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Pathways to pluralism about biological individuality

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Abstract What are the prospects for a monistic view of biological individuality given the multiple epistemic roles the concept must satisfy? In this paper, I examine the epistemic adequacy of two recent accounts based on the capacity to undergo natural selection. One is from Ellen Clarke, and the other is by Peter Godfrey-Smith. Clarke's position reflects a strong monism, in that she aims to characterize individuality in purely functional terms and refrains from privileging any specific material properties as important in their own right. I argue that Clarke's functionalism impairs the epistemic adequacy of her account compared to a middle-ground position taken by Godfrey-Smith. In comparing Clarke and Godfrey-Smith's account, two pathways emerge to pluralism about biological individuality. The first develops from the contrast between functionalist and materialist approaches, and the second from an underlying temporal structure involved in using evolutionary processes to define individuality.

Keywords Multi-level selection · Natural selection · Fitness · Function · Evolutionary transitions · Group selection

Introduction

What are the prospects for a monistic view of biological individuality given the multiple epistemic roles the concept must satisfy? At the outset, the existing diversity of accounts appears to offer little promise. Biological individuality has been defined, for example, by physical separation, sexual reproduction, an obligatory unicellular stage in development, physiological integration, and metabolic autonomy (Clarke 2011a; Wilson 2005). These definitions share little

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in common in terms of the physical properties or causal processes they privilege as important. However, perhaps this is too fine-grained of a perspective on the problem. Instead, we might abandon monism at this level and look to find unity in a functional capacity common to all biological individuals. Ideally, the properties and processes we had already identified as important would turn out to all contribute to this capacity in some way. The causal basis of individuality would therefore be multiply realizable even as we retained a monistic view at a functional level. Even so, we would still have to consider whether a pluralistic view that relied on multiple types of functional capacities could do an even better job.

In this paper, I will examine the epistemic adequacy of two recent evolutionary accounts of individuality. One is by Clarke (2011a, b, 2012, 2013, 2014), and the other is by Godfrey-Smith (2009, 2013). Clarke's position reflects a strong monism, in that she aims to characterize individuality in terms of an entity's functional capacity to undergo selection and refrains from privileging any specific material properties as important in their own right. She then has to accommodate the work of categorizing, modeling, and explaining individuality solely in terms of the effects these underlying properties and processes have on the capacity for selection. Godfrey-Smith, in contrast, takes a middle-ground position: he introduces a paradigmatic type of individual that is highly evolvable because it possesses three specific physical properties (a bottleneck in development, a reproductive division of labor between germ line and body, and physiological integration). These three physical properties then turn out to be crucial in satisfying the epistemic demands placed on the concept.[1]

I argue that Clarke's thoroughgoing functionalism about individuality impairs the epistemic adequacy of her account compared to Godfrey-Smith's middle ground. The functional categories she uses to analyze cases of individuality remain at too high a level of abstraction and turn out not to capture the most important distinctions for tasks such as evolutionary modeling. One key issue is that her account places no emphasis on the importance of interactions between mechanisms in the evolution of individuality.

In comparing Clarke and Godfrey-Smith's account, two pathways emerge to pluralism about biological individuality. The first develops from the contrast between functionalist and materialist approaches I have already introduced above. A deep question left unexplained by Godfrey-Smith's account is why we need only these three material properties to adequately define individuality. His account may indeed capture the most important reasons why something is a biological individual, but simply privileging these properties does not explain why individuality turns out to be that simple. One of the merits of Clarke's functionalist approach is that it allows individuality to be highly complex and realized in multiple, distinct ways. The real challenge for a functionalist approach, then, is to develop the theoretical apparatus necessary to explain why there are multiple pathways to individuality and why some causal processes turn out to be more important than others.

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[1] Additionally, Clarke equates organisms and biological individuals in her account, but Godfrey-Smith treats the two as intersecting but not identical. He therefore allows a global pluralism about the units of biology in a way that Clarke does not.

Both Clarke and Godfrey-Smith share an evolutionary approach to individuality, but the structural possibilities within this approach, along with their tradeoffs, have not been made fully explicit. There are several ways to anchor individuality in natural selection as an evolutionary process occurring over time. Emphasizing the present capacity for selection focuses on what evolution can do in a population at a particular moment in time. Evolution by natural selection does not guarantee that adaptation will occur, though: heritable fitness differences can drive change without maximizing some objective feature of the population that we can recognize as adaptive (Michod 1999; Gardner 2009; Birch 2015). By contrast, the capacity for adaptation is future-oriented in the sense that it depends on mapping the initial conditions of a population at some time to a long-term maximization. Another option is to define individuality in terms of a past history of adaptation, such as the functional integration we associate with being an organism (Queller and Strassmann 2009). Lastly, I suggest there is an underexplored, "atemporal" option that would define individuality in terms of a causal role function that can be studied separately from evolutionary processes. The epistemic demands of these options differ insofar as they require us to know about the past, present, or long-run effectiveness of natural selection, or none of the above.

The two accounts

What distinguishes the unity of cells in an animal from a set of free-living bacteria in the ocean? Ascribing biological individuality to some group, according to Clarke, is a matter of determining the group's capacity to undergo natural selection given that its parts may also be units of selection. In this way, a higher capacity for selection at the level of the group increases its individuality, but the same capacity at the level of its parts undermines the group's individuality. Clarke introduces two kinds of causal mechanism to reflect these two sources of influence: "an individuating mechanism is a mechanism that either limits an object's capacity to undergo within-object selection (policing kind) or increases its capacity to participate in a between-object selection process (demarcation kind)" (Clarke 2013, 427). The functional roles of demarcation and policing jointly provide necessary and sufficient conditions for individuality: "biological individuals are all and only those objects that possess both kinds of individuating mechanism" (Clarke 2013, 427).

