (Leroi et al. 2003, 226). Similarly, “the evolution of novel morphology might interfere with the quality control of development” (ibid). The vast array of morphological size and shape was “bought at the expense of untold numbers of deaths due to cancer...[but] cancer deaths select for modifiers that make development more precise” (ibid). Leroi et al. (2003, 227) discuss the evolution by selection of tumor suppressors to address cancerous activity as a side effect of evolutionary change. As a side effect, cancer should be common after rapid episodes of evolution, as in cases of artificial selection with chickens notorious for cancers of the reproductive tract (ibid).¹¹⁵ The assumption is that natural selection should produce anti-cancer adaptations, like tumor suppressors, to eliminate cancer:

¹¹⁵ Leroi et al. 2003 primarily discuss rapid evolution and cancers of the immune system and central nervous system. They say that “the immune system is expected to be among the fastest evolving systems in any species because it will be constantly selected in new directions by co-evolving pathogens and parasites.” (227). Immune system

Perhaps the simplest way in which evolutionary change can cause an increased risk of cancer is by bringing about an increase in the number of stem cells and cell divisions, so [as to increase] the opportunity for selfish lineages to arise. This would make larger bodies more oncogenic, so big dogs might be prone to osteosarcoma simply because they have more cells than smaller dogs (Leroi et al. 2003, 228).

However, despite finding that whales and humans are less cancer-prone than mice, Leroi et al. note that many evolutionary-minded oncologists suggest that cells of large animals “must somehow be more resistant to neoplastic transformation” (2003, 228).

Overall, the above consideration of cancer as a by-product of selection characterizes cancer as something controlled by selection for mechanisms that reduce mutation rates, such as cancer detection and suppression mechanisms. To say that cancer is a by-product of novel adaptation means that cancer is a functional manifestation of mechanistic failure—the functioning of mechanisms that maintain multicelled individuals fail or do not function properly. For example, Aktipis et al. (2015) recount the hallmarks of multicellularity, such as cell proliferation inhibition, controlled or programmed cell death also known as ‘apoptosis’, division of labour, resource allocation and transport, and extracellular environmental maintenance. These hallmarks are cooperative in nature—collectives of cells cooperate under this set of shared “rules” that cancer cells, as cheaters, ultimately violate in one way or another. They survey cancer across life and look for the absence of cancer to identify cancer detection and suppression

cancers, such as leukemia and lymphoma, are the most common class of cancers in human children. Mutations that give rise to these forms of cancer are caused by misplaced activity of enzymes that the adaptive immune system depends on. The second most common class of cancers are of the central nervous system attributed to the fact that our brains have increased three-fold in size (ibid). Such marked changes are only found in certain lineages, so Leroi et al. predict that immune system cancer will be common in all mammals, but not CNS cancers (228). This prediction comes from conceiving of cancer as a by-product of novel adaptations, and correspondingly, a side effect of rapid evolutionary change.

mechanisms (2015, 3). We have seen something like this project before: Pradeu (2010, 2012) discusses the role of immunogenic response—immune system response in the presence of antigenic discontinuous signals—in surveilling proper function of parts conducive to maintaining the whole individual. Leroi et al. (2008, 227) et. al. point out that the most common cancers in youth are cancers of the immune system, which is one of the most rapidly evolving systems in any species. They state that “if cancer arises as a side effect of evolutionary change, it should be particularly common after very rapid bouts of evolution before protective devices have had a chance to evolve” (227). Cancer is, in effect, something that *happens to* multicellular individuals, and so to at least one type of evolutionary individual, rather than a direct product of evolution by selection.¹¹⁶ Cancer and cancer-like phenomena, then, are dependent on the rapid evolution of multicelled life. The existence of cancer points to a fragility in the transition to multicelled life and the negative effects that can occur because of drastic change.

The above supports a rejection of considering cancer as an emergence of anything new. Rather, as Godfrey-Smith (2009, 101) puts it, cancer is “re-Darwinization” such that competition among parts of an individual increase that ultimately leads to the individual’s demise. Cancer as an affliction to multi-celled life is then something to overcome rather than a new product of evolution by selection. As a breakdown in multicelled individuality, cancer is also a case of transition failure. A complete transition failure will be the point at which there are too many

¹¹⁶ Additionally, another reason to think that cancer represents a breakdown in individuality, and therefore, a side effect of evolution, is to explore the nature of possible cancer adaptations if cancer were to be considered an evolutionary individual. Germain (2012) directly argues that because cancer cells do not develop complex adaptations, namely, “adaptations that are an accumulation of evolutionary changes” (787). Using Godfrey-Smith’s framework, he concludes that cancer cells are not paradigmatic Darwinian populations but consist of only marginally Darwinian individuals at best (799). This implies that adaptive explanations of cancer do no work, because cancer cells (nor the collectives, presumably) are units of selection. I am skeptical of Germain’s view for reasons I discussed in Chapter 4 concerning Clarke’s (2016) focus on complexity for evolutionary individuality.

instances of multicellulars exhibiting such a breakdown. Of course, the point at which an accumulation of instances counts as a full-blown transition failure will be contentious. The pervasiveness of cancer and cancer-like phenomena in all multicelled life certainly renders it a candidate for causing a failure to occur. We often think of transitions as complete and in the past, that is, that there *were* transitions to multicellularity and now we see the product of those changes, i.e. multicelled life. But the evolutionary story is not over. Some transitions might fail. Or more specifically, some transitions might currently be in a state of failure. If cancer amounts to the failure of functions that sustain multicellular creatures, then those functions as products of transitions are inadequately fulfilling their role in the maintenance of that organization. The causes of this failure are contingent upon the nature of the transition itself. For example, cancer as an uncontrolled proliferation of cells is only a problem if cell proliferation requires control in order to maintain the transition. On this view, so the story goes, selection corrects for this failure by selecting for detection and suppression mechanisms, such as improving the surveillance of the immune system. This is an expected selectionist story as cancer appears too disorganized and erratic to fit the typical mold of what selection takes as its objects. Because this dissertation focuses on the diverse outcomes of contingent evolution, a selection-centric story is suspicious. It moves focus away from the intricate details of cancerous cells and towards the general adaptive function (or lack thereof) of tumors to solve environmental challenges. There has been a shift in thinking, however, that explores cancer cells as products, rather than by-products of evolution by selection. That is, rather than a failure of multicelled function and breakdown of a token individual or entire transition, cancer cells are themselves products of evolutionary processes.

