

forthcoming in O. Bueno, M. B. Fagan, and R. Chen (eds.),  
*Individuation Across Experimental and Theoretical Sciences*,  
Oxford: Oxford University Press

preprint

## *Ask Not “What is an Individual?”*

C. Kenneth Waters

Department of Philosophy

University of Calgary

**Abstract:** Philosophers of biology typically pose questions about individuation by asking “what is an individual?” For example, we ask, “what *is* an individual species”, “what *is* an individual organism”, and “what *is* an individual gene?” In the first part of this chapter, I present my account of the gene concept and how it is used in investigative practices in order to motivate a more pragmatic approach. Instead of asking “what *is* a gene?”, I ask: “how do biologists individuate genes?”, “for what purposes?”, and “do their practices of individuating genes serve these purposes?” In the second part of this chapter, I propose that we use this approach when analyzing concepts of organisms and biological individuals. Following philosophical pragmatism, I argue that we should abstain from attempts to situate individuation of Darwinian individuals or of holobionts in a philosophy of nature. Instead, we should analyze practices of individuating organisms in terms of three-place relations between the world, ideas, and human purposes and actions. I conclude with three lessons: an ontological, an epistemological, and a meta-philosophical lesson, which I suggest, apply to philosophy of science generally and to philosophy and metaphysics at large.

**Keywords:** pragmatics, individuating, gene, organism, evolutionary individual, holobiont, actual-difference maker, selection, speciation, philosophy of nature, metaphysics

# *Ask Not “What is an Individual?”*

C. Kenneth Waters

Department of Philosophy

University of Calgary

## **1. Introduction**

Biologists and philosophers often ask ‘what is an X?’ with an emphasis on the word ‘is’. As Arthur Fine (1996) might remark, it is as if one can hear the stamping of feet upon utterance of the word ‘is’ when we ask, what *is* a species, what *is* an organism, or what *is* a gene? In the first part of this chapter, I motivate a more pragmatic approach to questions about individuals and individuation by presenting my account of conceptual practice in genetics. I contend that instead of asking “what *is* a gene?”, philosophers should ask: “how do biologists individuate genes?”, “for what purposes?”, and “do their practices of individuation serve these purposes?” In the second part of this chapter, I propose that we adopt this approach in our analyses of organisms and biological individuals. I illustrate how philosophical work on individuation typically focuses on questions about what it is to be an individual by discussing Peter Godfrey-Smith’s analysis of Darwinian individuals (2009). According to his analysis, animals exemplify the paradigm of Darwinian individuality. I contend that we should not interpret this claim as a “philosophy of nature.” Next, I turn to the idea that the real individuals are holobionts, not animals. I challenge the underlying presumption that one concept of individuals identifies the real individuals while others do not. But, I reappropriate Scott Gilbert, Jan Sapp, and Alfred Tauber’s argumentation (2012) for the holobiont view to advance pragmatism; instead of asking ‘what is an individual?’ as if there is an essence to (or a paradigm of) individuality, philosophers should examine how biologists individuate animals and assemblages of animals and commensals and ask what purposes these individuating practices can serve.

## **2. How biologists individuate genes**

The rise and practice of classical genetics involved individuating mutations and segments (i.e. genes) in which mutations occur. Individuating mutations

and genes continues to be an important part of practice in contemporary genetics. In classical genetics, the individuation of genes was intimately connected to the individuation of mutations. Experimental practice involved identifying mutations and using mutations to individuate genes. Geneticists believed that genes were the fundamental units of heredity, that genes were located in cellular structures called ‘chromosomes’, and that mutations were differences in genes. One of the central aims of classical genetics was to parse chromosomes into their basic functional units, i.e. into genes (the ‘mapping project’).<sup>1</sup>

Thomas Hunt Morgan and his collaborators established empirical strategies for individuating genes. Working on fruit flies, they searched laboratory populations for the appearance of flies with distinctive outward differences (compared to other flies in the laboratory population). Upon finding such a difference, they conducted breeding experiments to determine whether the outward difference was caused by one or a few differences in chromosome(s). If they learned that the outward difference was indeed caused by one or a few chromosomal differences, they would call the outward difference a difference in ‘phenotype’ and the chromosomal difference(s) a difference in ‘genotype’. The term ‘mutation’ was used to refer to individual differences in genotype.

The Morgan group developed sophisticated breeding strategies for determining whether a phenotypic difference was caused by one mutation or a few mutations. In cases where a phenotypic difference was caused by a few mutations, their breeding strategies enabled them to individuate the different mutations responsible for the phenotypic difference. By individuating mutations, they individuated genes in which mutations occurred. Morgan’s group also developed strategies for determining the relative locations of mutations, which effectively determined the relative location of genes in which mutations were located. The success of these strategies supported the idea that mutations and genes were located in linear fashion along the chromosomes.

Classical geneticists learned that different mutations could occur in one and the same gene, and as the individuation practices of the science advanced through the first half of the twentieth century, geneticists established an experimental method, called the *cis-trans test*, for determining whether two mutations were located in the same gene or in different genes. This effectively provided them with a means for individuating functional units in the chromosome, that is, for individuating ‘genes’. In time, geneticists learned how to determine the relative location of different mutations occurring within one and the same gene. Hence, they learned that genes are functional units positioned in linear fashion along chromosomes, that mutations are differences within genes, and that these differences are located in linear fashion within the genes.

---

<sup>1</sup> A more ambitious aim of classical genetics was to investigate a broad range of biological processes (see Waters 2004, 2008).

The individuating practices of classical genetics did not depend on knowledge about what genes were made of, how genes functioned, what the function of genes were, or even how differences in a gene could cause differences in phenotype. They did not need to answer the question, “what is a gene?” Of course, some theoretically inclined geneticists (especially Hermann Joseph Muller, see Carlson 1966) were carrying out investigations aimed at determining the material make-up of genes, the nature of gene action, and the individual functions of particular genes. One might view theoretical research into the question, “what is a gene?”, to have been a metaphysics of sorts—a metaphysics that incubated later genetics.<sup>2</sup> But, it was not central to the practice of the science. Most research involved using genetics to investigate a wide range of basic biological processes, not just hereditary processes (Kohler 1994, Waters 2004, 2008). If one wishes to understand the knowledge of classical genetics and how the science worked, one needs to understand how classical geneticists individuated mutations and genes. This is required because geneticists’ explanations of the transmission of phenotypic differences from one generation to the next (their major explanatory feat) and their strategies for using genetics to investigate biological processes (their greatest ambition) depended on individuating mutations and genes. But, one does not need to know how different geneticists might have speculated about the question, ‘what *is* a gene?’

In sum, classical geneticists shared a minimal concept of the gene. Geneticists knew that differences in genes could cause uniform differences in phenotype in particular genetic and environmental contexts (Waters 2009), and that was an important part of their conception of genes. But, ideas about the material make-up, function, or nature of gene action were not part of their basic gene concept. But, what about individuation practices in contemporary genetics? What concepts do contemporary biologists employ?

Contemporary geneticists individuate numerous elements in genetic materials: genes, introns, exons, regulatory regions, repetitive regions, transposable elements, and many more. For the purposes of this chapter, I focus on the individuation of genes at the molecular scale. According to textbook definitions, genes are segments of DNA that code for proteins. DNA consists of linear sequences of nucleotides. Proteins, roughly speaking, consist of polypeptides that are made up of linear sequences of amino acids. The textbook idea, as schoolchildren learn, is that genes are segments of DNA that produce RNA molecules and RNA molecules produce polypeptides. Linear sequences of nucleotides in DNA are said to ‘code for’ linear sequences of amino acids in polypeptides.