Clarke's definition represents a relatively low threshold for individuality, since most common examples of biological individuals (e.g. bacteria, animals, and plants) will possess multiple mechanisms of each type. However, we can distinguish among individuals by examining the extent of their ability to undergo selection. "One advantage of focusing on what a mechanism does, rather than on how it does it, is that it becomes more salient that the mechanism can fulfill its function to a greater or lesser extent. This is a welcome implication, because it encourages us to recognize that individuality is a property that an object can possess to a greater or lesser degree" (Clarke 2013, 429).

Clarke offers three criteria governing the capacity for selection, based on Richard Lewontin's classic account of the units of selection. It is sufficient for a population of things to undergo evolution by natural selection if

> 1. Different individuals in a population have different morphologies, physiologies, and behaviors (phenotypic variation).
> 2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness).
> 3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable) (Lewontin 1970, 1).

Clarke largely adopts these three conditions as criteria for how mechanisms can contribute to the capacity for selection. In (Clarke 2013), she also includes the criterion of increasing the heritability of traits regardless of whether they produce fitness differences. Policing mechanisms must therefore inhibit one or more these conditions for selection at the lower level, and demarcation mechanisms must contribute to these conditions at the higher level. A mechanism can simultaneously serve to police and demarcate, of course.

This is a functional view of individuality that accommodates massive multiple realizability. "The actual properties picked out by the classical views are red herrings, in so far as we are interested in finding general criteria for counting organisms. Pig cells are redundant as demographic units, not because bottlenecks prevent selection from acting within pigs, but just because there is no selection acting within pigs. In other words, it doesn't really matter what property or mechanism succeeded in preventing intra-pig evolution, only that something did" (Clarke 2012, 342). By allowing for multiple realizability, her account achieves the considerable virtue of showing how many apparently competing views can be unified by focusing on how the properties they pick out affect the capacity to undergo selection at the higher or lower level.

Clarke's approach shares much in common with Godfrey-Smith's historically prior account (2009, 2013). Both emphasize natural selection as the foundational principle for defining individuality, and both focus their analysis on collective individuals that are formed out of parts that may be individuals in their own right. However, Godfrey-Smith diverges from Clarke's approach in two ways. First, he makes use of two related but distinct functional accounts of individuality. Second, he introduces the notion of a "collective reproducer," defined in material terms, as a proxy for a functionalist understanding of collective individuals. As a result, his account of collective individuals is a hybrid of functional and material criteria.

Godfrey-Smith's two functionalist accounts of individuality are based respectively on the capacity of a population to undergo selection and to evolve complex adaptations. In the first case, a "minimal" Darwinian individual is a member of a population that meets the general criteria for evolution by natural selection, e.g. Lewontin's formulation above. In the second case, a "paradigm" Darwinian individual is a member of a population that meets a more stringent set of criteria that increase the population's capacity to adapt. The further criteria Godfrey-Smith formulates are: competitive interaction with respect to reproduction; the continuity of fitness values for nearby mutations (e.g. smoothness of the fitness landscape); and the dependence of reproductive differences on the intrinsic characters of the members of the population (Godfrey-Smith 2009, 63). Competitive interaction tracks the extent to which the reproductive success of one organism obstructs or ‘displaces’ the success of others. Continuity is a “rough measure of the overall extent to which similar organisms in a population have similar fitness,” which affects the capacity of selection to drive the population in a coherent direction toward higher fitness (Godfrey-Smith 2009, 58). The importance of a trait being intrinsic rather than extrinsic is that it can be inherited from parent to offspring independently of their relation to the environment. This last criterion is especially novel and controversial for biological individuality (Sterelny 2011; Godfrey-Smith 2011).

Minimal and paradigm Darwinian populations both depend on some notion of individual reproduction, of which Godfrey-Smith distinguishes three categories: simple, collective, and scaffolded. Since both he and Clarke focus their attention on collective reproducers, I will leave the other two aside here. As a supplement to the paradigmatic Darwinian population concept, Godfrey-Smith introduces the idea of a paradigmatic collective reproducer, which he defines in terms of three properties: an obligatory bottleneck stage in development (e.g. a single cell zygote), a reproductive division of labor separating the germ line from the rest of the body, and functional integration. These three criteria describe material properties that a living system must actually exhibit during its life cycle in order to count as a biological individual. They also each contribute in different ways to the individual’s capacity to adapt as part of a larger population (Godfrey-Smith 2009, 100–103 and 112–114). A germ line, for example, has the effect of de-Darwinizing the lower level population by decoupling what happens to the cells of the organism’s body and their intrinsic traits.

Epistemic tasks for individuality

In order to maintain a purely functionalist approach, an account must characterize what is important about the material properties of a phenomenon in terms of their effects on key capacities. In effect, a functionalist account weaves a fishing net out of different kinds of effects in order to capture all the relevant material properties. Each material property we manage to characterize functionally can then referenced as a basis for the epistemic work of the concept. Philosophers often describe the work of individuality, for example, as enabling biologists to count relevant units in evolutionary processes. As Clarke puts it, biologists “know that counting particular units, and not counting others, allows them to generate explanatory and predictive descriptions of evolutionary processes” (Clarke 2013). A functionalist account of individuality therefore proves insufficient if it fails to capture an aspect of a material property that is necessary for correctly counting units of evolution. It also fails in practical terms if we cannot actually assess whether a property has effects of the relevant kinds. As a result, if we simply graft the material property onto the account, then we have a hybrid definition that mixes functional and material components.