5.4.1.2 Cancer as a Product of Evolution Subject to Selection

Cancer as an object of selection calls for a fitness story about the individual cancer cells and the tumors they comprise that yield detrimental results for the multicelled host. Lean and Plutynski (2016) expand on the idea that cancer is a cellular population subject to selection.¹¹⁷ On this view, cancer progression from early stages of individual cells to tumor formation and eventual metastasis (or the spreading of cancerous cells to other sites) can be construed as cancer cells competing with, or coevolving with, other cell lineages (49). Cancerous lineages are, then, lineages of evolutionary individuals. These lineages comprise populations subject to the same selective pressures as other cellular populations, however, cancer cells monopolize the fitness advantage selfishness offers when in competition with other cells. “Cancer cells also recruit neighbouring cells in order to participate in tumor development,” for both structural support and blood supply (50). This is arguably a form of niche construction if cancer cells evolve and co-evolve with their surrounding environments—the behaviour of the tumor is not exclusively due to the behaviour of neoplastic (or cancer) cells. Ultimately, the “highly integrative functional organization of some tumors suggests that they should be considered as akin to organs” (51). The analogy to organs does, however, suggest that cancer is better viewed as part of an individual organism rather than a competing organism itself. And so, Lean and Plutynski argue against Germain (2012); the production of cancerous phenotypes will count as complex adaptations depending on grain of analysis. The general message of their paper is that while cancer is a by-product of the adaptation and evolution of complex organisms, it is a product as well if we accept that selection acts on multiple levels of biological organization. “cancer is both product

¹¹⁷ Lean and Plutynski (2016) also explain how cancer can be considered a by-product of selection from a multilevel perspective by utilizing multi-level selection theory.

and by-product of a multi-level selection process: the process of selection among cells *within* whole organisms and, a by-product of selection between *individual organisms*” (54).

On this picture, at the very least, cancer is not *only* a negative cost of evolution for multicellular creatures. That is, it is not only the failure of functions required to sustain the new level of organization that is multicelled life. Instead, cancer is also something new—a product of evolution—whose evolutionary trajectory is shaped by the processes which influence it, such as selection. If selection acts on individuals, then cancer falls under the category of evolutionary individuality in the relevant sense. Individuals in selection reside at the level of cells, if we indeed accept the multi-level selection theory upon which Lean and Plutynski’s conclusion rests.

In both cases, the discussions of cancer as a by-product and/or product of evolution by selection focus on the role cancer fulfills in that process. Even as a product of evolution, cancer is characterized insofar as it functions (or doesn’t function) to adapt to its surroundings, which is why research on the body’s own defenses against cancer, such as immunotherapy have commenced with great success. Notably, that cancer adapts to its surroundings still seems destructive—it recruits other cells and manipulates its own environment at the expense of the individual it is a part of. Rather than zooming in on the details of cancer, cancer is analyzed by what it does—how it functions within the greater context of evolutionary history. In the next section, I aim to briefly outline an addition perspective that demotes the role of selection in studying cancer. This highlights the generative qualities of cancer, rather than only its negative effects.

5.4.2 Cancer as a Product of Other Evolutionary Processes

Even if cancer evolves by selection, it is influenced by other evolutionary processes— evolution includes other processes besides selection and recall that according to the Evolutionary

Contingency Thesis, the power of selection is kept in check. Under ECT, other processes besides selection play significant roles in evolutionary change, such as mutation or drift. Notably, Lean and Plutynski (2016, 51-52) quickly mention the role of drift for a population of cancer cells, e.g. whether a cancer cell lives or dies may have to do with accidents of location, but they do not take the analysis further. However, this is exactly the direction I suggest philosophers should go.

By moving away from thinking about cancer in terms of how it functions according to selection alone, there is opportunity to move towards a more detailed account of cancer that functional classifications might gloss over. ECT provides a platform for doing so. Instead of treating cancer as a functional class, one gains insight into cancer as a diverse set or heterogeneous kind of disease. Recall that evolution's contingency causes diverse sets of outcomes. Notably, a turn towards the details of cancer, or better yet, towards the details that distinguish *cancers*, is well supported by studies. For example, Melo et al. (2013, 686) state, "cancers of various organs have been categorized into distinct subtypes...within a seemingly homogeneous subclass, individual cancers contain diverse tumor cell populations that vary in important cancer-specific traits" such as the ability to generate clones and potential to invade neighbouring organs. There are differences *between* tumor types and *within* a given tumor type—Melo et al. aim to understand the "biological causes that distinguish [kinds of] tumors" (ibid). Although all cancers are caused by somatic mutations, it looks as those classes of tumors are distinguished by certain mutational processes (Alexandrov et al. 2013, 415). Some mutations cross-classify cancers and so are present in many cancer types, however, others are "confined to a single cancer class" (ibid). Alexandrov et al. say,

Different mutational processes often generate different combinations of mutation types termed 'signatures'...to generate a mutational signature, a single mutation from each cancer sample is

entered into a mutation set aggregated from several cases of a particular cancer type...if multiple mutational processes are operative, a jumbled composite signature is generated (2013, 415).

Recall that mutation is an important source of evolutionary contingency—it not only supplies variation for selection to work with, but it also plays a role in the capacity for lineages to evolve and the strategies available to selection (Brown 2014, Sterelny 2007).¹¹⁸ Overall, these mutational signatures distinguish kinds of cancers that are also sometimes cross-classified by those very same mutational processes. By citing the studies above, I wish to point out that philosophers of biology and medicine who only analyze cancer functionally neglect the intricate details of different cancer types. Of course, understanding cancer from an evolutionary perspective is important, but we must be mindful of how an emphasis on selection characterizes cancer functionally. Part of the challenge of finding a cure is that the differences among multiple types of cancers likely call for multiple cures, if indeed the biological processes which distinguish cancer types function in importantly different ways. This is not to say that there are no common functional properties among different kinds of cancers. I only wish to suggest that distinguishing between kinds of cancers calls for more than contemplating its functional role with regards to selection. Such attention to detail is possible under an evolutionary perspective that highlights the role of other evolutionary processes besides selection, such as mutation and drift.

In summary, cancer within a contingency framework reveals alternatives to classifying cancer as a new evolutionary individual or a transition failure. Instead, one gains insight into the

¹¹⁸ I am suggesting here that evolvability points to the generative aspect of evolutionary contingency, that is, the potential possibilities available that can be realized as evolution moves forward.

diversity of different cancer kinds and the complexities that modern medicine must contend with. There are lessons gained from exploring cancer within a contingency framework. First, whether cancer is a new evolutionary individual or a by-product constituting an individuality breakdown sets up a false dichotomy—we should not think of cancer as either one or the other exclusively. Lean and Plutynski (2016) make a case in favourable to that claim. However, evolutionary contingency provides an avenue to challenge the focus on how cancer functions in selection alone. From this, one gains a second insight. Even if cancer can be both a product and by-product of selection, the adaptationist or functional classification of cancer glosses over the fact that different mutational signatures cause different cancer kinds. Yet, current philosophical treatment groups all kinds of cancers together. This is not mindful of the scientific studies I mentioned that distinguish kinds of cancer—the structural details matter from a medical perspective. If one’s research aim concerning cancer is to contribute to a cure, and multiple cancers require multiple cures, it is not clear how functional classifications are sensitive to that aim.