Philosophers have argued that this gene concept is ambiguous, hopelessly vague, and that it admits exceptions. Many contend that genes exist at the cytological scale, not at the molecular scale. I have addressed these arguments

---

<sup>2</sup> I thank an anonymous reviewer for pushing me on this point.

elsewhere (Waters 1994 and 2001) and will not repeat the details here. Instead, I present my analysis of the molecular gene concept and show how it is used in contemporary genetics to individuate segments of DNA. I will then describe what purposes this practice of individuating serves across biological and biomedical sciences.

My analysis is cast in causal terms because the common use of informational language typically muddles important issues and easily leads to exaggerated claims on behalf of contemporary genetics. I therefore refrain from characterizing the process of RNA synthesis as ‘transcription’ or the process of polypeptide synthesis as ‘translation’. Biologists have investigated and explained these processes as biochemical syntheses and it is helpful to conceive of them in these terms. But, the question remains, “what is the relation between genes and polypeptides?”

Some biologists and philosophers say that the segments of nucleotide sequences within DNA called genes ‘code for’ the amino acids comprising polypeptides. But, this language is unclear, and as I have already mentioned, it gives rise to exaggerated claims about the significance of genes. Others say that the segments called genes ‘produce’ polypeptides. But, this is also misleading. The synthesis of RNA molecules depends on many molecules, not just DNA, and the synthesis of polypeptide molecules depends on many molecules, not just RNA molecules. So, what, if anything, is the distinctive causal role of DNA in the synthesis of RNA molecules and what, if anything, is the distinctive role of RNA molecules in the synthesis of polypeptides?

The distinctive role of genes is that they are makers of actual differences in the synthesis of RNA molecules (I have called them ‘actual-difference makers’), and the distinctive role of RNA molecules is that they are makers of actual differences in the synthesis of different kinds of polypeptides. Cells contain many different kinds of polypeptides, each kind having a particular linear sequence of amino acids.<sup>3</sup> Although there are many causes of the synthesis of polypeptide molecules, most of the causes are uniform across the syntheses of different kinds of RNA molecules. RNA is a distinctive cause because it takes on different values in the synthesis of different kinds of polypeptides. That is, actual differences in the nucleotide sequences of different RNA molecules determine the actual differences in amino acid sequences in different polypeptide molecules. Hence, they are actual-difference makers. Likewise, actual differences in nucleotide sequences in different genes determine actual difference in nucleotide sequences in different

---

<sup>3</sup> Of course, there are always exceptions to general biological claims. In this case: some proteins, e.g. prions, take on different conformations *in vitro*. These different conformations could be regarded as different kinds of proteins that have identical amino acid sequences. But, this exception does not undermine my analysis of gene causation. What it shows is that RNA is not an actual-difference maker of these different conformations.

RNA molecules (in eukaryotes, differences in RNA molecules are often determined by differences in genes *and* differences in splicing agents—see below). This is to say that the DNA segments called genes are causes that determine differences in amino acid sequences that actually occur in a cell. Hence, DNA is a distinctive cause of these actual differences. It is an actual-difference maker. In this sense, we can say that the sequence of nucleotides in a gene determines the sequence of nucleotides in an RNA molecule, which determines the sequence of amino acids in a polypeptide.

This analysis treats the molecular gene concept as an indexical. DNA segments are not simply genes, they are genes for linear sequences. That is, the referent of an application of the term ‘gene’ depends on what sequence in an RNA molecule or polypeptide is set by the relevant investigative, explanatory, or technological context. DNA segments are not simply genes, they are genes for sequences at some stage of genetic expression in a particular cellular context. (See Waters 2007 for a fuller exposition of this account.)

The biological situation gets very complicated in eukaryotes because RNA molecules are often edited as they are being synthesized. That is, some regions of the RNA molecules, called ‘introns’ are removed and some or all of the remaining regions, called ‘exons’, are spliced together. The RNA molecule consisting of spliced exons move from the nucleus to the cytoplasm where it participates in polypeptide synthesis. Hence, one continuous segment of DNA determines the sequence of nucleotides in the primary RNA molecule, but a set of discontinuous segments in DNA (a set of exons) determines (or partially determines) the sequence of nucleotides in the mature RNA molecule and the sequence of amino acids in the polypeptide. What is individuated as the gene? Do biologists individuate the continuous segment that determines the linear sequence in the primary RNA molecules? Or, do they individuate the discontinuous set of DNA segments that determines the linear sequence within the RNA exons and partly determines the sequence of nucleotides in the polypeptide?

It turns out that biologists sometimes individuate genes by including both exon and intron regions in DNA, but other times, they individuate genes by including only the exon regions. Many philosophers have taken this ambiguity to be a serious problem and a reason to doubt that genes exist at the molecular scale. But, this is not a problem for individuating. When biologists are interested in primary RNA molecules, it serves their interests to individuate DNA segments containing both exons and introns. When they are interested in polypeptides, it often serves their interest to individuate discontinuous DNA segments containing just exons (i.e. ‘split genes’). The molecular concept is an indexical concept and its application involves individuating genes for particular linear sequences. This makes the practice of individuation both flexible and precise.

The flexibility of gene individuation practices is especially important in navigating the incredibly complicated processes of differential splicing.

Biologists have learned that one and the same kind of primary RNA molecule is sometimes spliced in hundreds, perhaps even thousands of different ways. This makes it possible for one continuous segment of DNA and different splicing agents to determine the amino acid sequences in hundreds or even thousands of different polypeptides. In one tissue at a particular stage of development, one polypeptide is synthesized; in another tissue or at a different stage of development, a different polypeptide is synthesized. The molecular gene concept is indexed to these different contexts. It is used to individuate many different overlapping and discontinuous segments of a DNA molecule as illustrated in Figure 1.

