

Biological Individuals

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The nature of biological individuals and their roles in natural selection, speciation, the history of life, and developmental biology have become lively topics of discussion at the intersection of philosophy and biology. To summarize and synthesize some of the contours to these discussions, and to indicate directions future work might take, we begin with the impressive variation within the category *biological individual* and the focal question in the literature: what are biological individuals? In Section 2 we clarify some of the complexities that arise when addressing this question before teasing apart and elaborating three subsidiary questions in Section 3. One of these clarifies ways in which traditional focus on organisms has left the nature of biological individuals that are *not* organisms unexplored and perhaps distorted (Section 3.1). Another summarizes distinctions that have been drawn between types of biological individuals, including between evolutionary individuals and physiological individuals (Section 3.2). A third subsidiary question seeks the best way to articulate the conceptual space surrounding biological individuals, given the preceding distortions and distinctions. This subsidiary question demands extra attention and so after its relation to pluralism is briefly discussed (Section 3.3), we devote Sections 4 through 6 to it. In Section 4 we introduce an organism-centred view to help frame exploration of the conceptual space surrounding biological individuals. On this view, every biological individual is either a part of an organism, an organism, or a group of organisms. We explore this organism-centred view in Section 5 by discussing three key features of organisms: their status as living things, their possession of reproductive life cycles, and their agency and autonomy. We further expand on this in Section 6 by taking up recent influential work on Darwinian and physiological individuals, conflict and cooperation, and the multiple realizability of biological individuals. We wrap-up by discussing group-level biological individuals in Section 7 and the evolution of biological individuals in Section 8.

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1. The Focal Question: What are Biological Individuals?

The biological world contains an incredibly diverse variety of individuals. At the ground level of common sense, there are alligators, ants, beetles, marmots, moles, mushrooms, ostriches, roses, trees, and whales. At this ground level, biological individuals are *organisms*, physically-bounded, relatively well-integrated, autonomous agents in the biological world, the ones listed being amongst those that we can readily detect with our senses—or so we think. Extending the reach of common sense through magnification, we see or infer flagella-propelled protists, tRNA molecules, prions, and bacteria of many kinds. At larger or collective scales, we find herds of zebra, sweeping and astonishing coral reefs, algae blooms, biofilms made up of many different species of organism, and even fungus complexes several hectares in area and with masses greater than that of an elephant. Although some of these entities are not themselves single organisms (e.g., a tRNA molecule or a herd of zebra), each is a candidate biological individual nonetheless, and each has been treated as such in the biosciences as those sciences attempt to discover generalizations, provide explanations, and make predictions about the biological world. So while it is harmless in some contexts to talk as though ‘organism’ and ‘biological individual’ are synonymous terms, we see, when the context requires more care about these things, that the terms are not equivalent – that ‘biological individual’ names a superordinate category whose nature and relation to the organism category is complex and worthy of investigation.

In the rapidly expanding literature on biological individuals (cf. Hull 1992 with Guay and Pradeu 2016a, 2016b, and Lidgard and Nyhart 2017a, 2017b), what we will call *The Focal Question* – what are biological individuals? – can be paraphrased in a number of ways:

- What constitutes being a biological individual?
- What makes something a biological individual?
- What is the nature of the category *biological individual*?
- What is the best explicative definition of the term ‘biological individual’?

Here we take *biological individual* as a quite general category that may subsume several kinds of biological individual (e.g., evolutionary, developmental, genetic, metabolic).

Philosophers of biology typically understand biological individuals to be distinct from other kinds of entities in the biosciences, such as properties, processes, and events (though see Dupré 2012, Nicholson 2018, Nicholson and Dupré 2018). Biological individuals have three-dimensional spatial boundaries, endure for some period of time, are composed of physical matter, bear properties, and participate in processes and events. Biological *processes* (such as photosynthesis) and biological *events* (such as speciation) lack such a suite of features. Although philosophers have explored the question of what makes anything an individual of *any* kind (e.g., Strawson 1959; van Inwagen 1990; Chauvier 2016; French 2014, 2016; Lowe 2016; Wiggins 2016), we bracket off such questions here to concentrate on *biological* individuals (cf. Love and Brigandt 2017).