“We live in a dappled world, a world rich in different things, with different natures, behaving in different ways.” —*Nancy Cartwright 1999, p.1*

Chapter Six: Concluding Remarks

In closing, and generally, I have inferred that diversity yields more diversity such that new products of evolution can (and often do) emerge. This inference is based on the identification of salient differences among mechanisms responsible for the phenomena discussed in the previous chapters: *that variety makes a difference*. Since the task has been to work from the bottom-up, the moral of the story should perhaps be construed as the following: the variety found in the biological domain *should* make a difference to our philosophical treatment of living things. Evolutionary contingency as an explanatory framework captures the diversity found in the organic world and provides a means to explain it. It is through this extension of the Evolutionary Contingency Thesis that we see diversity and disunity at work. Evolution’s contingency explains the diversity of life by embracing it as something to be explained, rather than to be easily captured by general abstractions and the like.

Overall, there are three broad themes of this dissertation—pluralism, disunity, and contingency. Evolutionary contingency, I contend, causes diverse outcomes, which can be categorized into a plurality of different kinds. When modelled, this plurality yields a disunified set that lacks commonality, such as in the case of major transitions. I have explored evolutionary reasons for pluralism in the cases of individuality, major transitions, and the nature of cancer. The pluralism defended in those cases is local, discovered on a case by case basis, and viewed through the lens of contingency present in biology.

I am left then with some topics to be explored further in future research.

- My view of evolutionary individuality might be construed as structuralist when compared to Ellen Clarke's functionalist account. Does the distinction between structural and functional views of individuality help or hinder the individuality pluralism present here?
- What is the relevance of the individuality debate to biology and will it have any effect on the empirical work of biologists? This question is concerned with the usefulness and application of individuality concepts.
- Is the aim of unity in major transitions properly construed as an "entrenched framework assumption" similar to Wylie's (2012) statement concerning feminist interventions in philosophy of science? Is there a sense in which a feminist intervention might transform the debate concerning major transitions? If so, then how?
- What sorts of medical, rather than just evolutionary, reasons support the consideration of cancer as a heterogeneous disease? Does a philosophical account of the pluralist nature of cancer better capture the way in which medical treatment is administered depending on the cancer kind?

Because of my interest in the extension and application of the Evolutionary Contingency Thesis, I also anticipate future work in debates concerning evolutionary contingency directly, as well as research concerning Gould's contributions to the philosophy of biology as a historical figure. Overall, the questions above build on the groundwork set in previous chapters. Some contain a shift in focus, while others are clarifications or extensions of the work in this dissertation.

References

- Aktipis, C. A., A. M. Boddy, G. Jansen, U. Hibner, M. E. Hochberg, C. C. Maley, and G. S. Wilkinson. 2015. "Cancer across the Tree of Life: Cooperation and Cheating in Multicellularity." *Philosophical Transactions of the Royal Society B: Biological Sciences* 370 (1673): 20140219–20140219. doi:10.1098/rstb.2014.0219.
- Alexandrov, Ludmil B, Serena Nik-Zainal, David C Wedge, Samuel a J R Aparicio, Sam Behjati, Andrew V Biankin, Graham R Bignell, et al. 2013. "Signatures of Mutational Processes in Human Cancer." *Nature* 500: 415–21. doi:10.1038/nature12477.
- Alvarez-Ponce, David, Philippe Lopez, Eric Bapteste, and James O McInerney. 2013. "Gene Similarity Networks Provide Tools for Understanding Eukaryote Origins and Evolution." *Proceedings of the National Academy of Sciences of the United States of America* 110 (17). National Academy of Sciences: E1594–1603. doi:10.1073/pnas.1211371110.
- Bapteste, Eric. 2014. "The Origins of Microbial Adaptations: How Introgressive Descent, Egalitarian Evolutionary Transitions and Expanded Kin Selection Shape the Network of Life." *Frontiers in Microbiology* 5 (MAR): 1–4. doi:10.3389/fmicb.2014.00083.
- Beatty, John. 1980. "What's Wrong with the Received View of Evolutionary Theory?" *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association* 1980 (2): 397–426.
- . 1994. "Theoretical Pluralism in Biology, Including Systematics." In *Interpreting the Hierarchy of Nature: From Systematic Patterns to Evolutionary Process Theories*, edited by Lance Grande and Olivier Rieppel, 33–60. San Diego, CA: Academic Press.
- . 1995. "The Evolutionary Contingency Thesis." In *Concepts, Theories, and Rationality in the Biological Sciences, The Second Pittsburgh-Konstanz Colloquium in the Philosophy*

- of Science*, edited by Gereon Wolters and James G. Lennox. Pittsburgh, PA: University of Pittsburgh Press.
- . 1997. “Why Do Biologists Argue like They Do?” *Philosophy of Science* 64 (S1): S432–43. doi:10.1086/392620.
- . 2006a. “Replaying Life’s Tape.” *The Journal of Philosophy* 103 (7): 336–362. doi:10.1111/j.1502-3931.1990.tb01787.x.
- . 2006b. “The Evolutionary Contingency Thesis.” In *Conceptual Issues in Evolutionary Biology*, edited by E. Sober, 3rd ed. Cambridge, MA: MIT Press.
- Bell, G. 1982. *The Masterpiece of Nature: The Evolution and Genetics of Sexuality*. Berkeley, CA: University of California Press.
- Birch, Jonathan. 2012. “Collective Action in Fraternal Transitions.” *Biology and Philosophy* 27: 363–80.
- Bonner, John Tyler. 1998. “The Origins of Multicellularity.” *Integrative Biology: Issues, News, and Reviews* 1: 27–36.
- . 2004. “Perspective : The Size-Complexity Rule.” *Evolution* 58 (9): 1883–90.
- . 2013. *Randomness in Evolution*. Princeton, NJ: Princeton University Press.
- Booth, Austin. 2014. “Symbiosis, Selection, and Individuality.” *Biology and Philosophy* 29: 657–73. doi:10.1007/s10539-014-9449-8.
- Bouchard, Frédéric, and Philippe Huneman. 2013. “Introduction.” In *From Groups to Individuals: Evolution and Emerging Individuality*. Cambridge, MA: MIT Press.
- Bouratt, Pierrick. 2014. “From Survivors to Replicators: Evolution by Natural Selection Revisited.” *Biology and Philosophy* 29 (4): 517–38.
- . 2015. “How to Read ‘heritability’ in the Recipe Approach to Natural Selection.” *British*

