

Contingency and Individuality: A Plurality of Evolutionary Individuality Types  
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**Abstract:** Recently, philosophers have sought to determine the nature of individuals relevant to evolution by natural selection or *evolutionary individuals*. The Evolutionary Contingency Thesis (ECT) is a claim about evolution that emphasizes the role dependency relations and chance-based factors in how evolution unfolds. In this paper I argue that if we take evolutionary contingency seriously, then we should be pluralists about the types of individuals in selection.

**1. Introduction: Evolutionary Individuals Evolve.**

Although there are general approaches to biological individuality, often philosophers focus on what it takes to be an individual in selection. They cite various features as important markers of evolutionary individuals, such as reproduction, replication, integration, immunology, policing and demarcation mechanisms (Godfrey-Smith 2009; Pradeu 2010; Ereshefsky and Pedroso 2015; Clarke 2013). Rather than a push for any particular account, I explore how evolutionary individuality is informed by a view about the nature of evolution itself.

One common theme is the call for evolutionary individuality concepts that are consistent with evolutionary change. For example, Haber recommends a notion of individuality that includes how individuals are expressed, maintained, and continuing to *evolve* (2013, 213). Godfrey-Smith's account of individuality, though dynamic, is confined to a particular set of parameters ranging from marginal to paradigm individuals (Godfrey-Smith 2009). Ultimately, he argues that evolutionary individuals are reproductive units forming lineages which *evolve* by natural selection. And finally, Ereshefsky and Pedroso (2015) develop a pluralistic and open-ended account of individuality that captures the vast array of heterogeneous entities including multispecies consortia, such as biofilms. My goal is to provide a framework for thinking about the evolution of individuals in selection. I argue that the Evolutionary Contingency Thesis gives good reason to be individuality pluralists—there are many types of individuals in selection. I

turn to the details of this framework next. In the final sections I illustrate contingent individuality and show why pluralism makes sense in that context.

## 2. The Evolutionary Contingency Thesis

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 1995; Desjardin 2011; Turner 2011). 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). I argue that something analogous occurs for evolutionary individuality.

On the one hand, 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. One upshot is that evolutionary history constrains future possibilities—the direction of evolution is shaped by the trajectories of prior evolutionary pathways (Desjardin 2011, 734). On the other hand, there is another aspect of contingency that tends to be forward-looking—the occurrence of a particular prior state is insufficient to bring about a future outcome (Gould 1989, 278). For example, the survival of the primitive vertebrate *Pikaia* was potentially necessary, but alone provided no guarantee, for the existence of humans. This is because many more factors affected the sequence of evolutionary events that took place between *Pikaia* and *Homo sapiens*. Occurrences in the past do not guarantee an evolutionary outcome often due to a dependence on stochasticity or randomness of processes, such as mutation and mutational order.

According to Beatty (1982), 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. They are true necessarily because any exception would be considered physically impossible (Beatty 1982, 398). However, biological generalizations 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.

### *2.1 Mendelian Inheritance and Mutational Change: Non-Disjunction 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 chromosome pair fail to separate into different gametes during meiosis. It is the failure of homologue separation, which results in one gamete that receives two of the same type of chromosome, while the other gamete receives no copy.

Meiotic mutants, such as nondisjunction, are not just exceptions to Mendel’s Law of Segregation. They help illustrate what it means to be a contingent outcome of evolution, which is important if different types of individuals are outcomes of evolution. Biological generalizations, such as Mendel’s laws, describe contingent outcomes. The agents of evolutionary change—directed and random mutation, natural and sexual selection, random drift, etc.—all have ‘rule-making and rule-breaking’ capabilities (Beatty 1982). Generalizations

emerge as certain traits are selected for: “What the agents of evolution render general, they may later render rare” (222). Mutations, such as nondisjunction, demonstrate that Mendelian meiosis has a genetic basis, and therefore, undergoes evolutionary change. This is no mere philosophical conjecture. Marcy Uyenoyama proposed that the process of genetic transmission itself evolves by natural selection (1987, 21). More recently, Van Leeuwen et al. investigates how mitochondria inheritance is non-Mendelian because there is no recombination through meiosis (2008, 5980). Non-Mendelian inheritance is not only theoretically possible, it has been identified. Abnormal meiotic mutations can be viewed as evidence of evolutionary change.

## *2.2 Evolutionary Outcomes: A Transition to Contingent Individuality*

Lewontin’s recipe for evolution by selection is cited as constraints for evolutionary individuality (Godfrey-Smith 2009). Individuals in selection will 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, in Lewontin’s framework there is room for a plurality of types of evolutionary individuals. This is the case even if types of individuals in selection share common overarching features that distinguish them from other biological individuals.<sup>1</sup> 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; the wings of bats, birds, and insects that all yield the ability to fly. 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 types will not classify biological entities in the same way. For example, one type of

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<sup>1</sup> Examples of other biological individuals besides evolutionary individuals are metabolic, immunological, etc.

individuality might exclude biofilms, whereas another type of individuality includes them. The different types of individuality are underpinned by different trait transmission mechanisms—the types are distinguished by the causal roles in which ancestors and descendants relate to one another.

Inheritance mechanisms matter for individuals in selection because they facilitate a pattern of ancestor-descendant relationships. 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. 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 bottlenecks and germ-soma distinctions, whereas Ereshefsky and Pedroso (2015) call for other trait transmission mechanisms besides narrow views of reproduction. 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. But what does it mean for individuals to be contingent? We should find evidence that the trait transmission mechanisms responsible for individuality types are contingent and liable to evolve. In the next section I introduce some markers of contingency.