Unifying parochial definitions of individuality under a general functionalist account is therefore only a first step for philosophical analysis, since individuality has a number of important epistemic roles to play in scientific research. To rigorously evaluate the merits of any account of individuality, we need to be clear about (a) what sort of work the concept should do and (b) what sort of criteria will adequately track its performance in these roles (c.f. Love 2008; Brigandt 2011). Although philosophers and biologists working on individuality are broadly aware of the relevant roles and criteria they rely on, no one to my knowledge has developed an explicit and comprehensive list of what these are. Indeed, the idea that the concept should enable us to count evolutionary units actually runs together a number of distinct roles. An explicit list would also be particularly fruitful for investigating how well evolutionary conceptions of individuality serve the needs of other fields in biology, such as immunology (Pradeu 2012), paleontology, or developmental biology. This section contributes to that larger project by making explicit four epistemic roles that individuality should play for evolutionary biology.

First, arguably the most basic epistemic role for individuality is to provide a coherent and justified categorization of biological entities. We can evaluate this extensionally, i.e. in terms of what degree of individuality an account assigns to various cases. We might, for example, look at the individuality ascribed to viruses, chromosomes, and insect colonies in order to see whether these meet our independently justified expectations. We would also want to evaluate whether the classification is coherent both internally and with respect to background knowledge, such as evolutionary theory.

A second task is guiding the correct choice of evolutionary models, which has been a major topic in the group selection debate (Okasha 2006; Sober and Wilson 1998; Godfrey-Smith and Kerr 2013). Correctly modeling the origins of altruistic behavior, for example, depends on being able to tell when a collection of organisms should be treated as a fitness-bearing individual in its own right or as a context for selection at the lower level. As Clarke puts it, “Population-biological models should measure trait frequencies (in other words, count) at any level at which objects have a non-negligible capacity for heritable variance in fitness… A population biological model that omits objects with a weak capacity for participating in a selection process will make smaller errors than a model that omits objects with a stronger capacity. It is a matter of pragmatics to decide how much individuality the objects at some level can possess before that level can no longer be safely omitted from a population-dynamical model (that is, what exactly qualifies as ‘non-negligible’)” (Clarke 2013, 430).

It is also important, as a third role, to know when and why we can use our categorization of individuals to support inductive generalizations. One important use for individuality, then, is to determine which entities are comparable individuals across a set of taxa (Pepper and Herron 2008). In philosophical terms, is individuality projectable?

Fourth and last is the challenge of explaining evolutionary transitions in individuality (Michod 1999; Okasha 2006). These transitions involve the evolution of a new, higher level of individual through the loss of individuality of units at the lower level, which then comprise the new whole. Individuality must therefore be the sort of thing that can evolve into and out of existence. An account of individuality should ideally support biologists in “compiling comparative measures of different lineages’ progress through a transition” (Clarke 2013, 430).

Categorizing individuals

Consider any living system. What degree of individuality does it exhibit? Each account of individuality must answer this question for real cases of biological interest. An account’s practical value in this regard will depend on the gap between what sort of knowledge about the living system the account demands and what we can reasonably expect to acquire. At first glance, accounts based on the capacity for selection or adaptation are in danger of being highly impractical. Fitness is difficult to measure experimentally, and biologists must often rely on imperfect proxies. Many individuating mechanisms will have multiple distinct effects on a population’s status as Darwinian, and these effects may vary depending on environmental context and what other mechanisms are present. Talk of capacities also requires evaluating what a system would do in many potential situations rather than simply what it actually does in the wild or the lab. For example, it is generally more important for evolvability if the traits of a population exhibit unbiased variation (Godfrey-Smith 2009, 47–48), but this is not always required in special situations. Furthermore, functional criteria such as the extent of variation or the intrinsicality of a trait purchase their generality at the cost of vagueness.[2]

In nearly every case, then, the functional capacities picked out by Clarke and Godfrey-Smith will be very difficult for biologists to determine directly. Faced with a new population of living systems exhibiting questionable individuality, biologists have no ready-made toolkit of methods to measure the population’s capacity to undergo selection or adapt. However, there is another way to organize the task of categorizing individuals: study the effects of general kinds of mechanisms or material properties and then search for their presence or absence in particular cases. Austin Booth’s application of Godfrey-Smith’s account to the case of heterokaryotic fungi is a good example of how a functional account can proceed by using biologists’ background knowledge about the material aspects of the case (Booth 2014). As we will see, the practicality of a functional approach depends on its

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[2] The universality of functionalist approaches partly derives from introducing ambiguities in the meaning of evolution by natural selection (ENS) that can only be removed by adding back in material details, e.g. about life cycle structure. Godfrey-Smith has argued that our most general definitions of ENS, such as Lewontin’s criteria above, fall short of giving necessary and sufficient conditions (Godfrey-Smith 2007, 2009). Instead, we should understand the different formulations of ENS as providing models whose explanatory and predictive value depends on various idealizations and approximations. For example, some popular formulations of ENS depend on the idealization of synchronized generations, but this rules out a case where differences in generation time drive population change even when every parent has the same number of offspring (Godfrey-Smith 2007, 495–496). As a result, the material details of reproduction lead us to apply different formulations of ENS across contexts and thereby exert influence on its overall meaning rather than simply factoring into the capacity for selection once a formulation has already been selected. Failing to be precise about these material aspects of a case may lead us to mischaracterize the effects of individuating mechanisms, e.g. by focusing solely on the number of offspring per generation and overlooking generation time.

ability to characterize the “importance” of these different kinds of mechanisms or properties.