- Journal for the Philosophy of Science* 66 (4): 883–903.
- Boyd, Richard. 1999. “Homeostasis, Species, and Higher Taxa.” In *Species: New Interdisciplinary Essays*, edited by Robert A. Wilson, 141–85. Cambridge, MA: MIT Press.
- Brandon, R.N. 1990. *Adaptation and Environment*. New Jersey: Princeton University Press.
- Brown, Rachael L. 2014. “What Evolvability Really Is.” *British Journal for the Philosophy of Science* 65: 549–72. doi:10.1093/bjps/axt014.
- Burnet, F.M. 1960. “Immunological Recognition of the Self.” *Nobel Lectures in Physiology or Medicine* 3: 689–701.
- Buss, Leo W. 1987. *The Evolution of Individuality*. Princeton, NJ: Princeton University Press.
- Calcott, Brett. 2011. “Alternative Patterns of Explanation for Major Transitions.” In *The Major Transitions in Evolution Revisited*, 35–52. Cambridge, MA: MIT Press.
- Calcott, Brett, and Kim Sterelny. 2011. *The Major Transitions in Evolution Revisited*. Edited by Brett Calcott and Kim Sterelny. Cambridge, MA: MIT Press.
- Cartwright, Nancy. 1983. *How The Laws of Physics Lie*. Oxford UK: Oxford University Press.
- . 1999. *The Dappled World: A Study of the Boundaries of Science*. Cambridge, MA: Cambridge University Press.
- Cat, Jordi. 2017. “The Unity of Science.” *Stanford Encyclopedia of Philosophy*.
- Charles, Hubert, Séverine Balmand, Araceli Lamelas, Ludovic Cottret, Vicente Pérez-Brocal, Béatrice Burdin, Amparo Latorre, et al. 2011. “A Genomic Reappraisal of Symbiotic Function in the Aphid/buchnera Symbiosis: Reduced Transporter Sets and Variable Membrane Organisations.” *PLoS ONE* 6 (12): e29096. doi:10.1371/journal.pone.0029096.
- Clarke, Ellen. 2013. “The Multiple Realizability of Biological Individuals.” *The Journal of Philosophy* CX (8): 413–35.

- . 2014. “Origins of Evolutionary Transitions.” *Journal of Biosciences* 39 (2): 303–17.
doi:10.1007/s12038-013-9375-y.
- . 2016. “Levels of Selection in Biofilms: Multispecies Biofilms Are Not Evolutionary Individuals.” *Biology and Philosophy* 31 (2). Springer Netherlands: 191–212.
doi:10.1007/s10539-016-9517-3.
- Clement, L.W., S.C. Koppen, W.A. Brand, and M Heil. 2008. “Strategies of a Parasite of the Ant-Acacia Mutualism.” *Behavioural Ecology and Sociobiology* 62 (6): 953–62.
- Conway Morris, Simon. 2003. *Life’s Solution: Inevitable Humans in a Lonely Universe*.
Cambridge, MA: Cambridge University Press.
- . 2006. “Evolutionary Convergence.” *Current Biology* 16 (19): R826-827.
doi:10.1016/j.cub.2006.08.077.
- . 2010. “Evolution: Like Any Other Science It Is Predictable.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 365 (1537): 133–45.
- . 2012. “Creation and Evolutionary Convergence.” In *The Blackwell Companion to Science and Christianity*, 258–69. New Jersey: John Wiley and Sons Ltd.
- Crow, J. 1979. “Genes That Violate Mendel’s Rules.” *Scientific American* 240 (2): 134–46.
- Currie, Adrian. 2012. “Convergence, Contingency, and Morphospace.” *Biology and Philosophy* 27: 583–93.
- . 2013. “Convergence as Evidence.” *The British Journal for the Philosophy of Science* 64 (4): 763–86.
- Darden, Lindley, and Nancy Maull. 1977. “Interfield Theories.” *Philosophy of Science* 44 (1): 43–64.
- Dawkins, Richard. 1976. *The Selfish Gene*. Oxford UK: Oxford University Press.

- . 1978. “Replicator Selection and The Extended Phenotype.” *Zeitschrift für Tierpsychologie* 51: 184–200.
- Dennett, Daniel C. 1991. “Real Patterns.” *The Journal of Philosophy* 88 (1): 27–51.
- Desjardins, Eric. 2011a. “Historicity and Experimental Evolution.” *Biology and Philosophy* 26: 339–64. doi:10.1007/s10539-011-9256-4.
- . 2011b. “Reflections on Path Dependence and Irreversibility: Lessons from Evolutionary Biology.” *Philosophy of Science* 78 (5): 724–38. doi:10.1086/662560.
- Dettman, Jeremy R, and Bart J van der Kamp. 2001. “The Population Structure of *Armillaria Ostoyae* in the Southern Interior of British Columbia.” *Canadian Journal of Botany* 79 (May): 612–20. doi:10.1139/cjb-79-5-600.
- Doolittle, Ford. 2013. “Microbial Neopleomorphism.” *Biology and Philosophy* 28: 351–78.
- Dupré, John. 1993. *The Disorder of Things: Metaphysical Foundations of the Disunity of Science*. Cambridge, MA: Harvard University Press.
- . 2014. “Animalism and the Persistence of Human Organisms.” *The Southern Journal of Philosophy* 52 (Sindel Supplement): 6–23. doi:10.1111/sjp.12065.
- Dupré, John, and Maureen A O Malley. 2009. “Varieties of Living Things : Life at the Intersection of Lineage and Metabolism.” *Philosophy and Theory in Biology* 1: 1–25.
- Egel, Richard. 2008. “Overt and Hidden Layers of Description and Control.” In *Recombination and Meiosis: Crossing-Over and Nondisjunction*, edited by Richard Egel and Dirk-Henner Lankenau, 27–68. Springer-Verlag Berlin Heidelberg. doi:10.1007/7050.
- Ereshefsky, Marc. 2001. *The Poverty of the Linnaean Hierarchy: A Philosophical Study of Biological Taxonomy*. Cambridge, MA: Cambridge University Press.
- . 2012. “Homology Thinking.” *Biology and Philosophy* 27 (3): 381–400.

doi:10.1007/s10539-012-9313-7.

Ereshefsky, Marc, and Makmiller Pedroso. 2013. "Biological Individuality: The Case of."

Biology & Philosophy 28: 331–49.

———. 2015. "Rethinking Evolutionary Individuality." *Proceedings of the National Academy of Sciences of the United States of America* 112 (33): 10126–32.

doi:10.1073/pnas.1421377112.

———. 2016. "What Biofilms Can Teach Us about Individuality." In *Individuals Across Sciences*, edited by Alexandre Guay and Thomas Pradeu, 1–30. Oxford, UK: Oxford University Press.

Ereshefsky, Marc, and Thomas A.C. Reydon. 2015. "Scientific Kinds." *Philosophical Studies* 172: 969–86. doi:10.1007/s11098-014-0301-4.

Erkko, Hannele, Bing Xia, Jenni Nikkila, Johanna Schleutker, Kirsi Syrjakoski, Arto Mannermaa, Anne Kallioniemi, et al. 2007. "A Recurrent Mutation in PALB2 in Finnish Cancer Families." *Nature* 446 (7133). Nature Publishing Group: 316–19.
<http://dx.doi.org/10.1038/nature05609>.