As our initial list of the variety of biological individuals suggested, organisms are at once prominent but not the only examples of biological individuals. We should thus walk a fine line when addressing The Focal Question about biological individuals. On one hand we should reflect closely on the related question “What is an organism?”, a question that is also of historical importance when thinking about the biological world (Nicholson 2014). On the other hand, we should also focus on biological individuals that are not organisms (Dupré and O’Malley 2009; R. Wilson 2005:ch.3; Pradeu 2016a, 2016b), and resist the recurrent temptation (e.g., Queller and Strassman 2009, Clarke 2013) simply to identify biological individuals with organisms.

When addressing The Focal Question we will say more about the relationships between the organism and biological individuals categories. But first we want to provide a sense of the complexities that an answer to that question must address and highlight the intimate interplay between empirical data gathered by biologists and conceptual clarification in answering it. Consider two examples, the first introduced into discussions of biological individuals by the philosopher of biology Jack Wilson (1999: 23-25), the second by the physiologist Scott Turner (2000: ch.2).

2. Some Complexities: the Humungous Fungus and Coral Reefs

In the early 1990s, a team of biologists reported in the journal *Nature* that they had found high levels of genetic identity in samples of a species of fungus (*Armillaris bulbosa*), which had taken over a large geographic region in Michigan’s Upper Peninsula. They used this data to make a case for viewing these samples as constituting parts of one gigantic fungus with an estimated biomass of more than ten tons and an estimated age exceeding 1500 years. They concluded that “members of the fungal kingdom should now be recognized as among the oldest and largest organisms on earth” (Smith, Bruhn, and Anderson 1992:431). Some scientists have questioned whether this final claim about the organismal status of the humungous fungus is warranted, and some have argued that the claim is mistaken. Since then, other scientists have recognized even larger funguses as organisms (Schmitt and Tatum 2008).

How do we judge such claims and disputes? Minimally, we seem to need more empirical information about the example. Is the fungus a continuous biological structure? Does it

have a determinate growth pattern? Can it reproduce? But this information alone can't settle the matter. We must also draw on our antecedent concept(s) of an organism and the status of organisms as a kind of biological individual. The empirical information, in turn, also allows us to fine-tune, amend, or challenge our antecedent concept(s), better so than would common sense reflection alone. If the humungous fungus is not an organism but seems another sort of biological individual, which empirical considerations motivate this distinction?

Consider a more elaborately described example (Turner 2000: ch.2). Coral reefs are spectacular and beautiful parts of the living world, despite rapidly becoming a thing of the past due to the climate changes associated with global warming. At least at the ground level of common sense, they are often thought of as consisting of two chief components. The first are accretions of calcite deposits. The second are the small animals, polyps, which produce and grow on the deposits. (Coral polyps belong to the same Linnaean class as sea anemones, and to the same Linnaean phylum as jellyfish.) The polyps are indisputably organisms. But further, conservation biologists also often describe the coral reefs themselves, consisting of the polyps *and* the deposits considered together, as living things that can grow and die.

The reefs are at least biological individuals, typically being thought of as ecosystems; formal methods already exist for modeling them, and even expansive ecosystems, as such (e.g., Huneman 2014). And taking seriously their life, growth and death leads to the question of whether they too might be organisms: to a first approximation, metabolically-circumscribed entities that are relatively well-integrated and function as a whole. The dependence relation between the reefs and the polyps does not rule this out, since such dependence is common in organisms. We humans depend on internal bacteria that outnumber our own cells by about ten to one, and yet we are organisms (Ackerman 2012). Similarly, the polyps that reefs depend on are themselves dependent on single-celled algae, zooxanthellae, for the glucose that provides the energy necessary for polyp respiration, which in turn drives the process of calcification. Moreover, it is the zooxanthellae that supply the pigments that give living corals their spectacular colours; when zooxanthellae are absent or diminished, this signals a problem for the long-term survival of a coral reef. Neither are the zooxanthellae free of dependence. By infecting the polyps they gain a feeding den crucial to their survival.