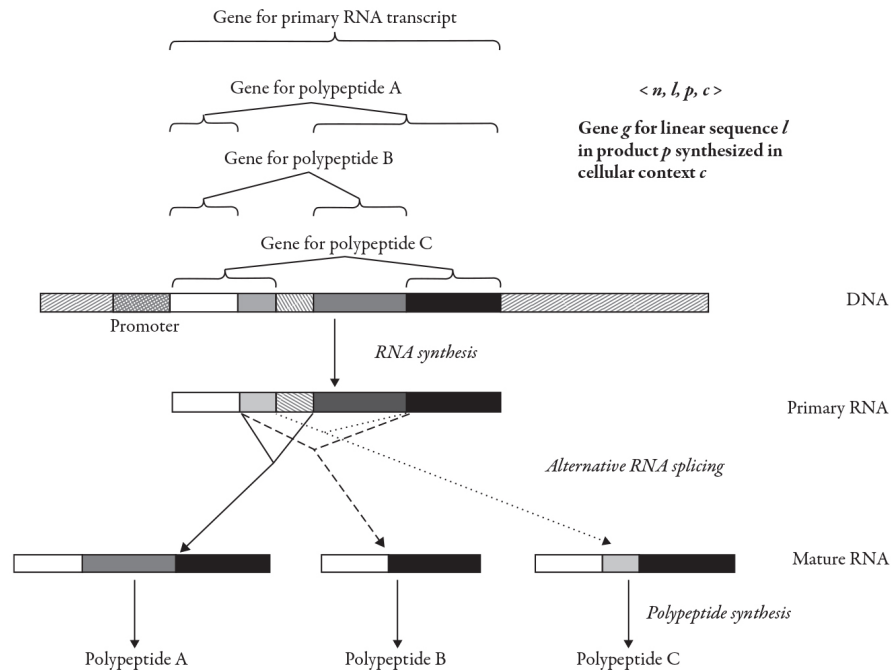


FIG. 1 The molecular gene concept enables biologists to partition DNA in multiple ways. With respect to this figure, if biologists are interested in the synthesis of the primary RNA transcript (see above), then the DNA segment covered by the bracket directly under ‘gene for primary RNA segment’ is the relevant gene (the continuous region of five segments in the DNA molecule starting with the solid white segment and ending with the solid black segment). If biologists are interested in the synthesis of polypeptide B occurring in some tissue at a particular stage of development, then the relevant gene is the discontinuous region marked by the brackets directly under ‘gene for polypeptide B’ (the white and grey segments in DNA and not the segments between).

The molecular gene concept provides flexibility for individuating DNA segments in precise ways. But, this individuation does not yield a unique partition of DNA. Classical geneticists might have speculated that there was a unique partition of a chromosome into its genes. To employ a commonly used metaphor, geneticists might have assumed that DNA could be cut at its joints. But, molecular biologists have learned that (in eukaryotes least) this is impossible. There are simply too many joints yielding overlapping genes. The division of DNA into molecular genes is a complicated mess. Nevertheless, the piecemeal practice of individuating genes for particular purposes is an important scientific activity across the biological and biomedical sciences.

### **3. Purposes served by individuating genes**

Individuating molecular genes is useful and serves a multiplicity of scientific aims: to explain, predict, manipulate, and, most importantly, to investigate. Consider explanation. Individuating a molecular gene and identifying its nucleotide sequence can provide a basis for explaining the linear sequence in an RNA and/or polypeptide molecule. Identifying a difference in a gene can explain the differences in linear sequences in RNA and/or polypeptide molecules. When the difference in linear sequences in RNAs and/or polypeptides is simply linked to an outward difference in phenotype, identifying the difference in the gene can also explain the difference in phenotype. But, these explanations are partial, and their significance is typically modest.

Gene-based explanations are partial because genes do not control the timing of synthesis. At any one time, most genes are not participating in a synthesis. Complex regulatory processes determine when the synthesis of particular kinds of RNA and polypeptide molecules occur. In multicellular organisms, complex regulatory processes also determine where (e.g. in what tissue) and when (e.g. at what stages of development) the synthesis of particular kinds of RNA and polypeptide molecules occur. The regulatory processes are incredibly complex, and it appears impossible to fully explain the development of a multicellular creature, or even the functioning of a single prokaryotic cell, in terms of genes. The significance of gene-based explanations is modest. Genes can be individuated to explain why particular molecules have the linear structures they do, but that by itself does not explain much. With respect to the countless processes going on within an organism, gene-based explanations leave a vast explanatory void.

Similar points can be made regarding prediction. Individuating genes is useful for making predictions, but most of these predictions are made in the context of experimentally manipulated situations. This prompts the question: if genes don't explain or predict that much, why is the individuation of genes so central to biological and biomedical practice?



Individuating genes is central to practice because it provides a basis for manipulating all kinds of different processes within organisms. This is important for medicine, agriculture, and technology. It is also important for investigation. The *genetic approach* to investigation involves using genes to manipulate biological structures and processes in ways that will reveal the functions of these structures or important aspects of these processes (Waters 2004, 2008). The results of these investigations are often local and partial. In addition, it is worth emphasizing that the explanations yielded from intervening on genes are typically not gene-based. Genes are like the scalpels of classical physiology. They are used as tools to investigate, not as elements in the eventual explanations.

The foremost purpose of individuating genes is to forge epistemological entry points for explaining and predicting a very narrow range of biological phenomena and for manipulating and investigating a much wider breadth of phenomena. Genes are not important categories of being (Waters 2017). Answering the question “what is it to be a gene?” does not provide important metaphysical insights into the functioning or development of organisms. The processes by which organisms function and develop are incomprehensibly complex. But, biologists have yielded partial and piecemeal accounts of aspects of these processes, and they have gained a degree of control over parts of them. Given the complexities of the biological world, these are impressive achievements. A key to this success involves the individuation of genes. So, ask not, “what is a gene?”. Ask “how do biologists individuate genes and for what purposes?”

#### **4. Darwinian Individuality**

Perhaps the stamping of feet is loudest when biologists and philosophers ask “what *is* an organism?” The search has been for a universal analysis, one that gets at the essentials of what it is to be an organism. This question has recently drawn more attention as biologists have been investigating major evolutionary transitions, such as the transition from unicellular organisms to multicellular organisms. Theoretical evolutionary biologists need an explanatory target; they want to know what features make multicellular entities organisms rather than collections of cells so they can construct theoretical models of the transition to multicellularity (e.g. Buss 1987, Maynard-Smith and Szachmary 1995, Queller and Strassmann 2009). Experimental evolutionary biologists also need to have an experimental target (Ratcliff et al 2012). They want to know what features would mark evolution towards becoming a multicellular organism so they can determine whether their experimental populations of unicellular organisms are evolving traits of multicellular individuality.

Meanwhile, philosophers interested in questions about individuality have moved the target of analysis. What began as the question “what is an

organism?” has shifted to “what is a biological individual?”, to “what is an evolutionary individual?”, and in some of the most recent work, “what is a Darwinian individual?” This shift helps make inquiry more tractable. It is much easier to construct a universal answer to a question if it is reframed in terms of a theory. Trying to answer “what is an organism?” might force one to analyze the incredibly messy world of life, a world that resists essentialist analyses. Trying to answer the question, “what is a Darwinian individual?” leads one to analyze abstract principles, which are constructed in a tidy theoretical framework. One is much more likely to find an answer that appears universal, that seems to get at the essentials, if one moves from the question “what is an organism?” to the question “what is a Darwinian individual?”

Take, for example, Peter Godfrey-Smith’s primary work on individuality (2009). Godfrey-Smith answers the question about Darwinian individuality by carrying out a careful examination of important elements of contemporary Darwinian theory. The details of his analysis do not matter for the purposes of this chapter and I will not examine them here. I am not interested in joining the lively debate about what it is to be a Darwinian individual.<sup>4</sup> My interest is to advance a form of pragmatism by proposing that we shift attention away from seeking an analysis of individuality, as if it could be read off the best scientific theories, to seeking an understanding of individuation practices in science with respect to the purposes they serve in scientific inquiry.

Godfrey-Smith begins by arguing that reproduction is “at the heart of Darwinian evolution”. His subsequent analysis of reproduction leads him to identify three parameters defining what it is to be a ‘paradigm’ Darwinian individual:

**B:** passing through a bottleneck between generations such as through the production of a fertilized egg that consists of a single cell.

**G:** featuring reproductive specialization of parts such as the distinction of a germ line from somatic cells.

**I:** exhibiting overall integration among parts.

Godfrey-Smith points out that each of these parameters admits of degrees. For example, a bottleneck might be a narrowing to a single cell, as in the case of animals like us, or a narrowing to a relatively small number of cells as in the case of plants like aspens.