Franklin-Hall, Laura R. 2015. "Natural Kinds as Categorical Bottlenecks." *Philosophical Studies* 172 (4): 925–48. doi:10.1007/s11098-014-0326-8.

French, Steven, and Kerry McKenzie. 2012. "Thinking outside of the Toolbox: A More Productive Engagement between Metaphysics and Philosophy of Physics." *European Journal of Analytic Philosophy* 8 (1): 42–59.

Germain, Pierre-Luc. 2012. "Cancer Cells and Adaptive Explanations." *Biology and Philosophy* 27: 785–810.

Ghiselin, Michael T. 1974. "A Radical Solution to the Species Problem." *Systematic Zoology* 23:

536–44.

- . 1981. “Categories, Life, and Thinking.” *Behavioural and Brain Sciences* 4: 269–313.
- . 1987. “Species Concepts, Individuality, and Objectivity.” *Biology & Philosophy* 2: 127–43.
- . 2016. “Homology, Convergence and Parallelism.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 371 (1685): 20150035. doi:10.1098/rstb.2015.0035.
- Gilbert, Scott F, Jan Sapp, and Alfred I Tauber. 2012. “A Symbiotic View of Life : We Have Never Been Individuals.” *The Quarterly Review of Biology* 87 (4): 325–41.
doi:<http://www.jstor.org/stable/10.1086/668166>.
- Gillhooly, James F., Chen Hou, and Michael Kaspari. 2010. “Eusocial Insects as Superorganisms: Insights from Metabolic Theory.” *Communicative and Integrative Biology* 3 (4): 360–62.
- Godfrey-Smith, Peter. 2009. *Darwinian Populations and Natural Selection*. New York, NY: Oxford University Press.
- . 2011. “Darwinian Populations and Transitions in Individuality.” In *The Major Transitions in Evolution Revisited*, edited by Brett Calcott and Kim Sterelny, 65–82. Cambridge, MA: MIT Press.
- . 2013. “Darwinian Individuals.” In *From Groups to Individuals: Evolution and Emerging Individuality*, edited by Frédéric Bouchard and Philippe Huneman, 18–36. Cambridge, MA: MIT Press.
- Gould, Stephen J., and Richard C. Lewontin. 1979. “The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme.” *Proceedings of the Royal Society of London Series B Containing Papers of a Biological Character Royal*

- Society Great Britain* 205 (1161): 581–98. doi:10.1098/rspb.1979.0086.
- Gould, Stephen Jay. 1989. *Wonderful Life: The Burgess Shale and the Nature of History*. New York, NY: W.W. Norton & Company.
- . 2002. *The Structure of Evolutionary Theory*. Cambridge, MA: The President and Fellows of Harvard College.
- Graham, James. 1992. *Cancer Selection: The New Theory of Evolution*. Lexington, VA: Aculeus Printing.
- Griesemer, J. 2000. “Development, Culture, and The Units of Selection.” *Philosophy of Science* 67 (348–368).
- Griffiths, Paul E. 1994. “Cladistic Classification and Functional Explanation.” *Philosophy of Science* 61 (2): 206–27.
- Grosberg, Richard K, and Richard R Strathmann. 2007. “The Evolution of Multicellularity: A Minor Major Transition?” *Annu. Rev. Ecol. Evol. Syst* 38: 621–54.
doi:10.1146/annurev.ecolsys.36.102403.114735.
- Gross, Jeferson, and Debashish Bhattacharya. 2010. “Uniting Sex and Eukaryote Origins in an Emerging Oxygenic World.” *Biology Direct* 5: 53. doi:10.1186/1745-6150-5-53.
- Haber, Matthew H. 2013. “Colonies Are Individuals: Revisiting the Superorganism Revival.” In *From Groups to Individuals: Evolution and Emerging Individuality*, edited by Frédéric Bouchard and Philippe Huneman, 195–218. Cambridge, MA: MIT Press.
- Hacking, Ian. 1996. “The Disunities of Science.” In *The Disunity of Science: Boundaries, Contexts, and Power*, edited by P Galison and D. Stump, 37–74. Stanford, California: Stanford University Press.
- Hammerschmidt, Katrin, Caroline J. Rose, Benjamin Kerr, and Paul B. Rainey. 2014. “Life

- Cycles, Fitness Decoupling and the Evolution of Multicellularity: Supplementary Information." *Nature* 515 (7525): 75–79. doi:10.1038/nature13884.
- Harrison, R. D. 2000. "Repercussions of El Niño: Drought Causes Extinction and the Breakdown of Mutualism in Borneo." *Proceedings of the Royal Society B: Biological Sciences* 267 (1446): 911–15. doi:10.1098/rspb.2000.1089.
- Hempel, Carl. 1965. *Aspects of Scientific Explanation*. New York, NY: Free Press.
- Hull, David L. 1976. "Are Species Really Individuals?" *Systematic Zoology* 25 (2): 174–91.
- . 1978. "A Matter of Individuality." *Philosophy of Science* 45 (3): 335–60. doi:10.4324/9780203133972.
- . 1980. "Individuality and Selection." *Annual Review of Ecology and Systematics* 11: 311–32. doi:10.1146/annurev.es.11.110180.001523.
- . 1992. "Individual." In *Keywords in Evolutionary Biology*, edited by Evelyn Fox Keller and Elisabeth A. Lloyd, 180–87. Cambridge, MA: Harvard University Press.
- Hummert, Sabine, Katrin Bohl, David Basanta, Andreas Deutsch, Sarah Werner, Günter Theißen, Anja Schröter, and Stefan Schuster. 2014. "Evolutionary Game Theory: Cells as Players." *Molecular BioSystems* 10: 3044–65. doi:10.1039/C3MB70602H.
- Huneman, Philippe. 2014a. "Individuality as a Theoretical Scheme. I. Formal and Material Concepts of Individuality." *Biological Theory* 9 (4): 361–73. doi:10.1007/s13752-014-0192-9.
- . 2014b. "Individuality as a Theoretical Scheme. II. About the Weak Individuality of Organisms and Ecosystems." *Biological Theory* 9 (4): 374–81. doi:10.1007/s13752-014-0193-8.
- Huxley, Julian S. 1912. *The Individual in the Animal Kingdom*. Cambridge, MA: Cambridge

University Press.

———. 1953. *Evolution in Action*. New York, NY: Harper.

Inkpen, Rob, and Derek Turner. 2012. “The Topography of Historical Contingency.” *Journal of the Philosophy of History* 6 (1): 1–19. doi:10.1163/187226312X625573.

Jablonski, David. 2007. “Scale and Hierarchy in Macroevolution.” *Palaeontology* 50 (1).

Blackwell Publishing Ltd: 87–109. doi:10.1111/j.1475-4983.2006.00615.x.