Further reflection along these lines may suggest that an integrated network of dependence relations is itself a mark of being an organism. If that were so, then we may come to view the coral reef as a better example of an organism than either the polyps or zooxanthellae, as the reef enjoys a kind or degree of complex, functional integrity that polyps and zooxanthellae arguably lack when considered singly (see also Combes 2001). Alternatively, perhaps we should continue to think of the reef as some other kind of biological individual, such as an ecosystem, that contains several distinct organisms, the polyps and the zooxanthellae, as proper parts.

Again, knowing what to say about the striking claim that the polyp-zooxanthellae-calcite deposit complex is an organism turns in part on the empirical facts, but on more than just

those. Polyps, zooxanthellae and whole reef complexes do not wear placards that state which is an example of an organism, and whether all three should be viewed as biological individuals of some kind or other. Knowing what to say about this case also turns on our conceptions of an organism and the kind of work that we expect a general notion of biological individuals to do. The interplay between our conceptions and empirical complexities both allows us to unpack those conceptions and informs how we might regiment them to better capture nuances of the biological world inaccessible to commonsense reflection alone.

As we will see, that interplay heightens with the broader and deeper consideration of those empirical complexities that has become central to the ongoing work on biological individuals. This has involved attending more squarely to the microbial world (O'Malley, Simpson, and Roger 2013, O'Malley 2014), recognizing the various tight integrative and collaborative relations between what *prima facie* are distinct organisms (Dupré and O'Malley 2009, Ereshefsky and Pedroso 2015) and trying to make sense of the diversity one finds in the processes of reproduction, metabolism, and development (Godfrey-Smith 2016b, Griesemer 2016).

3. Subsidiary Questions: Conceptual Space, Distinctions, and Organism-Centrism

Adequate responses to The Focal Question should themselves answer, or at least clearly advance discussion of, at least three closely related subsidiary questions:

1. *Conceptual Space*: What is the best way to articulate the conceptual space surrounding the concept of biological individuals?
2. *Distinctions*: What are the most useful distinctions between the various kinds of biological individuals that exist?
3. *Organism-Centrism*: In what ways does the traditional focus on organisms help and hinder us in thinking about biological individuals?

Since the last of those questions anchors our discussion in the historical trajectory of thinking about biological individuals, we begin with it.

3.1 Organism-Centrism and Two Challenges

In the history of recent thinking about biological individuals, scientists themselves—following common sense—have been drawn first and foremost to organisms when beginning their theorizing about biological individuals. For example, one impetus for thinking about biological individuals was provided by John Maynard Smith and Eörs Szathmáry's influential *The Major Transitions of Life* (1995). This wide-ranging book on the origins and evolution of life has stimulated much work on the evolution of individuality (Buss 1987) and the Darwinian dynamics (Michod 1999) that governs emerging kinds of biological entities (see section 8 below). The book opens with a simple point about the living world and a characterization of the book's chief theme:

“Living organisms are highly complex, and are composed of parts that function to ensure the survival and reproduction of the whole. This book is about how and why this complexity has increased in the course of evolution. The increase has been neither universal nor inevitable” (p.3). Here organisms are viewed as exemplars of complex living things composed of many parts, and their complexity is taken to have increased—albeit unevenly and contingently—through evolution by natural selection.

Likewise, the early collection on evolutionary developmental biology by Gerd Muller and Stuart Newman (2003) focuses on how *organismal form* originated and on the evolutionary, developmental, and ecological processes that have shaped it over many generations. The essays in that volume concentrate on the relationships between basic body plans of organisms over phylogenetic time, rather than the evolution of individuality as such, and do not really take up The Focal Question about biological individuals. But like that of Maynard Smith and Szathmáry, the project of exploring these relationships is naturally expressed in terms of the concept of an organism.

This should occasion no surprise, since, as we saw in Section 1, organisms are prominent examples of biological individuals. But the snippet that we have drawn from Maynard Smith and Szathmáry about organisms also further elaborates why equating biological individuals with organisms would be a mistake. The parts that compose organisms in all their complexity are, often enough, themselves biological individuals, and even if some of those parts are also organisms (e.g., the microbes that live on and in macrobes), many are not. Precisely the same is true of the populations and lineages that individual organisms in turn constitute. They may sometimes be organisms—as has been suggested in the case of “superorganisms”—but in many cases they are biological individuals that are not organisms. If either this internal compositional complexity to organisms or their formation into populations and lineages are *necessary* features of organisms (which we tend to think they are) then this would prove a stronger conclusion: given that there are organisms, there *must be* some biological individuals that are not organisms.