---

<sup>4</sup> Although I am not interested in joining the debate, I acknowledge that it has led to fruitful philosophical inquiry about (what I would view as) conceptual tools in biology. For example, see Jim Griesemer’s critique of Godfrey-Smith’s analysis of reproduction and Griesemer’s alternative (2014a and 2014b).

Godfrey-Smith claims that entities that exhibit the highest degree of all three features, what he calls ‘paradigm Darwinian individuals’, evolve most effectively through Darwinian processes. As he puts it, populations consisting of paradigm Darwinian individuals are “*the kind of system that can produce novel and complex organisms, highly adapted to their circumstances*” (p. 6, my emphasis). Populations made up of “marginal” Darwinian individuals, i.e. those that exhibit the three features to lesser degrees, can still evolve, but apparently not to the degree of novelty, complexity, and adaptedness of paradigm cases. He illustrates his analysis of Darwinian individuality with a cube. See Figure 2.

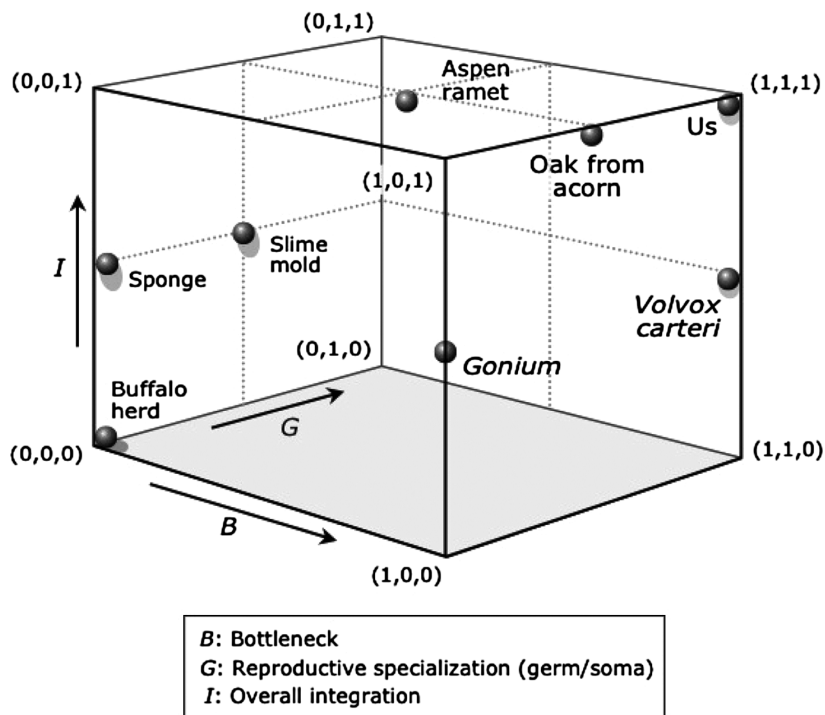


Figure 1.1  
 Forms of collective reproduction.

FIG. 2: Godfrey-Smith’s representation of forms of collective reproduction (from Peter Godfrey-Smith *Darwinian Populations and Natural Selection*, Oxford: University Press, 2009).

Godfrey-Smith applies his framework to major evolutionary transitions. He explains:

*The framework developed here is intended to be useful when thinking*

*about transitions, especially their intermediate stages. We often find populations that have a marginal Darwinian status – for example, collective entities that are somewhat organism-like, but not all the way there. A great array of this can also be seen in aquatic life, in which there is a variety of forms of partial integration of cells and simple organisms into collective entities, including seaweeds, corals, and sponges. (Godfrey-Smith 2009, 8–9)*

He posits that “marginal” Darwinian individuals can get ‘all the way there’ by evolving into “paradigm” Darwinian individuals:

*As a transition of this kind occurs, a population may appear first as a marginal case, from a Darwinian point of view – an ensemble of collective entities who can only be said to reproduce in an extended, generous sense, who barely count as individuals at all. But there may be successive increases in integration [and presumably in B and G as well], until the entities display a well-defined mode of reproduction at the higher level, with heritable variation in the traits found at that level. The collective becomes a paradigm case. (Godfrey-Smith 2009, 9)*

According to Godfrey-Smith’s account, evolutionary processes themselves evolve—a point John Beatty made forcefully to challenge the received view of theories (Beatty 1982). Beatty argued that there are no necessary, that is, no non-contingent, laws of evolution. He used the Hardy-Weinberg equilibrium from population genetics as an example. This principle depends on the individual alleles of a diploid pair being segregated in processes that give them equal probabilities of being transmitted to any given gamete. But, as Beatty argued, there are known exceptions to this kind of random segregation. In exceptional cases, some alleles have a greater than 50% chance of being transmitted. The Hardy-Weinberg principle, a central principle of the evolutionary theory called population genetics, does not apply to these alleles. Beatty argued that organisms could evolve such that the Hardy-Weinberg equilibrium rarely applied to any of them. The processes underlying evolution are evolving and the so-called laws that describe today’s processes might not describe tomorrow’s.

Alison McConwell has recently extended Beatty’s contingency thesis to argue that, since evolutionary individuality is a contingent result of evolution, we should expect it to take on a plurality of forms (2017a, 2017b). Like Beatty’s, McConwell’s conception of biological diversity is not progressive. She does not assume that there is any directionality to second-order evolutionary processes. She also does not assume that there is a hierarchy of evolutionary processes associated with a hierarchy of forms of individuality. Instead, there is a contingent plurality.

Ellen Clarke has also argued for a plurality of individuality (2013), but Clarke’s conception is quite different than McConwell’s. Clarke’s argument assumes that Darwinian processes are unchanging in the sense that the basic principles of Darwinian theory always apply. She argues that to evolve via these processes, organisms must have certain features, and that these features define what it is to be an evolutionary individual. Plurality enters into her picture because these features can be instantiated in different ways. So, individuality is bounded by the stability of evolutionary dynamics, but within these bounds, there can be abundant diversity. Whereas McConwell follows Beatty’s idea that evolution itself evolves (what I am calling ‘second-order evolution’) and hence, imposes no fixed boundaries on individuality, Clarke’s analysis assumes that evolution itself is stable.

Godfrey-Smith’s conception of the plurality of individuality is different from both Clarke’s and McConwell’s conceptions. Like Beatty, he believes evolutionary processes are themselves evolving. Godfrey-Smith maintains that as collectives of entities in an evolving population take on the three features of being a paradigm Darwinian individual, the evolutionary process itself changes. At an early stage of evolution, when the collectives are merely marginal Darwinian individuals, the system can evolve these collectives. In some cases, as the collectives (or “marginal individuals”) evolve, they increasingly take on the features of being a paradigm Darwinian individual. In these cases, the evolutionary process itself changes and it “can produce novel and complex organisms, highly adapted to their circumstances” (p. 6). Godfrey-Smith’s account of the transition to multi-cellularity proceeds from the evolution of collectives of unicellular organisms to the evolution of marginal Darwinian individuals, and then, from the evolution of marginal Darwinian individuals to the evolution of paradigm Darwinian individuals. The second-order evolutionary process is viewed as leading towards a more effectively evolving population with individuals that are more fully integrated, and hence, in an important sense, as being progressive.<sup>5</sup> The plurality of multicellular individuality evidently represents different stages of a second-order evolutionary process.