Jacob, F. 1977. “Evolution and Tinkering.” *Science* 196 (4295): 1161–66.

doi:10.1126/science.860134.

Janicke, Marie A., Loren Lasko, Rudolf Oldenbourg, and James R. LaFountain Jr. 2007.

“Chromosome Malorientations after Meiosis II Arrest Cause Nondisjunction.” *Molecular Biology of the Cell* 18: 1645–56. doi:10.1091/mbc.E06.

Janzen, Daniel. 1977. “What Are Dandelions and Aphids?” *The America Naturalist* 111 (979): 586–89.

Keller, Laurent, and Michael G. Surette. 2006. “Communication in Bacteria: An Ecological and Evolutionary Perspective.” *Nat Rev Micro* 4 (4). Nature Publishing Group: 249–58.

<http://dx.doi.org/10.1038/nrmicro1383>.

Kellert, Stephen H., Helen E. Longino, and C. Kenneth Waters. 2006. *Scientific Pluralism*.

Minneapolis, MN: University of Minnesota Press.

Kerr, B., and J.R. Nahum. 2011. “Setting the Stage for an Egalitarian Major Transition: The Evolution of Restraint.” In *The Major Transitions in Evolution Revisited*, edited by Brett Calcott and Kim Sterelny, 127–40. Cambridge, MA: MIT Press.

Kirk, D.L. 2005. “A Twelve-Step Program for Evolving Multicellularity and a Division of Labour.” *BioEssays* 27: 299–310.

- Knoll, A.H., E.J. Javaux, D. Hewitt, and P. Cohen. 2006. "Eukaryotic Organisms in Proterozoic Oceans." *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361 (1470): 1023-1038.
- Knoll, Andrew H. 2003. "The Geological Consequences of Evolution." *Geobiology* 1 (1). Blackwell Science Ltd: 3–14. doi:10.1046/j.1472-4669.2003.00002.x.
- Koschwanez, John H., Kevin R. Foster, and Andrew W. Murray. 2011. "Sucrose Utilization in Budding Yeast as a Model for the Origin of Undifferentiated Multicellularity." *PLoS Biology* 9 (8): e1001122. doi:10.1371/journal.pbio.1001122.
- Kripke, S. 1972. "Naming and Necessity." In *Semantics of Natural Language*, edited by D Davidson and G Harman, 253–55. Reidel, Dordrecht.
- Ku, Chuan, Shijulal Nelson-Sathi, Mayo Roettger, Sriram Garg, Einat Hazkani-Covo, and William F Martin. 2015. "Endosymbiotic Gene Transfer from Prokaryotic Pangenomes: Inherited Chimerism in Eukaryotes." *Proceedings of the National Academy of Sciences of the United States of America* 112 (33): 10139–46. doi:10.1073/pnas.1421385112.
- Lean, Christopher, and Anya Plutynski. 2016. "The Evolution of Failure: Explaining Cancer as an Evolutionary Process." *Biology and Philosophy* 31 (1). Springer Netherlands: 39–57. doi:10.1007/s10539-015-9511-1.
- Leeuwen, Thomas Van, Bartel Vanholme, Steven Van Pottelberge, Pieter Van Nieuwenhuyse, Ralf Nauen, Luc Tirry, and Ian Denholm. 2008. "Mitochondrial Heteroplasmy and the Evolution of Insecticide Resistance: Non-Mendelian Inheritance in Action." *Proceedings of the National Academy of Sciences of the United States of America* 105 (16): 5980–85. doi:10.1073/pnas.0802224105.
- Leroi, Armand M, Vassiliki Koufopanou, and Austin Burt. 2003. "Cancer Selection." *Nature*

- Reviews Cancer* 3: 226–31. doi:10.1038/nrc1016.
- Lewontin, Richard C. 1970. “The Units of Selection.” *Annual Review of Ecology and Systematics* 1: 1–18.
- . 1983. “The Organism as the Subject and Object of Evolution.” *Scientia* 118: 63–82.
- Li, Min, Baohong Wang, Menghui Zhang, Mattias Rantalainen, Shengyue Wang, Haokui Zhou, Yan Zhang, et al. 2008. “Symbiotic Gut Microbes Modulate Human Metabolic Phenotypes.” *Proceedings of the National Academy of Sciences* 105 (6): 2117–22. doi:10.1073/pnas.0712038105.
- Libby, Eric, William Ratcliff, Michael Travisano, and Ben Kerr. 2014. “Geometry Shapes Evolution of Early Multicellularity.” *PLoS Computational Biology* 10 (9): e1003803. doi:10.1371/journal.pcbi.1003803.
- Markov, A.V. 2014. “Horizontal Gene Transfer as a Possible Evolutionary Predecessor of Sexual Reproduction.” *Paleontological Journal* 48 (3): 219–33. doi:10.1134/S0031030114030149.
- Maynard-Smith, John, and Eörs Szathmáry. 1995. *The Major Transitions in Evolution*. New York, NY: Oxford University Press.
- Mayr, Ernst. 1970. *Populations, Species, and Evolution*. Cambridge, MA: Harvard University Press.
- McConwell, Alison K. 2015a. “Review of Maureen O’Malley’s Philosophy of Microbiology (2014).” *The British Journal for the Philosophy of Science* 0: 1–5.
- . 2015b. “Review of Thomas Pradeu’s The Limits of the Self: Immunology and Biological Identity (2012).” *Philosophy in Review* 35 (3): 171–73.
- McConwell, Alison K, and Adrian Currie. 2016. “Gouldian Arguments and the Sources of Contingency.” *Biology {&} Philosophy*, 1–19. doi:10.1007/s10539-016-9556-9.

- McGhee, George. 2011. *Convergent Evolution: Limited Forms Most Beautiful*. Cambridge, MA: MIT Press.
- McKenzie, Kerry. 2013. "Priority and Particle Physics: Ontic Structural Realism as a Fundamentality Thesis." *The British Journal for the Philosophy of Science* 65 (2): 353–80.
- Mcshea, Daniel W., and Carl Simpson. 2011. "The Miscellaneous Transitions in Evolution." In *The Major Transitions in Evolution Revisited*, edited by Brett Calcott and Kim Sterelny, 19–34. Cambridge, MA: MIT Press.
- Michod, Richard E., and D. Roze. 1999. "A Multi-Level Selection Theory of Evolutionary Transitions in Individuality." *Artificial Life*. http://www.ugr.es/~jmgreyes/michod_roze.pdf.
- Michod, Richard E. 1999. *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. Princeton, NJ: Princeton University Press.
- Michod, Richard E., and Matthew D. Herron. 2006. "Commentary: Cooperation and Conflict during Evolutionary Transitions in Individuality." *European Society for Evolutionary Biology* 19: 1406–9.
- Michod, Richard E, and Aurora M Nedelcu. 2003. "On the Reorganization of Fitness During Evolutionary Transitions in Individuality." *Integrative and Comparative Biology* 43 (1): 64–73. <http://dx.doi.org/10.1093/icb/43.1.64>.
- Moran, Nancy A. 2006. "Symbiosis." *Current Biology* 16 (20). Elsevier: R866–71. doi:10.1016/j.cub.2006.09.019.
- Moya, Andres, Juli Pereto, Rosario Gil, and Amparo Latorre. 2008. "Learning How to Live Together: Genomic Insights into Prokaryote-Animal Symbioses." *Nat Rev Genet* 9 (3). Nature Publishing Group: 218–29. <http://dx.doi.org/10.1038/nrg2319>.
- Muijres, Florian T., L. Christoffer Johansson, Melissa S. Bowlin, York Winter, and Anders