Both Clarke and Godfrey-Smith discuss importance in particular cases, such as with bottlenecks or germ lines, but do not fully theorize this aspect of biologists’ knowledge about individuality. Clarke, for example, states that “the properties relevant to being an organism are just those properties which determine the extent to which, or the efficacy with which, natural selection can occur” (Clarke 2013, 427). We can further analyze the extent to which natural selection can occur into distinct components, however, such as the scope (i.e. number) of traits that can undergo selection and the robustness of this capacity for each trait over evolutionary conditions.

To see why a notion of importance matters for epistemic practice, it will help to appreciate just how intractable the problem of categorization is from a top-down, functional approach. I will use Clarke’s framework here. Identifying a group’s degree of individuality appears to depend only on the capacity for selection at either level, but a second, implicit variable is what we decide to count as a member in the group. For example, we might compare the set of all the human cells in a person’s body versus one that also includes bacteria from the gut. To illustrate the issue, imagine introducing a heritable parasite into a clump of genetically identical cells bound together by an extracellular matrix. Without the parasite, there is little capacity for selection at the lower level because no relevant genetic variation exists for selection to act on. If we count the parasite as a member of the group, though, there is now a strong potential for selection: we can count the homogeneous cells as one genotype, and the parasite as a second genotype, so if there is a constraint on the total number of cells that can survive in the clump—for example, due to limited resources—then competition for resources can drive change in the relative frequency of the genotypes.

If we exclude the parasite, then the capacity for selection at the lower level is unchanged and the parasite’s effects count as an external, ecological influence on the fitness of the homogeneous group. If we include the parasite, then the capacity for selection increases and individuality drops (assuming the cost of competition outweighs the presence of the parasite as a heritable, group-level trait). The relevant mechanisms introduced by the parasite therefore would count as anti-individuating mechanisms.

One might think that inclusion could be settled by whether something contributes to individuation or not, and so the heritability of the parasite would lead us to place it in the group. However, Clarke is explicitly agnostic about whether individuating mechanisms must be “intrinsic” to the individual, so the entities involved in the mechanism can be either inside or outside the collection (Clarke 2013, 427).

To avoid this indeterminacy, we might instead try to consider a number of possible groupings and pick the one with the greatest individuality. Unfortunately, there may be a combinatorially explosive number of possibilities—consider deciding whether to include or exclude each species of bacteria in our digestive systems. Another issue is that since a group must simply possess one policing and one demarcating mechanism to be an individual, it will be common to find a number of overlapping groups that count as individuals but vary in their degree of individuality.

The difficulty ramifies even further when we consider how most biological individuals will contain a large number of individuating mechanisms with complex effects and interactions. Although Clarke has discussed a few of the most important individuating mechanisms studied by biologists, her definitions of policing and demarcating mechanisms are much broader. For instance, recall that many of the cells in a multicellular organism have lost the ability to survive on their own and are metabolically dependent on other cells in the group. This incapacity constrains the potential for selection to act at the lower level and therefore increases the individuality of the group. In a similar manner, we can expect the mechanisms involved in any division of labor to have some effect on individuality. As a result, the set of individuating mechanisms at work in any context will often incorporate some or all of the cells' metabolic and reproductive systems. Calculating the "net" individuality for a group will therefore involve aggregating the effects of a large number of mechanisms.

In practice, then, many living systems present us with an intractably large number of individuating mechanisms and candidate groupings. In order to simplify the problem, we can first of all distinguish more important individuating mechanisms from less important ones in terms of their robustness, scope, and strength of effect on the capacity for selection. We can then argue that the degree of individuality is largely fixed by the most important mechanisms, and the lesser ones can be ignored. This strategy is viable if there are not too many large, context-dependent interactions between individuating mechanisms.

Choosing among multiple candidate groups would still be a challenge, however. The issue arises in the parasite example because the effects of individuating mechanisms apply to different sets of lower-level entities. The parasite is inside the physical boundary of the extracellular matrix, but it would be excluded by any functional integration among the genetically identical cells. In theory, if we had N different individuating mechanisms, their effects could apply to N different sets of entities with no universally shared intersection. One way out would be to prioritize individuating mechanisms that tend to share common targets, so the boundaries of the groups they pick out would coincide. Where possible, we could even rank individuating mechanisms as more important to the extent that they cause other mechanisms to share a common set of targets, either dynamically during development or as an entrenched outcome of evolutionary history. Still, we are stuck assuming that cases without strong overlap tend to be marginal.

As a matter of practical epistemology, then, functionalist accounts of individuality are not free from having to worry about the ways it is realized in the world. Despite this, a pure functionalism must still find a way to describe and justify the importance of various kinds of material properties solely in terms of their effects—not how the effects are produced. Godfrey-Smith's definition of the paradigmatic collective reproducer implicitly addresses this problem by stipulating that only three kinds of properties have primary importance. He argues for the functional relevance of these properties but does not defend why these are the only three. Is this a historically contingent feature of biological individuality or a necessary consequence of the phenomenon? To what extent is it a product of our current ignorance about the material basis of biological individuality?