## 5. The Great Cube of Being?

What might readers take to be the metaphysical significance of Godfrey-Smith’s analysis? On the one hand, Godfrey-Smith sometimes qualifies his statements with phrases such as ‘from a Darwinian view’, which suggests that

---

<sup>5</sup> In later writings, Godfrey-Smith says that the transition can be reversed, that populations of paradigm individuals can evolve into populations of marginal individuals. This, however, is consistent with the idea that the transition towards paradigm individuality is progressive in the sense that it leads towards populations that can evolve *more* effectively and individuals that are *more* integrated.

his analysis is not intended to have metaphysical significance. On the other hand, in the introduction of *Darwinian Populations* (2009), he explicitly states that his account does have such significance. He distinguishes between science, philosophy of science, and philosophy of nature. The third kind of investigation, the philosophy of nature, is a form of metaphysics. He says his book “moves constantly between these three kinds of investigation.”

“The focus of *science*”, Godfrey-Smith writes, “is the natural world.” He envisions *philosophy of science* (as many philosophers do) as a theory-focused meta-discipline:

*The focus of philosophy of science is science itself. The aim is to understand how science works and what it achieves. Here we ask what kinds of contact with the world theories can have – how they function as representations, how they can yield understanding. We ask about the role of worthy but vexed goals such as truth, simplicity, and explanatory power and about the nature of evidence, testing and scientific change. (Godfrey-Smith 2009, 2)*

*Philosophy of nature*, Godfrey-Smith writes:

*is the project of taking science as developed by scientists, and working out what its real message is, especially for larger questions about our place in nature. (Godfrey-Smith 2009, 3)*

As mentioned above, he claims that his book (2009) constantly moves between science, philosophy of science, and philosophy of nature. With this in mind, readers might ask about philosophy of nature. What is the “real message” implied by this analysis about “our place in nature?” Godfrey-Smith never says.<sup>6</sup> But, readers searching for its “real message” might wonder whether the three-dimensional cube of individuality could represent the *Great Cube of Being* with animals like us perched at the pinnacle, plants “not all the way there”, and creatures like sponges and slime molds having a long way to go. It is unclear where bacteria and archaea would fit in. Viewed as a philosophy of nature, the cube suggests a grand metaphysical view, and possibly, a seductive one. After all, it reinforces some traditional Western ideas about our place in nature.

I suggest we resist such interpretations by abandoning the project of

---

<sup>6</sup> In the rest of this section, my intention is to identify what readers might take to be ‘the real message ... about our place in nature’ of Godfrey-Smith’s account of individuality. I am not claiming that what follows describes Godfrey-Smith’s own views about the metaphysical significance of his cubic analysis. Other than implying that his account has metaphysical significance, he is coy with respect to this issue.

philosophy of nature altogether. Instead of viewing scientific theories as having some “real message” about our place in nature, or even about our place on the cube of Darwinian being, we can view science more modestly, as a system for investigating the world that provides us means for describing, explaining, predicting, manipulating and investigating aspects of parts of the world that are important to us.

## 6. Holobionts

A number of biologists and philosophers have recently argued that animals, as traditionally conceived, are not biological individuals at all. Rather, they are parts of individuals. The real individuals are multispecies assemblages made up of the animal and the symbiotic microbes (bacteria, archaea, and viruses) living with it, for example living within their guts or on their skins. More generally, they argue that holobionts, collectives consisting of eukaryotic hosts and symbiotic microbes, are the real individuals.

Again, I am not interested in joining the debate about whether this or that kind of biological entity is a *real* individual. My interest is to advance pragmatism. I will not be defending or criticizing the idea that holobionts, rather than the eukaryotic hosts within holobionts, are the real individuals (just as I have not defended or criticized Godfrey-Smith’s conception of Darwinian individuality). Instead, I will propose that the concepts of animal and of holobiont should be understood as tools biologists use to individuate entities. On this view, philosophers should analyze how and why biologists use the holobiont concept (as well as other concepts) to individuate. The literature on holobionts is a rich source for motivating my pragmatic perspective on individuation because it connects to a broad range of scientific and medical interests. I will use a thought-provoking article “A Symbiotic View of Life: We Have Never Been Individuals” by Scott Gilbert, Jan Sapp, and Alfred Tauber (2012) to develop my position.

Before turning to Gilbert, Sapp, and Tauber’s paper, it is useful to point out two features of holobionts that have figured into the debate about whether it is these assemblages, or alternatively whether it is the eukaryotic hosts within them, that are the real individuals. The first feature is that holobionts are functionally integrated. Eukaryotic hosts could not survive or reproduce without their microbial collaborators. And many holobiont microbes critically depend on their hosts as well. Considerations about functional integration motivate the idea that holobionts are individuals. But, another feature of holobionts pulls in the other direction. Holobiont reproduction typically involves ‘horizontal’ as well as ‘vertical’ transmission. Parent/descendant relationships are usually conceived of in terms of vertical transmission. The cells in an offspring are all descendants of cells in the offspring’s parent(s). This conception of transmission generally applies to plants and animals. But,

holobionts are different. The microbes in a holobiont are often recruited from the environment, rather than inherited from the parent holobiont. That is, many of the microbes in a holobiont are not descendants of microbes in the parent holobiont(s); they are descendants of microbes that were transmitted from the environment. Considerations about horizontal transmission motivate the idea that holobionts are not individuals because evolution by natural selection presumably requires vertical transmission.<sup>7</sup>

Much of the philosophical literature in the debate about whether holobionts are real individuals concerns whether the means by which they reproduce are consistent with the mechanism of evolution by means of natural selection. But Gilbert, Sapp, and Tauber's paper takes a broader perspective to argue for two theses: (1) entities we usually consider individuals, such as multicellular plants and animals, are not genuine individuals, and (2) the real individuals are holobionts.

The central line of reasoning leading to the first thesis in Gilbert, Sapp, and Tauber (2012), hereafter 'GST', proceeds as follows:

1. from an *anatomical* conception of individuality, animals are not individuals
2. from a *developmental* conception of individuality, animals are not individuals
3. from a *physiological* conception of individuality, animals are not individuals
4. from a *genetic* conception of individuality, animals are not individuals
5. from an *immunological* conception of individuality, animals are not individuals

Although it is not necessary for my purposes to examine how they justify each of these claims, it will be instructive to briefly examine a couple of their arguments. I begin with their argument that from a physiological conception, animals are not individuals.

The physiological view of individuality is traced by GST to the early and mid-nineteenth century writings of Henri Milne-Edwards and Rudolf Leuckart. The basic idea was that the parts of a complex organism cooperate for the good of the whole. After Darwin, this developed into the view that evolution led to an "ever-increasing integration through the division of labor." (p. 329). This integration evolved within cells and also among the cells of multicellular

---

<sup>7</sup> For a different idea of what is required for evolution by natural selection, see Roughgarden et al 2017.



organisms. The idea that cooperation of parts is an important feature of being an organism is indeed a central theme in the scientific literature on individuality. For example, it is one of the two axes that Queller and Strassman set out to map the space of organismality (2009).

Biologists have learned that the division of labor favored by selection can be achieved through an integration of functioning among different species living together—for example, by an integration of activities carried out by an animal host and its microbial symbionts. GST list numerous findings about how microbial symbiosis contributes to the physiological functioning of animals ranging from insects to mammals. They cite research that shows that bacterial symbionts are required for lipid metabolism, detoxification, colonic pH regulation, vitamin synthesis, intestinal permeability, and suppression of dangerous immune responses. They conclude that examples such as these show that “on classic physiological grounds, animals are not individuals.” (Gilbert, Sapp, and Tauber 2012, p. 330).