- Hedenström. 2012. “Comparing Aerodynamic Efficiency in Birds and Bats Suggests Better Flight Performance in Birds.” *PLoS ONE* 7 (5). doi:10.1371/journal.pone.0037335.
- Nishiguchi, M.K. 2002. “Host-Symbiont Recognition in the Environmentally Transmitted Sepiolid Squid-Vibrio Mutualism.” *Microbial Ecology* 44 (1): 10–18. doi:10.1007/s00248-002-0002-y.
- Nyholm, Spencer V., and Margaret McFall-Ngai. 2004. “The Winnowing: Establishing the Squid–vibrio Symbiosis.” *Nature Reviews Microbiology* 2 (8): 632–42. doi:10.1038/nrmicro957.
- O’Malley, Maureen. 2014. *Philosophy of Microbiology*. Cambridge, UK: Cambridge University Press.
- Odenbaugh, Jay. n.d. “A Sense of Scale: Integration in Ecology.” *An Afternoon of Philosophy and Ecology 2016*.
- Okasha, Samir. 2006. *Evolution and the Levels of Selection*. New York, NY: Oxford University Press.
- Oppenheim, Paul, and Hilary Putnam. 1958. “Unity of Science as a Working Hypothesis.” In *Minnesota Studies in the Philosophy of Science Vol. 2*, edited by H. Feigl, 3–36. Minneapolis, MN: Minnesota University Press.
- Otto, Sarah P. 2017. “Evolution of Modifier Genes and Biological Systems.” In *The Princeton Guide to Evolution*, edited by Jonathan Losos, 255–62. New Jersey: Princeton University Press.
- Pace, Norman R. 2006. “Time for a Change.” *Nature* 44 (18): 289.
- Paracer, Surindar, and Vernon Ahmadjian. 2000. *Introduction. Symbiosis: An Introduction to Biological Associations*. 2nd ed. Oxford UK: Oxford University Press.

- Pigliucci, Massimo. 2008. "Is Evolvability Evolvable." *Nature Reviews: Genetics* 9: 75–82.
- Pinto, Daniel, and Hans Clevers. 2005. "Wnt, Stem Cells and Cancer in the Intestine." *Biology of the Cell* 97 (3): 185–96.
- Piotrowska, Monika. 2013. "From Humanized Mice to Human Disease: Guiding Extrapolation from Model to Target." *Biology and Philosophy* 28 (3): 439–55. doi:10.1007/s10539-012-9323-5.
- Powell, Russell. 2009. "Contingency, Convergence, and Macroevolution: A Reply to John Beatty." *The Journal of Philosophy* 106 (7): 390–403.
- Powell, Russell, and Carlos Mariscal. 2015. "Convergent Evolution as Natural Experiment: The Tape of Life Reconsidered." *Interface Focus* 5: 20150040. doi:10.1098/rsfs.2015.0040.
- Pradeu, Thomas. 2010. "What Is an Organism? An Immunological Answer." *History and Philosophy of the Life Sciences* 32: 247–67.
- . 2012. *The Limits of the Self: Immunology and Biological Identity*. Oxford UK: Oxford University Press.
- Putnam, Hilary. 1975. *Mind, Language and Reality: Philosophical Papers Volume 2*. Cambridge, MA: Cambridge University Press.
- Queller, David C. 2000. "Relatedness and the Fraternal Major Transitions." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 355: 1647–55. doi:10.1098/rstb.2000.0727.
- Queller, David C., and Joan E. Strassmann. 2009. "Beyond Society: The Evolution of Organismality." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364: 3143–55. doi:10.1098/rstb.2009.0095.
- . 2012. "Experimental Evolution of Multicellularity Using Pseudo-Organisms." *Biology*

- Letters*, 1–5. doi:10.1098/rsbl.2012.0636.
- Ragan, Mark A., and Robert G. Beiko. 2009. “Lateral Genetic Transfer: Open Issues.” *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364: 2241–51. doi:10.1098/rstb.2009.0031.
- Rainey, Paul B., and Benjamin Kerr. 2010. “Cheats as First Propagules: A New Hypothesis for the Evolution of Individuality during the Transition from Single Cells to Multicellularity.” *BioEssays* 32 (10): 1–9. doi:10.1002/bies.201000039.
- Ratcliff, William C, R. Ford Denison, Mark Borrello, and Michael Travisano. 2012. “Experimental Evolution of Multicellularity.” *Proceedings of the National Academy of Sciences* 109 (5): 1595–1600. doi:10.1073/pnas.1115323109.
- Ratray, Alison, Gustavo Santoyo, Brenda Shafer, and Jeffrey N. Strathern. 2015. “Elevated Mutation Rate during Meiosis in *Saccharomyces Cerevisiae*.” *PLoS Genetics* 11 (1): e1004910. doi:10.1371/journal.pgen.1004910.
- Ray, Robert P., Toshiyuki Nakata, Per Henningsson, and Richard J. Bomphrey. 2016. “Enhanced Flight Performance by Genetic Manipulation of Wing Shape in *Drosophila*.” *Nature Communications* 7 (10851). Nature Publishing Group: 1–8. doi:10.1038/ncomms10851.
- Rioux, John D., and Abul K. Abbas. 2005. “Paths to Understanding the Genetic Basis of Autoimmune Disease.” *Nature* 435 (7042): 584–89. <http://dx.doi.org/10.1038/nature03723>.
- Rosenberg, Alexander, and Karen Neander. 2009. “Are Homologies (Selected Effect or Causal Role) Function Free?” *Philosophy of Science* 76 (3): 307–34. doi:10.1086/649807.
- Ruse, Michael. 1969. “Definitions of Species in Biology.” *The British Journal for the Philosophy of Science* 38: 225–42.
- . 1987. “Biological Species: Natural Kinds, Individuals, or What?” *The British Journal*