By contrast, Clarke makes no such commitments about the importance of certain mechanisms within her account. However, the difficulty of multiple overlapping groups highlights an important constraint for her account. Since individuating mechanisms are defined solely in terms of their effects on target populations, no distinctive functional roles can be assigned to mechanisms based specifically on their effects on other mechanisms. Hence we cannot capture the special importance of individuating mechanisms that cause other individuating mechanisms to align their effects on a shared group of targets, since this alignment has no necessary consequence of increasing either policing or demarcation and thus is not a logical subcategory of Clarke's two types of individuating mechanisms. The issue of interactions among individuating mechanisms will also come up in a different epistemic context in "Evolutionary transitions in individuality" section.

Modeling individuality

The topic of biological individuality today has subsumed several prior philosophical discussions about group selection and the units of selection. Earlier debates usually took for granted the idea of a biological hierarchy, e.g. from genes to chromosomes, organisms, populations, and species. The idea that selection could act on a group at a higher level than genes came under heavy attack (Leigh 2010). Nonetheless, from the 1990's to the present, group selection has undergone a revival and is now widely acknowledged to be an important process in evolution. One important reason for this change has been the recognition that the units at all levels of the hierarchy are themselves the product of evolution (Maynard Smith and Szathmary 1995). If we identify biological individuals with units of selection, then it turns out that these individuals are typically also groups formed out of things that either were or still are biological individuals in their own right. The question "What is a biological individual?" is therefore closely aligned with the question "What is a group?"

For this reason, the concept of individuality gets caught up in the problem of specifying how we should model group selection. In particular, modeling the evolution of new forms of group-level individuality requires us to rely on a temporal sequence of models with qualitatively different mathematical structures. Okasha, for example, suggested that these transitions start off with group fitness corresponding to the average fitness of individuals within each group, while at the end group fitness takes on its own emergent value (Okasha 2006; but see Shelton and Michod 2009). Similarly, Godfrey-Smith and Kerr list a sequence of five stages that parameterize natural selection in distinctive ways (Godfrey-Smith and Kerr 2013). We can understand the emergence of group fitness here as the mathematical decoupling of the fitness value of the group from the average fitness value of its members (Michod 1999). Most human cells, for example, have a long-term fitness of zero because they are isolated from the reproductive process, but this tells us little about the fitness of human individuals.

What changes in the nature of individuality (if any) correspond to these changes in mathematical modeling? On Clarke's account, a group has a non-zero degree of individuality if it possesses at least one policing and one demarcating mechanism, which in general will fall short of guaranteeing fitness decoupling. Moreover, the effect of some demarcating mechanisms may be representable as contextual effects of group membership on the parts' fitness values. Consider, for example, a situation where groups form by aggregation according to similarity in some trait that is also linked genetically to a second trait which affects the lifespan of the groups. Variation in the trait controlling lifespan can then be heritable in a statistical sense across group generations and produce effects on the average fitness of members without implying emergent group fitness. The existence of demarcating mechanisms therefore does not directly translate into emergent group-level fitness or reproduction.

On Godfrey-Smith's account, though, paradigmatic collective reproducers have exactly the sort of properties necessary to possess emergent group-level fitness. Indeed, a germ line was the exemplary mechanism Michod had in mind in his discussion of fitness decoupling (Michod 2006). The presence or absence of a bottleneck, germ line, and functional integration can therefore guide our choice of which model to apply to the situation. One can broadly justify the importance of a germ line for modeling based on how it reduces the ability of selection to act on the intrinsic traits of the lower-level units. However, this is not the same as defining a principled measure for any property's importance for producing emergent group-level fitness. In particular, Godfrey-Smith does not advance his own functional account of reproduction, which could index how important a material property is to the emergence of group fitness by how it contributes to the capacity for reproduction. As a result, the material properties of collective reproducers take precedence over the functional criteria for paradigm Darwinian individuals.[3]

A pure functionalism must find another route to supporting the epistemic work of modeling. As Clarke writes about objective principles for choosing groups in multi-level selection models, "we must avoid elevating proximate mechanisms into definitional criteria if we want to arrive at a truly level-neutral and general analysis of an evolutionary transition" (Clarke 2014, 7). Her solution is that "groups are generated by mechanisms which cause fitness alignment amongst their member objects" (Clarke 2014, 7). In this manner, she follows a number of other authors who have connected individuality to sharing a common evolutionary fate, such as (Wilson and Sober 1989; Folse and Roughgarden 2010). On Clarke's view, "the essential point is merely that something in the world itself, rather than in the modeller's choice of representation, is sorting objects into groups, in such a way that the fitness of one object is more predictive of the fitness of each of its group mates, on average, than it is of the fitness of a randomly chosen object from the rest of the population" (Clarke 2014, 7). An assortment mechanism that generates fitness alignment is therefore relevant because "it drives selection up to a higher level, by

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[3] I should note that Godfrey-Smith has developed other resources for guiding modeling practice in collaboration with Benjamin Kerr that do not rely on the concept of individuality (Godfrey-Smith and Kerr 2013).

shifting the expression of heritable variance in fitness up to the between-aggregate level" (Clarke 2014, 8).