GST argue that animals are not individuals from a genetic conception of individuality on the grounds that allelic variations in the host genome are not the basis for phenotypic variation in the host. Biologists have learned, they contend, that the genome of importance is what is called the hologenome (the combined genome of the host and microbial symbionts). They support this idea by describing how the synthesis of phenylalanine in the mealy bug *Planococcus* requires several enzymes. Only one of them is encoded in the genome of the host; the others are encoded in the genomes of two nested bacteria contained in the host. They argue:

*the genomes of all three organisms have been altered through this symbiosis. ... genomes evolve in such a manner that they need their partners to achieve complex genetic integration. None of the three species ... has a “complete” genome. It is the holobiont that does.*  
(Gilbert et al. 2012, 329 - 330)

On the basis of examples such as this one, GST conclude, that on genetic grounds, animals are not individuals.

Similar example-based arguments are offered for GST’s claims that animals are not individuals from anatomical, developmental, and immunological conceptions (claims 1, 2, and 5 above). But, arguing that animals are not individuals is not the same as arguing that holobionts are individuals. GST shift their emphasis to their second main thesis, the thesis that holobionts are genuine individuals, when they consider individuality from an evolutionary perspective.

GST begin by noting that evolutionary individuality has been conceived in terms of ‘that which can be selected’ in the process of evolution. They continue:

Usually, these individuals are genes or monogenomic organisms. But, from

the above discussion, it is evident that organisms are anatomically, physiologically, developmentally, genetically, and immunologically multigenomic and multispecies complexes. Can it be that organisms are selected as multigenomic associations? Is the fittest in life's struggle the multispecies group, and not an individual of a single species in that group? (Gilbert et al. 2012, p. 331)

They answer this question by describing an example of a holobiont, pea aphids and their endogenous microbes, which they argue satisfies the conditions for group selection. Much of their discussion is aimed at showing that the holobiont immune system provides a mechanism against cheating, a potential constraint inhibiting group selection.

It is worth noting that the example chosen by GST to advance their case that holobionts are evolutionary individuals has a distinctive feature: one of the bacterial symbionts is nested within the other and both are nested within the aphids. This means that reproduction of these assemblages is vertical. Hence, Godfrey-Smith classifies these holobionts as Darwinian individuals while he maintains that holobionts which exhibit horizontal transmission count as 'organisms' but not as 'Darwinian individuals' (2012). In contrast, GST do not seem concerned with modes of transmission and draw a general conclusion:

*Thus, animals can no longer be considered individuals in any sense of classical biology: anatomical, developmental, physiological, immunological, genetic, or evolutionary. ... the holobiont, with its integrated community of species, becomes a unit of natural selection whose evolutionary mechanisms suggest complexity hitherto largely unexplored.* (Gilbert et al. 2012, p. 334)

As mentioned, I will not take sides in debates about questions of the form "who are the *real* individuals?" But, it is worth mentioning that just as the cube of being a Darwinian individual resonates with the idea of the great chain of being, the idea that real individuals are assemblages of diverse organisms cooperating as functional wholes has its romantic appeal.

*For animals, as well as plants, there have never been individuals. This new paradigm for biology asks new questions and seeks new relationships among the different living entities on Earth. We are all lichens.* (Gilbert et al. 2012, p. 336)

But, microbiologists and biomedical scientists would note that many of the microbes within us and on us are not cooperating, and many that cooperate at certain times or in certain contexts do not cooperate at other times or in other contexts. Gilbert and other proponents of the holiobiont view explicitly acknowledge this. For example, Roughgarden et al. (2017) include pathogens

as an integral part of the holiobiont assemblage. Relationships between hosts and their microbes are dynamic, potentially adversarial, and often fragile.

Readers should resist interpreting the view offered by GST as a philosophy of nature, as a metaphysics that identifies the “real message” of the science about our place in nature. On the other hand, the idea they develop in the concluding section of their paper (and mentioned in the above quotation) that conceiving holobionts as individuals opens up new opportunities for numerous fields ranging from medicine to conservation biology is an idea worth philosophical attention.

## 7. Purposes served by individuating organisms and the like

Maureen O’Malley suggests that questions about individuality should be framed in terms of the explanatory usefulness of different concepts (forthcoming). She begins by pointing out that distinguishing between biological individuals (or ‘metabolic individuals’) and evolutionary individuals (or ‘Darwinian individuals’) is becoming standard practice among philosophers writing on questions about individuality. In this paper, she challenges the idea that one of these concepts has explanatory priority. Instead, she maintains:

*There are explanatory and descriptive aims that can only be achieved when the constituent entities of multispecies biological individuals are separated, and other aims that rule out such separation. These explanatory differences rest on the distinction between biological and evolutionary (i.e., Darwinian) individuals, and an acknowledgement that neither has out-and-out priority free of explanatory context. (O’Malley forthcoming, 4)*

Although O’Malley’s focus is on explanatory utility and (in the paper quoted here) on the explanation of major evolutionary transitions in individuality, her idea that different concepts of individuality serve different aims can be generalized and localized. First, it can be generalized with respect to more than two distinctive sets of explanatory aims. The idea that biologists tune their individuations of entities to different explanatory interests is a powerful one. We can use this idea as a basis for reappropriating the argumentation of GST.

The examples discussed in GST connect to a broad range of explanatory interests: anatomical, developmental, physiological, genetic, and immunological. Their mode of argumentation identifies numerous examples where a property or process depends not just on the animal host, but also on its symbiotic microbes. They infer from these dependencies that the animal host is not a genuine individual. Recall their example of the synthesis of phenylalanine in the mealy bug *Planococcus*. The synthesis, they point out, depends on an enzyme from the animal host and on several enzymes of two

different symbiotic bacteria. The individual, they argue, could not be the animal host, and presumably, must be the assemblage of host plus bacterial symbionts. We can reframe this reasoning in terms of the usefulness of individuating entities. If one's aim is to explain (or for that matter, to manipulate—see below) the synthesis of phenylalanine in these creatures, then it is useful to individuate the assemblage. Individuating the animal within might obscure explanatorily relevant enzymes and DNA.

I propose that we interpret the arguments of GST as arguments about the usefulness of individuating assemblages for various purposes. We can drop O'Malley's tacit assumption that there must be one correct way to individuate organisms. And, we can think of the purposes in a more fine-grained, localized manner. One could entertain the possibility that for the purpose of explaining the synthesis of phenylalanine in *Planococcus*, it is best to individuate assemblages, whereas for the purposes of explaining other biochemical syntheses, it might be more useful to individuate the animal host.

The idea that biologists can individuate in a multiplicity of ways to serve a variety of explanatory purposes can be generalized in a second way. The purposes of individuation extend beyond the descriptive and explanatory. They also include purposes of investigation, manipulation, and prediction. Broadening philosophical attention to these purposes could move inquiry well beyond the areas of biological science that currently receive the most philosophical attention. It could also reveal that the conceptual division between biological individuals and evolutionary individual is too blunt; biologists fine-tune their individuation practices to serve specific interests. Consider the concept of 'evolutionary individual'.