So one way in which the traditional focus on organisms can hinder us in thinking about biological individuals is if by equating the two we ignore all of those biological individuals that are not organisms. But hindrance here could take a different form. We might think that a focus on organisms commits not just an error of omission but proves *positively misleading* about what biological individuals are. Consider two challenges to the privileging of organisms in discussions of The Focal Question:

- A. To understand life we should focus more than we have on *collaborations* between varieties of things (e.g., viruses, prions, plasmids, symbionts) that may not all be organisms; this is because these collaborations are characteristic and explanatory features of living systems, which may even suggest that a great variety of things other than organisms are parts of the living world (Dupré and O'Malley 2009).
- B. Far from being *paradigmatic* biological individuals, organisms may be marginal or unusual special cases of biological individuals and we should consider eliminating them from our ontology (Haber 2013, Okasha 2011).

Challenge A has been part and parcel of Dupré and O'Malley's complaint against the "macrobiotic bias" in the philosophy of biology and the case they have made for the significance of the microbial world for reconceptualizing biological individuals (O'Malley 2014, 2015, O'Malley, Simpson, and Roger 2013; Dupré 2010). One direction that this has been taken is Dupré's (2012) *promiscuous individualism*.

Promiscuous individualism is not simply the view that there are many legitimate ways to classify the world into biological individuals, including organisms, but the corresponding ontological view that such legitimation is provided by there being multiple biological individuals there to classify. To illustrate this view, consider lichens, which are typically regarded as composite organisms made up of a fungus and either a cyanobacterium or some other photosynthesizing organism, such as green algae. Challenging the view that there is just one organism (the lichen) or two organisms (the fungus and the cyanobacterium), an advocate of promiscuous individualism can readily make the case that there are three organisms (the lichen, the fungus, and the cyanobacterium), pointing to the different purposes and goals one might have in opting for either of the more monistic counts of organism numbers here.

Yet given that it is a population of millions of cyanobacteria inhabiting any given fungus that jointly compose a lichen, and that there are multiple ways to draw the boundary between individual fungi of a given species (Molter 2016), note how rampant promiscuity runs here. Dupré himself holds that populations of organisms, including multispecies populations such as those found in microbial biofilms, can themselves be both biological individuals and organisms (2012:89, 175-176, 194, 203). He also says that "[w]hether a group of microbes is a closely connected ecological community or an organism may be a matter of biological judgment" (p.153). Promiscuous individualism thus implies that there are many, many different numbers of individuals present in this paradigm case. It seems even to suggest that whether there are *any* biological individuals at all is "a matter of biological judgment", rather than something determined by the biological facts.

The emphasis on collaborations between living things in Challenge A can undermine the focus on organisms without entering (at least directly) into these deep metaphysical waters. Simultaneously it can also join with Challenge B. One way it can do so is by embracing the idea that it is not organisms but *holobionts* that are really the paradigmatic biological individuals. The holobiont is roughly "the multicellular eukaryote plus its colonies of symbionts" (Gilbert and Tauber 2016:842). This concept is attractive to some scientists (e.g., Zilber-Rosenberg and Rosenberg 2008; Bordenstein and Theis 2015; Bosch and Miller 2016; cf. Douglas and Werren 2016) while also sparking ongoing philosophical work (Theis et al. 2016, Booth 2014, Doolittle and Booth 2017). For example, a recent special issue of the journal *Biology & Philosophy* on biological individuality (volume 31, issue 6) contains papers that focus on the significance of the holobiont for immunology (Chiu and Eberl 2016, Gilbert & Tauber 2016) and for the evolution of individuality and its major transitions (Queller and Strassmann 2016, Skillings 2016; cf. Bourrat and Griffiths 2018).