In theoretical terms, however, fitness alignment is not equivalent to a joint increase of demarcation and policing. Consider a hypothetical case where lower-level individuals associate into groups and vary in a trait that influences the optimality of their functional integration during group co-existence. When a group forms, assume that its degree of functionality is randomly determined by the optimality of either the worst or the best individual in the group. This increases fitness correlation within groups, producing the required alignment. However, it also increases the variation in fitness across the population of individuals as a whole, increasing the potential for selection. Fitness alignment within groups is not identical to a decrease in the capacity for selection at the lower level, nor does it necessarily produce a net increase in group individuality. Hence the kind of effect produced by mechanisms generating fitness alignment is not a subset or necessary result of the kinds of effects produced by individuating mechanisms.

A similar point holds true of fitness decoupling, defined as a decrease in the correlation between group fitness and the average fitness of lower-level individuals. The standard way to think about achieving decoupling is by eliminating competition at the lower level and enforcing the early segregation of a germ line. The long-run fitness of almost every individual in the group thus becomes zero, with the exception of the several individuals that contribute to group-level reproduction. However, the same mathematical outcome could be produced by running a few winner-takes-all competitions among individuals in a group. Most individuals would still have zero long-run fitness, yet reproductive competition is high and there is no pre-determined germ-soma distinction. In logical terms, then, the classes of mechanisms that count as fitness aligners or fitness decouplers are not identical to subcategories of policing or demarcation mechanisms or a combination thereof. To put it another way, the importance of a mechanism as a fitness aligner or fitness decoupler does not follow necessarily from its importance as a demarcator or policing mechanism. One can certainly augment Clarke's account with these additional functional categories, but their role in guiding modeling practice is not derivable from her definition of individuality.

Projectable individuality

In addition to guiding biologists' decisions about which units to count for explaining evolutionary change, biological individuality also plays a role in supporting comparative generalizations: "The primary reason for adopting an operational definition of the organism is that evolutionary biology relies heavily on the comparative method, and effective comparison requires that we first define a class of comparable entities… For comparisons among species, organism concepts are critical to ensure that we are comparing apples to apples. Imagine, for example, that we are interested in organismal senescence, and we want to correlate lifespan with some environmental factor across a wide taxonomic range. For a given species of coral, should we record the lifespan of a single polyp or of the entire colony?"

(Pepper and Herron 2008, 625). Similarly, "the putative insect endosymbiont called Carsonella ruddii has a number of unusual features, including a much smaller genome than that of any other organism, but this is unusual only if it is indeed an organism (a bacterium), rather than part of the host organism (an organelle)" (Pepper and Herron 2008, 625).

The expectation that we should be able to form inductive generalizations based on classes of biological individuals raises an interesting question about whether individuality is projectable.[4] That is, does individuality have an underlying nature that would explain why the concept gives reliable results as a tool for comparative generalization? Or, do we need to supplement a functional account of individuality with specialized concepts that are defined in material terms?

The ability of a functionalist view to accommodate the open-ended complexity of individuality is a clear virtue for Clarke. "Perhaps the most important lesson we can learn about individuality in general is not to assume that criteria of individuality are transferable across different examples. It might be that none of the features I have so far singled out [for plants] are going to be relevant in determining individuality in bacteria, for example, or social insect societies. On the other hand, many of the conclusions found here are consequences of the modularity of plant growth, and will therefore generalise to modular organisms in other kingdoms" (Clarke 2012, 351). Hence the class of all biological individuals might contingently share some material properties due to evolutionary descent or common environmental forces, but this common nature is not a necessary outcome according to her functional account. The fact that a class of systems had low individuality might underwrite some comparisons, such as separating symbionts from organelles, yet falter on others that depend on specific aspects of life cycle structures, such as senescence. The same issue here would apply to Godfrey-Smith's minimal and paradigm definitions.

By contrast, paradigm collective reproducers do have a shared material nature that is informative about both the capacity for selection and life cycle structure. Indeed, part of what makes bottlenecks, germ lines, and functional integration so important is the relative universality of their effects. Single cell bottlenecks, for example, ensure that every generation starts with a high degree of genetic identity, erasing the history of any competition that arose among lower-level units during the last generation. The division of a group into germ-line and somatic units has a similarly robust consequence, preventing somatic cells from producing ancestors beyond the lifetime of the group and thereby lowering the payoffs for cheating. Integration makes a more ambiguous contribution in this regard, but insofar as it depends on mutually obligatory functional relationships between members of the group, we can expect it to have consistent consequences for the properties of individuals.

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[4] Note that Clarke simply equates organisms and individuals in her account (Clarke 2013).

Evolutionary transitions in individuality

Arguably the most important motivation driving recent theorizing about biological individuality is its role in explaining the evolution of new levels of selection (Maynard Smith and Szathmary 1995; Michod 1999). During such an evolutionary transition in individuality, the capacity for selection generally increases at the higher level and decreases at the lower-level. The challenge, then, is not merely to explain why entities at the higher and lower levels are capable of undergoing selection; rather, we need to explain why the transition is expected given certain initial conditions and heritable variation of fitness in the lower-level population. This challenge highlights an important difference between the capacity for selection and the capacity for adaptation (Gardner and Grafen 2009; Gardner 2009; Sober and Wilson 2011; Birch 2015), since recipes for natural selection such as Lewontin's do not guarantee that new variants appearing in a population with initially higher fitness values will evolve to fixation or even become relatively common. This proves to be a problem once we realize that even a population of highly individuated groups may be incapable of adapting.