Philosophers writing on the concept of 'evolutionary individual' generally assume that evolutionary individuals must be the units of Darwinian evolution, which is generally taken to mean the units of selection. This is why Godfrey-Smith grounds his analysis of Darwinian individual in terms of selection theory. It is also why in seeking to establish that holobionts are individuals from an evolutionary perspective, GST argue that holobionts meet the conditions for group selection. But, Darwinian theory cannot be reduced to the theory of transmutation by natural selection. Darwin's *Origin of Species* was based on two main ideas: (1) transmutation by means of natural selection; and (2) common ancestry. The idea that species differentiate into varieties and varieties further differentiate by means of natural selection was critical to the explanatory power of Darwin's theory (Waters 2003).

In contemporary Darwinian (or no-Darwinian) theory, the processes responsible common ancestry (for the origin and differentiation of varieties) are conceived as speciation. Speciation has been and continues to be a central investigative topic in evolutionary biology. Yet, it has largely escaped the attention of philosophers writing about evolutionary individuality. Starting with Hull (1978), philosophers have written a lot about whether species are individuals, but they haven't paid much attention to the question of how

entities (organisms) making up species should be conceived for the purposes of explaining speciation processes.

An integral part of speciation involves populations becoming reproductively isolated from one another. A prominent idea is that differential mating preferences play an important role in the evolutionary development of reproductive isolation. Laboratory biologists have investigated how this development might proceed. Consider the following empirical study. In laboratory experiments with *Drosophila* flies, Diane Dodd randomly divided a homogenous population of flies into two groups. She propagated one group on a molasses medium and the other group on a starch medium. The populations developed mating preferences. Flies propagated on one medium developed a preference to mate with flies propagated on the same medium. That is, molasses flies (flies evolved on the molasses medium) preferred to mate with other molasses flies rather than starch flies (Dodd 1989). Recently, experimenters demonstrated that this diet-induced mating preference depends on microbial symbionts (Sharon et al. 2010 and 2011). When the two populations were treated with antibiotics, thus eliminating the bacteria, the flies no longer exhibited mating preferences. These experiments indicate that it can be useful to individuate holobionts, rather than just animals, when investigating processes of speciation. In some scientific contexts, e.g. the context of theorizing about transmutation by means of natural selection, individuating evolutionary entities at the level of animal hosts might be most useful. But, in other scientific contexts, e.g. the context of investigating speciation, individuating evolutionary entities at an assemblage level might be better. The brute conceptual division between biological individual and evolutionary individual does not do justice to what should be nuanced practices of individuation.

This case reveals three things. First, biologists have a multiplicity of purposes for individuating organisms. Second, purposes for individuating, even evolutionary biologists’ purposes for individuating, are best served by fine-grained practices of individuation that cross-individuate entities. Third, biologists’ individuation of entities in the context of experimentation may reveal scientific aims, such as the aim to investigate speciation that can be lost in the context of abstract theorizing. Philosophers’ preoccupation with analyzing abstract theories obscures the diversity of purposes in science and leads us to oversimplify our philosophical understanding of biological practices of individuation.

## **8. Three lessons**

Following philosophical pragmatism, we should view practices of individuation in terms of three-place relations, between the world, ideas, and human purposes and actions. My three lessons can be viewed in terms of

Charles Morris's account of semiosis (1938). Although I draw these lessons with respect to philosophy of biology, I believe they apply to philosophy of science more generally, and in fact, to philosophy at large.

The first lesson concerns the world, that is, ontology. Much of the general philosophical literature on individuality is based on the assumption, or perhaps I should say the faith, that the world is neatly divided into individuals. This is also evident in philosophy of biology. With respect to genes, when philosophers learned that DNA is not neatly divided into genes, they decided that genes must not exist at the molecular scale. The real entities of heredity, they inferred, must be found elsewhere. Indeed, the findings of genetics indicate that DNA is not neatly divided into elements that line up with a uniquely correct and comprehensive partition of developmental processes. But, the ontological conclusion we should draw is that the processes by which organisms function and develop are, *as a whole*, incomprehensibly complex. They are a mess; a mess with lots of structure, but no overall structure. That's the way it is.

With respect to the ontology of organisms, philosophers have become increasingly open to the idea that the world might not be neatly divided into just one kind of individual, that there might be multiple kinds of individuals, perhaps even cross-identifying kinds of individuals (e.g. organisms versus evolutionary individuals). But, almost all recent philosophical attention has been devoted to analyzing what it is to be an evolutionary individual, not what it is to be an organism. It is as if the processes of evolution must define what it is to be an organism because, after all, organisms are products of evolution. In addition, the distribution of philosophical attention suggests there is an assumption among many philosophers that what it is to be an evolutionary individual can be established by analyzing the best scientific theory, which is taken to be the theory of natural selection as developed in the framework of population genetics. But, scientific findings discussed in this chapter indicate that the empirical world (as contrasted with the abstract world of Darwinian theory) is not neatly divided into evolutionary individuals. The processes of evolution are extremely complex and the results of these complex processes have not yielded a neat parsing of life into individuals. The processes of evolution are a mess; a mess with lots of structure, but no overall structure. That's the way the world is (Waters 2017).

The second lesson concerns epistemology. Concepts should be conceived as tools, used to help achieve particular purposes. Biologists use concepts to individuate different entities and processes. These tools serve a number of scientific and technological interests, but they do not provide the basis for a philosophy of nature or for grand views about the living world and our place within it. To be clear, my targets are not particular analyses of individuality, such as Godfrey-Smith's or Gilbert, Sapp, and Tauber's. My target is the metaphysical presumption that scientific theories have a "real message" about

‘our place in nature.’ The molecular gene concept is used to individuate segments of DNA in ways that serve a multiplicity of purposes, including purposes to investigate, explain, predict, and manipulate biological entities and processes. But, this tool does not provide the means to draw a univocal parsing of DNA that structures the overall processes of development or the functioning of organisms. Likewise, concepts of organismality including those based on metabolic, immunological, symbiotic, and evolutionary viewpoints, are used to individuate life in a multiplicity of ways that serve different human purposes. Philosophers have emphasized explanatory purposes, and particularly purposes related to explaining the evolution of creatures like us. But, description and explanation do not exhaust the aims of science. Scientists also aim to manipulate, control, investigate, and predict. This brings us to the third lesson, which is meta-philosophical.

The meta-philosophical lesson is future looking and pertains to what questions should guide philosophical inquiry. I conclude that instead of asking, “what is a biological individual?”, philosophers should ask what ways of conceiving biological individuality could be useful? In what contexts and for what purposes would they be useful? Could one concept be useful for situations in which biologists use several concepts? In situations where biologists use one concept, could a different concept, or a multiplicity of concepts better serve their purposes? Might purposes exist in medicine, public health, or environmental science that would be better achieved by using new concepts of individuality? Pursuing these kinds of questions, couched in terms of purposes, could move philosophers beyond analyzing science solely in terms of description, explanation, and prediction. It could decrease our obsession with the philosophical methodology of grounding analysis in abstract theories. Pursuing these questions could also lead to deeper and more inclusive understandings of science, and a more useful philosophy of science.