### **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 1982; Turner 2011, 164). In this section, I outline how evolutionary individuals are products of evolution, which are determined by processes that affect their likelihood as evolutionary outcomes. We know random mutation plays a role in providing the variation needed for selection to occur and that it is a source of evolutionary contingency. On this picture, selection opportunistically draws from what is available (Jacob 1977). Although mutations might be rare, if selected for they can eventually become the norm. And so, I will be looking for evidence of mutation and evolution of the biological mechanisms responsible for trait transmission in evolutionary individuals. I will introduce two markers of contingency within the context of individuality, namely, [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.

### *3.1 Two Markers of Contingency*

First, nothing necessitates the existence of individuality types; evolutionary or otherwise. 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 chance-contributing factors that affect the likelihood of their existence. The relevant mutation or mutational order may or may not occur, for instance. As products of stochastic processes individuals require complicated evolutionary pathways riddled with contingency.

Second, types of evolutionary individuals are impermanent and undergo evolutionary change. So long as they remain the object of processes that drive evolution, they potentially continue to evolve. The sources of contingency as evolutionary processes themselves help to drive evolutionary change. For instance, mutations arise and are selected for that may or may not be passed on 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 1982, 405).

In summary, accounts of individuality describe outcomes of evolution 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. Specific conditions for evolutionary individuality will emerge as genetically-based individuality mechanisms, e.g. trait transmission mechanisms, are selected for. What was at one time rare may become “normal,” so 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. It’s time to move to more concrete examples.

### *3.2 Two Cases from Biology*

In the following I search for evidence of contingency and evolutionary change in two cases: [1] Meiosis and lateral gene transfer (LGT), as well as [2] bottleneck versus aggregative means of forming new individuals.

#### *3.2.1 Mixing Up Genes: Meiosis and Lateral Gene Transfer.*

There are different ways to mix genes into new combinations, thus creating variation selection works with. So meiosis and LGT are ways to facilitate the variation needed for biological entities to be visible to selection. Meiosis is one way to facilitate variation; new combinations of genes are generated by the disjoining of chromosome pairs into different gametes. However, consider how Rattray et al. (2015) study the mutation rate during meiosis in *S. 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 (11). This increase contributes to variation generally.

We know there are other ways of mixing up 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.

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. Meiosis and LGT look to function as facilitators for variation and provide a platform for mutational change. These identified types 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 (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 individuals. Trait transmission does the rest.

### *3.2.2 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 a 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 the 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 transmitted through sexual reproduction. There is a type of evolutionary individuality such that its 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. But there is evidence that this type of evolutionary individuality evolves.

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, e.g. 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. 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.

Alternatively, 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 individual emerging through a different process by which it inherits traits from its predecessor. Ereshefsky and Pedroso make a case for biofilms as another type of evolutionary individuality because biofilm-level traits are transmitted to new biofilms (2015, 10128). Because a new biofilm can be formed by cells that have broken off from another biofilm, through LGT those preliminary colonizers will transfer traits throughout the new biofilm to later colonizers as they attach. By way of aggregation, then, we have a new individual. 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 start with small amounts of cells compared to the previous biofilm they departed from. And so, a new token individual emerges that inherits material from a predecessor biofilm.

If the nature of sexual reproduction evolves as discussed above (Zimmer and Riffell, 2011), and if meiosis evolves (Beatty 1982; Uyenoyama 1987; Van Leeuwen, et al. 2008), then the types of evolutionary individuality that rely on that machinery evolve. If we take the Evolutionary Contingency Thesis (ECT) seriously, the history of these mechanisms will be riddled with contingency and sourced by stochastic processes. Natural selection is not the only evolutionary process that drives change (Gould 1989; Beatty 1994, 36). If the evolutionary history of trait transmission mechanisms relevant for individuality is 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. Recall that the processes driving evolution have both rule-making and rule-breaking capacities (Beatty 1995; Gould 1989). 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. This individuality pluralism makes sense within the purview of evolutionary contingency.

#### **4. Making Sense of Individuality Pluralism**

There are good reasons to be individuality pluralists against 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 any convergence is not inevitable. Having diverse and contingent mechanisms that meet Lewontin's general constraints for evolutionary individuality means there are different types of individuals in selection. These are not just instances of trait transmission, but are alternative ways to form parent-offspring relationships needed for selection to occur. The contingency of the evolution of such mechanisms means we cannot ignore the role of stochastic processes, especially when genetically-based mechanisms underpin individuals. But how does individuality pluralism follow from this?

Evolutionary contingency gives good reason to reject the idea that there is only one type of evolutionary individuality. This is because any monistic account of individuality—ones that cite a single set of conditions, which 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 those criteria. Therefore, it is reasonable to explore a plurality of evolutionary 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 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. One could say that individuality accounts should be judged on the extent of their applicability in the biological domain and not their correctness per se (Beatty 1994, 41). But how does an ontological plurality of individuality types follow from ECT?

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 here. The case of biofilms only gives further credence to the idea that there can be different types of evolutionary individuals. Types of individuals in selection undergo evolutionary change and the entities which comprise them are affected by processes other than selection. If different types of evolutionary individuals emerge, evolve, and disappear analogous to speciation 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, different types of individuals exist synchronically as well. 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 an evolved individuality mechanism is and will continue to be maintained (Beatty 1994, 52).

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