One major reason natural selection can fail to maximize the fitness of a population in the long run is because the ability of a new and better variant to dominate the population is obstructed by frequency-dependent effects. This situation is common in evolutionary transitions: as cooperation (altruistic behaviors) increase in a group or population, so does the benefit of cheating, i.e. taking advantage of the benefits of cooperative behavior without contributing to any of the costs. As a result, natural selection may act to increase the initial frequency of cooperation and then balance its benefit for the group against the benefit of cheaters, failing to produce a group adaptation.

Michod has introduced a new kind of functional interaction among mechanisms to describe an escape route from frequency-dependence: the appearance of a "modifier" trait that rebalances the cost-benefit analysis in favor of cooperation and thereby allows group adaptation to proceed (Michod 1999, 109–121). Two of the most important examples are the early segregation of a germ line and internal policing using mechanisms such as an immune system or programmed cell death. These modifiers each have their own costs—germ line segregation, for instance, removes some fraction of cells from contributing to the broader functioning of the group. However, under the right conditions the appearance of a modifier can change the balance between cooperation and cheating in order to allow both the cooperative and modifier trait to go to fixation.

Michod argues that the evolution of modifiers represents a major milestone in an evolutionary transition. "The main criterion of significance is whether within-organism variation leads to selection of modifiers to reduce it. We have found that such modifiers increase in frequency, leading to an evolutionary transition that we have interpreted as the emergence of individuality, because these modifiers represent the first higher-level functions" (Michod 1999, 125). In addition, "the evolution of modifiers of within-organism change is a necessary prerequisite to the emergence of individuality and the continued well-being of the organism" (Michod 1999, 132).

Can this concept of a modifier be captured by Clarke's account? As I argued in the "Categorizing individuals" section, policing and demarcation are defined in terms of their effects on populations of lower or higher-level entities, not in terms of how one mechanism modifies the effects of another. Individuating mechanisms and modifiers therefore have different kinds of targets for their effects and are conceptually distinct.

However, perhaps every modifier mechanism is also a policing mechanism that lowers the capacity for selection by preventing frequency-dependence. To see why this does not work, notice that whether a cooperative trait can propagate through a group on its way to fixation (potentially over several group-level generations) is logically independent from the capacity for selection at the lower level. For instance, a multicellular group with both a single cell bottleneck and a segregated germ line largely eliminates lower-level selection. Any mutation in a germ line cell is also automatically propagated to fixation in descendant groups as a result of the bottleneck. On the other hand, if the capacity for selection is eliminated in a multicellular group without such a propagation mechanism, a mutation in one cell will never spread and become universal across members of the group. A purely hypothetical example would be if group reproduction happened by each cell dividing and contributing one offspring to each of the new groups. More realistically, policing mechanisms could sufficiently dampen the effectiveness of propagation as to significantly hinder the potential for adaptation. The multicellular, prokaryotic species *Magnetoglobus multicellularis* offers an interesting comparison case in this regard (Abreu et al. 2007). In sum, eliminating frequency-dependent effects by eliminating selection at the lower level does not guarantee an increased capacity for adaptation because mechanisms responsible for propagating traits that are adaptive for the group can also be weakened as a side effect.

Paradigm collective reproducers indirectly capture what is arguably the most important modifier trait, germ line segregation, as well as any mechanisms involving functional integration. However, it is unclear how to specify the distinctive importance of the interaction between a modifier and a cooperative trait based on Godfrey-Smith's functional notion of a paradigm Darwinian individual. Indeed, neither Clarke nor Godfrey-Smith's functional accounts have any special place for mechanisms whose importance derives from their effects on other individuating mechanisms.

Pathways to pluralism

In spite of the basic similarities between Clarke and Godfrey-Smith's accounts, an interesting thematic difference has emerged between Clarke's preference for thorough-going functionalism and Godfrey-Smith's compromise between evolvability on the one hand and specific material properties on the other. I have argued that Godfrey-Smith's reliance on material properties provides his account with better resources to address the various epistemic tasks I considered. Nonetheless, there are tradeoffs involved in this choice that may be sufficient to motivate keeping a functionalist approach alive, especially a strengthened version that incorporates important interactions between mechanisms that contribute to the capacity for adaptation. In this section, I discuss the contrast between functional and material strategies for defining individuality as one pathway to pluralism. I also introduce another pathway internal to functionalism based on how one incorporates the temporal component of evolutionary processes into individuality.

The arguments for pluralism I give in this section are motivated by differences in practical epistemic utility that result from different metaphysical natures that accounts assign to individuality. To put it another way, are there good epistemic reasons for maintaining both a functionalist and a materialist approach to individuality, at least until one approach captures the merits of the other? The durability of this pluralism will depend on how deeply the epistemic limitations of these approaches are built into their ontology.

It seems likely, for example, that functional accounts of individuality will continue to have a more principled basis in evolutionary theory but will also be more difficult to operationalize for practical use. I have also argued that key components of the epistemic work to categorize individuals, guide modeling, establish projectability, and explain transitions are not captured by the concepts of policing and demarcating mechanisms. The effects of mechanisms that biologists actually rely on to address these tasks remain under-theorized.

Although more successful at addressing the epistemic needs of biologists, Godfrey-Smith's account is not necessarily more satisfying in explaining why three and only three properties are sufficient to define a paradigmatic individual. Indeed, some recent criticism of Godfrey-Smith's account has explored whether there are other ways to be a Darwinian individual than recognized by the paradigmatic type. Ereshefsky and Pedroso (2012), for example, have argued that bacterial biofilms challenge some of Godfrey-Smith's assumptions by providing a relatively high level of individuality on his account without depending on genetic bottlenecks or a single lineage connecting parents to offspring. Biofilms are aggregates of bacterial cells, often involving multiple species, which are bound together on a surface by a carbohydrate matrix. They can achieve moderate levels of genetic homogeneity using lateral gene transfer across the aggregate. One consequence of new empirical knowledge for Godfrey-Smith's account, then, may be the need for multiple exemplars of individuality (Wilson and Barker 2014).