## **Acknowledgments**

I thank audiences at Taiwan National Chung Chang University, the University of Pittsburgh, and the Final Conference of the ERC Project ‘A Process Ontology for Contemporary Biology’ for helpful feedback. I am grateful that a number of individuals offered useful critiques and discussion of earlier drafts of this paper: Ananya Chattoraj, Antoine Dussault, Scott Gilbert, Brian Hanley, Ka Ho Lam, Oliver Lean, Celso Neto, Maureen O’Malley, Isobel Ronai, Ruth Shaw, Bill Wimsatt, Marcel Weber, Helen Zhao, and especially Marc Ereshefsky, Alan Love, and Dan Molter. I am indebted to Javier Suarez Diaz for sharing an enlightening manuscript of his with me. Anonymous referees provided helpful critiques. I thank my patient editors, Otávio Bueno, Ruey-Lin Chen, and Melinda B. Fagan. The research and writing of this chapter was supported in part by a grant from the John Templeton Foundation:

#50191; From Biological Practice to Scientific Metaphysics; [http:// biological-practice-to-metaphysics.org](http://biological-practice-to-metaphysics.org) and Canada's generous CRC program. The research and writing of this chapter was supported in part by a grant from the John Templeton Foundation: #50191; From Biological Practice to Scientific Metaphysics; [http:// biological-practice-to-metaphysics.org](http://biological-practice-to-metaphysics.org) and Canada's generous CRC program.

## References

- Beatty, J. 1982. "What's Wrong with the Received View of Evolutionary Biology?" In P. D. Asquith, R. N. Giere (eds.), *PSA 1980, Proceedings of the 1980 Biennial Meetings of the Philosophy of Science Association, Volume 2*. East Lansing, Michigan: Philosophy of Science Association.
- Buss, L. W. 1987. *The Evolution of Individuality*. Princeton, NJ: Princeton University Press.
- Carlson, E. A. 1966. *The gene: a critical history*. W. B. Saunders, republished 1989. Ames, Iowa: Iowa State University Press.
- Clarke, E. 2013. "The Multiple Realizability of Biological Individuals." *Journal of Philosophy* 110(8):413-435.
- Dasgupta, S., B. Westlake (eds.). Forthcoming. *Current Controversies in Philosophy of Science*. London: Routledge.
- Dodd D. M. B. 1989. "Reproductive isolation as a consequence of adaptive divergence in *Drosophila pseudoobscura*." *Evolution* 43:1308–1311.
- Fine, A. 1996. *The Shaky Game: Einstein, Realism, and the Quantum Theory*. Chicago, IL: University of Chicago Press.
- Gilbert, S. F., J. Sapp, A. I. Tauber. 2012. "A Symbiotic View of Life: We Have Never Been Individuals." *The Quarterly Review of Biology* Volume 87, No. 4:325-341.
- Godfrey-Smith P. 2009. *Darwinian Populations and Natural Selection*, Oxford: University Press.
- Godfrey-Smith P. 2012. "Darwinian Individuals." In F. Bouchard, P. Huneman (eds.), *From groups to individuals: Evolution and Emerging Individuality*. Cambridge, MA: MIT Press.
- Griesemer, J. R. 2014a. "Reproduction and the Scaffolded Development of Hybrids." In L. R. Caporael, J. R. Griesemer, W. C. Wimsatt (eds.), *Developing Scaffolds in Evolution, Culture, and Cognition*. Cambridge, MA: MIT Press, 23-55.
- Griesemer, J. R. 2014a. "Reproduction and Scaffolded Developmental Processes: An Integrated Evolutionary Perspective." In A. Minelli, T. Pradeu (eds.), *Towards a Theory of Development*, Oxford University Press, 183-202.
- Hull, D. 1978. "A Matter of Individuality." *Philosophy of Science* 45:335–360.
- Kohler, R. 1994. *Lords of the fly: Drosophila genetics and the experimental life*. Chicago: Chicago University Press.
- Maynard-Smith, J., E. Szathmáry. 1995. *The Major Transitions in Evolution*. Oxford, England: Oxford University Press.
- McConwell, A. 2017a. *Individuality, the Major Transitions and the Evolutionary Contingency Thesis*, PhD Dissertation, University of Calgary.



- McConwell, A. 2017b. “Contingency and Individuality: A Plurality of Individuality Types.” *Philosophy of Science* 84:1104–16.
- Morris, C. 1938 “Foundations of the Theory of Signs.” In O. Neurath, R. Carnap, C. Morris (eds.), *International Encyclopedia of Unified Science, Volume 1*, Chicago: University of Chicago Press, 79–137.
- O’Malley, M. A. forthcoming. “Is evolution fundamental when it comes to defining biological ontology? No.” Forthcoming in S. Dasgupta, B. Westlake (eds.), *Current Controversies in Philosophy of Science*. London: Routledge.
- Queller, D., J. Strassmann. 2009. “Beyond Society: The Evolution of Organismality.” *Philosophical Transactions of the Royal Society* B364:3143-3155.
- Ratcliff, W. C, R. F. Denison, M. Borrello, M. Travisano. 2012. “Experimental evolution of multicellularity.” *Proceedings of the National Academy of Sciences USA, Volume 109, Issue 5*: 1595-1600.
- Roughgarden, J., S. F. Gilbert, E. Rosenberg, I. Zilber-Rosenberg, E. A. Lloyd. 2017. “Holobionts as Units of Selection and a Model of Their Population Dynamics and Evolution.” *Biological Theory* <https://doi.org/10.1007/s13752-017-0287-1>.
- Sharon G, Segal D, J. M. Ringo, A. Hefetz, I. Zilber-Rosenberg, E. Rosenberg. 2010. “Commensal bacteria play a role in mating preference of *Drosophila melanogaster*.” *Proceedings of the National Academy of Sciences USA* 107:20051–20056. <http://dx.doi.org/10.1073/pnas.1009906107>.
- Sharon G, Segal D, Zilber-Rosenberg I, E. Rosenberg. 2011. “Symbiotic bacteria are responsible for diet-induced mating preference in *Drosophila melanogaster*, providing support for the hologenome concept of evolution.” *Gut Microbes* 2:190–192. <http://dx.doi.org/10.4161/gmic.2.3.16103>.
- Waters, C. K. 1994. "Genes Made Molecular." *Philosophy of Science*, 61:163–85.
- Waters, C. K. 2001. "Molecules Made Biological." *Revue Internationale de Philosophie*, 4/2000—n 214—(2000), 539–64.
- Waters, C. K. 2003. “The Arguments in Darwin’s *Origin of Species*.” In *The Cambridge Companion to Darwin*, J. Hodge, G. Radick (eds.), Cambridge: Cambridge University Press, 116–139.
- Waters, C. K. 2004. "What was Classical Genetics?" *Studies in History and Philosophy of Science* 35:783–809.
- Waters, C. K. 2007. “Causes that Make a Difference.” *The Journal of Philosophy*. Volume CIV, Number 11:551–579. [pre-print on PhilSci-Archive.pitt.edu]
- Waters, C. K. 2008. “Beyond Theoretical Reduction and Layer-cake Antireduction: How DNA Retooled Genetics and Transformed Biological Practice”, in Michael Ruse (ed.) *Oxford Handbook to the Philosophy of Biology*. New York, NY: Oxford University Press, 2008, 238–62. [pre-print on PhilSci-Archive.pitt.edu]
- Waters, C. K. 2017. "No General Structure." In M. Slater, Z. Yudell (eds.), *Metaphysics and the Philosophy of Science: New Essays*. Oxford: Oxford University Press, 81-108. [pre-print on PhilSci-Archive.pitt.edu]