- for the Philosophy of Science* 38 (2): 225–42.
- Sánchez Alvarado, Alejandro, and Shinya Yamanaka. 2014. “Rethinking Differentiation: Stem Cells, Regeneration, and Plasticity.” *Cell* 157: 110–19. doi:10.1016/j.cell.2014.02.041.
- Santelices, Bernabé. 1999. “How Many Kinds of Individual Are There?” *TREE* 14 (4): 152–55. doi:10.1016/S0169-5347(98)01519-5.
- Sarka, Sahotra. 2016. “Ecology.” *The Stanford Encyclopedia of Philosophy*, Edited by Edward N. Zalta. URL=<<https://plato.stanford.edu/archives/win2016/entries/ecology/>>.
- Slater, Matthew H. 2015. “Natural Kindness.” *The British Journal for the Philosophy of Science* 66 (2): 375–411. <http://dx.doi.org/10.1093/bjps/axt033>.
- Sober, Elliott. 1991. “Organisms, Individuals, and Units of Selection.” In *Organism and the Origins of Self*, edited by Alfred I Tauber, 275–96. Netherlands: Kluwer Academic Publishers. doi:10.1007/978-94-011-3406-4_13.
- Sousa Melo, Felipe E De, Louis Vermeulen, Evelyn Fessler, and Jan Paul Medema. 2013. “Cancer Heterogeneity—a Multifaceted View.” *Nature Publishing Group* 14 (8): 686–95. doi:10.1038/embor.2013.92.
- Stebbins, G.L. 1969. *The Basis for Progressive Evolution*. Chapel Hill, N.C.: University of North Carolina Press.
- Sterelny, Kim. 2003. “Last Will and Testament : Stephen Jay Gould ’ S The Structure of Evolutionary Theory” 70 (2): 255–63.
- . 2007. “What Is Evolvability?” In *Philosophy of Biology*, edited by Mohan Matthen and Christopher Stephens, 163–92. Holland: Elsevier.
- Suppes, P. 1978. “The Plurality of Science.” *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association* 2: 3–16.

- Szathmáry, Eörs, and Christantha Fernando. 2011. "Concluding Remarks." In *The Major Transitions in Evolution Revisited*, edited by Brett Calcott and Kim Sterelny, 301–10. Cambridge, MA: MIT Press.
- Szathmáry, Eörs, and John Maynard-Smith. 1995. "The Major Evolutionary Transitions" 374 (16): 227–32.
- Travisano, Michael, Judith A. Mongold, Albert F. Bennett, and Richard E. Lenski. 1995. "Experimental Tests of the Roles of Adaptation, Chance, and History in Evolution." *Science, New Series* 267 (5194): 87–90.
- Turner, Derek. 2011a. "Gould's Replay Revisited." *Biology and Philosophy* 26: 65–79. doi:10.1007/s10539-010-9228-0.
- . 2011b. "Evolutionary Contingency." In *Paleontology: A Philosophical Introduction*. Cambridge, MA: Cambridge University Press.
- . 2015. "Historical Contingency and the Explanation of Evolutionary Trends." In *Biological Explanation: An Enquiry into the Diversity of Explanatory Patterns in the Life Sciences*, edited by Christophe Malaterre and Pierre-Alain Braillard, 73–90. New York, NY: Springer. doi:10.1007/978-94-017-9822-8.
- Uyenoyama, Marcy K. 1987. "Genetic Transmission and the Evolution of Reproduction: The Significance of Parent-Offspring Relatedness to the 'Cost of Meiosis.'" In *Meiosis*, edited by P.B. Moens. London, UK: Academic Press.
- Van Valen, L. 1976. "Ecological Species, Multispecies, and Oaks." *Taxon* 25: 233–39.
- Vermeij, G.J. 1987. *Evolution and Escalation. An Ecological History of Life*. Vol. 1. Princeton, NJ: Princeton University Press. doi:10.1046/j.1420-9101.1988.1040369.x.
- Waters, C. Kenneth. 1990. "Why the Anti-Reductionist Consensus Won't Survive: The Case of

- Classical Mendelian Genetics.” *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association* 1990 (1): 125–39.
- . 2005. “Why Genic and Multilevel Selection Theories Are Here to Stay*.” *Philosophy of Science* 72: 311–33. doi:10.1086/432426.
- . 2006. “A Pluralist Interpretation of Gene-Centered Biology.” In *Scientific Pluralism*, edited by Helen E. Longino, Stephen H. Kellert, and C. Kenneth Waters, 190–214. Minneapolis, MN: University of Minnesota Press.
- Wiggins, D. 2001. *Sameness and Substance Renewed*. Cambridge, MA: Cambridge University Press.
- Wilson, Robert A., and Matthew Barker. 2017. “The Biological Notion of Individual.” In *Stanford Encyclopedia of Philosophy*, edited by Edward N. Zalta.
- Wimsatt, W.C., and J.C. Schank. 2004. “Generative Entrenchment, Modularity, and Evolvability: When Genic Selection Meets the Whole Organism.” In *Modularity in Development and Evolution*, edited by G. Schossler and G. Wagner, 359–94. Chicago, IL: Chicago University Press.
- Wolpert, Lewis, and Eörs Szathmáry. 2002. “Multicellularity: Evolution and the Egg.” *Nature* 420: 745. doi:10.1038/420745a.
- Worrall, James J., Kelly F. Sullivan, Thomas C. Harrington, and Joseph P. Steimel. 2004. “Incidence, Host Relations and Population Structure of *Armillaria Ostoyae* in Colorado Campgrounds.” *Forest Ecology and Management* 192: 191–206. doi:10.1016/j.foreco.2004.01.009.
- Wylie, Alison. 2012. “Feminist Philosophy of Science: Standpoint Matters.” *American Philosophical Association Presidential Address Abstract*.

- Yamaguchi, Masashi, Yuko Mori, Yoshimichi Kozuka, Hitoshi Okada, Katsuyuki Uematsu, Akihiro Tame, Hiromitsu Furukawa, Tadashi Maruyama, Cedric O’Driscoll Worman, and Koji Yokoyama. 2012. “Prokaryote or Eukaryote? A Unique Microorganism from the Deep Sea.” *Journal of Electron Microscopy* 61 (6): 423–31.
<http://dx.doi.org/10.1093/jmicro/dfs062>.
- Yamaguchi, Masashi, and Cedric O Driscoll Worman. 2014. “Deep - Sea Microorganisms and the Origin of the Eukaryotic Cell.” *Japanese Journal of Protozoology* 47 (1): 29–48.
- Yong, Ed. 2012. “Yeast Suggests Speedy Start for Multicellular Life.” *Nature News*.
- Young, J. Z. 1962. “The Retina of Cephalopods and Its Degeneration After Optic Nerve Section.” *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 245 (718). The Royal Society: 1–18. <http://www.jstor.org/stable/2992647>.
- Zimmer, Richard K., and Jeffrey A. Riffell. 2011. “Sperm Chemotaxis, Fluid Shear, and the Evolution of Sexual Reproduction.” *Proceedings of the National Academy of Sciences of the United States of America* 108 (32): 13200–205. doi:10.1073/pnas.1018666108.