Comparing the limitations of both approaches suggests some positive directions for future work. Clarke's account currently treats the effects of each mechanism in isolation, and I have argued that this limits our ability to capture important interactions between mechanisms that drive evolutionary transitions. The causal structure of the transition process is not simply a cumulative increase of additive effects of policing and demarcation mechanisms. Similarly, we also need a more rigorous accounting of how concepts such as fitness alignment or fitness decoupling relate to individuating mechanisms. As an empirical matter of fact the categories overlap considerably, but is this simply a contingent feature of how living things happen to have evolved? For a materialist approach, one way to expand Godfrey-Smith's hybrid account would be to investigate whether categories such as organelles or colonies are useful for inductive generalization in part because they are defined in material rather than functional terms.

Furthermore, the contrast between the capacity for selection and the capacity for adaptation indicates a second pathway to pluralism within functionalism. Clarke relies solely on the capacity for selection, while Godfrey-Smith presents one version of individuality from each. Arguably the strongest merit of focusing on selection rather than adaptation is its greater practicality: it is generally easier to show that a mechanism influences the degree of variation, heritability, viability, or reproductive capacity in a population than to demonstrate that adaptation can occur. Nonetheless, I have argued that the capacity for selection alone is too weak a foundation for a functionalist approach to address all the epistemic roles required, and our theoretical understanding is improved by paying attention to the outcomes of selection beyond the next generation.

In fact, there are two additional stances available that fit within a larger conceptual landscape of possibilities. Articulating this underlying structure will help clarify the relationships between different ontological choices we can make in giving functional accounts of individuality. These ontological differences may then lead to particular epistemic strengths and weaknesses in practice, but I will not argue for the relative merit of each option here.

One way to resist the idea that the capacity for selection or adaptation is sufficient to define individuality is to note how there are clear cases of unitary, living things that are not capable of undergoing selection. Mules, for example, are the male offspring of a mating between a female horse and a male donkey. They are sterile, in part because they have an intermediate number of chromosomes between horses and donkeys that cause problems with meiosis and prevent the generation of viable sperm. Should that mean that a mule has zero individuality? Surely it is still a relevant unit to count in various biological contexts—an evolutionary biologist, for example, might still care to count mules for the sake of estimating the cost that hybridization places on the reproductive fitness of donkeys and horses.

We can easily escape this difficulty if we allow an additional sense of individuality that is not dependent on the present capacity for selection. This connects with the lingering issue of how we should define the concept of organism in light of biological individuality (Gardner 2009; Pepper and Herron 2008; Queller and Strassmann 2009). Queller and Strassman write that “the most salient feature of organisms is adaptation, the seeming goal-directedness that makes organisms different from merely physical entities” (Queller and Strassmann 2009, 3144). Hence “the parts work together for the integrated whole, with high cooperation and very low conflict,” and the organism is “the largest unit of near-unanimous design” (Queller and Strassmann 2009, 3144). One important feature of this approach is that what matters for individuality is actual cooperation and conflict based on the actual adaptations that have evolved, not the potential for conflict or the capacity for selection. Queller and Strassman describe their account as an empirically-oriented counterpart to theoretical modeling, oriented toward making comparative generalizations, although they do not give a fully general set of functional criteria for what counts as cooperation or conflict.

In addition, an analogy to the philosophical literature on biological function suggests there is an underexplored, "atemporal" option for defining individuality based on causal role functions (Cummins 1975; Amundson and Lauder 1994). Instead of framing individuality in terms of selection or adaptation, we could instead define it in terms of the systemic capacity to complete a life cycle (Sterner forthcoming). Recent work on agency and autonomy could also fit in this category (Arnellos and Moreno 2015; Arnellos et al. 2013). This role function approach clearly would not replace evolutionary senses of individuality but could be useful for understanding how scientific research can proceed on individuality while bracketing issues of fitness or selection via heuristic assumptions about the relevance of life cycle processes to evolutionary change. Indeed, this might provide a way to connect conceptions of individuality used in other fields, such as developmental biology or ecology, to existing work in evolutionary biology.

Conclusion

Monism about biological individuality is misplaced once we consider the complexity of both the phenomena itself and the epistemic demands we place on the concept to cope with this complexity. With a plurality of meanings for individuality in hand, it is worth emphasizing the importance of explicitly tracking the roles each conception must satisfy in order to be epistemically adequate (Love 2008; Brigandt 2011). One aim of this paper has been to list these epistemic roles for individuality and assess the merits of Clarke and Godfrey-Smith's accounts based on these practical needs. In this regard, an important motivation for pluralism arises when different contexts of use demand that a concept satisfy overlapping but distinct epistemic demands. This can underwrite the value of maintaining multiple strategies as a result of how they assign different metaphysical natures to individuality and thus exhibit characteristic epistemic limitations for one or more roles. One major theoretical challenge to maintaining a plurality of conceptions over time, then, is to ensure that the results derived under particular contexts remain relevant to the aims of the larger research program. Tracking the relevant contexts of use and epistemic roles therefore seems an essential prerequisite to a productive pluralism about individuality.

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