Like the concept of an organism that it putatively supplements or supplants, that of the holobiont encompasses a huge diversity of entities. These include macro-organisms and the microbial endosymbionts living within their cells (such as *Chlamydia* and other obligate parasites); those that live beyond their cells but in close symbiotic relations (such as cyanobacteria); and the multispecies microbiota that inhabit the human intestine (Booth 2014). There are challenges in how to delineate individual holobionts that, as we will see in section 3.2, may be met by shifting to particular physiological criteria (Pradeu 2012). Yet those challenges have suggested to some that the take-away from reflection on holobionts is that we should emphasize not another kind of individual, a holobiont, but the process of *holobiosis* (Doolittle and Booth 2017). Whether the concept of the holobiont lives up to its promise of revolutionizing thinking about biological individuals remains unclear.

3.2 Distinctions: The Evolutionary and the Physiological

Consider now our second subsidiary question, Distinctions: what are the most useful distinctions between the various kinds of biological individuals that exist? Prominent here is the work of Peter Godfrey-Smith on what he calls “Darwinian individuals”, a specification of what others call “evolutionary individuals” (Pradeu 2016b, Clarke 2016b). On the view of evolution and natural selection defended in Godfrey-Smith’s *Darwinian Populations and Natural Selection* (2009), what evolves are “Darwinian populations”, collections of things in which at least three conditions hold: there is *variation* in the traits had by things in the collection, those traits are *heritable* within the collection, and some variants of the traits confer reproductive advantage on the things that bear them. In such a Darwinian population, the members are Darwinian individuals (Godfrey-Smith 2013:19).

At least three features of Darwinian individuals are important for Darwinian populations to express the heritable variation in fitness that is required for evolution by natural selection. First, the members are the *bearers* of the traits that vary within the evolving population. Second, population members are the *reproducers* that help enable trait heritability. Third, some heritable trait variants *tend to help cause* their bearers to reproduce more offspring than bearers of other variants of the trait in question (Godfrey-Smith 2013:19-20).

Consider a population of finches. There is variation in beak length: some finches have long beaks, others short. Beak length is heritable. And the finches occupy a habitat where long beaks help cause finches with those beaks to produce more off-spring than those with short beaks, because longer beaks make it easier to eat seeds that have fallen between rocks, helping finches with the energy needed for competing with mates and so on. In this example, the finches that make up the evolving population are Darwinian individuals. They are bearers of the trait that varies (beak length), they reproduce (new finches), and one variant of the trait (the long one) helps cause relative reproductive success.

Godfrey-Smith's approach to evolutionary individuals is intended to contrast with the replicator-based views developed by Richard Dawkins and others and that have been central in discussions of the levels and units of selection (Godfrey-Smith 2015, Sober and Wilson 1994, 1998, Okasha 2007). Here genes are paradigmatic replicators, being housed in *interactors*, such as organisms, and it is their survival that matters in evolution. Rather than the emphasis on the importance of high-fidelity copying across generations in the replicator framework, what matters for natural selection in Godfrey-Smith's framework is the establishment of parent-offspring lineages that feature heritability, as well as the variety of forms that *reproduction* can take in their establishment and stabilization.

This shift from replication to the process of reproduction in accounts of the biological world has a longer history, particularly amongst those sensitive to the relationships between evolution and development. For example, James Griesemer (2000) has argued that biological reproduction involves fission and fusion requiring what he calls *progeneration*, a process that creates new entities through *material overlap*, and that that process is a crucial feature of how living things evolve. We will return to this in section 5 in discussing reproduction, life cycles, and lineages.

Whichever way evolutionary individuals are conceptualized, they do not exhaust the realm of biological individuals any more than organisms do. Although evolution is foundational when thinking about Darwinian individuals, it does not play this role for all kinds of biological individual. Indeed, Godfrey-Smith (2013) proposes that some organisms, understood from a metabolic point of view, are not Darwinian individuals. Although he acknowledges that some other authors count more entities within this sub-category of biological individual than he is willing to count, he believes there are significant examples. These, such as the squid-*Vibrio* complex he discusses, are organisms made out of symbiotic relationships between members of different species (e.g., between the squid and *Vibrio* bacteria they contain). Figure 1 reproduces Godfrey-Smith's diagrammatic depiction of distinctions here.

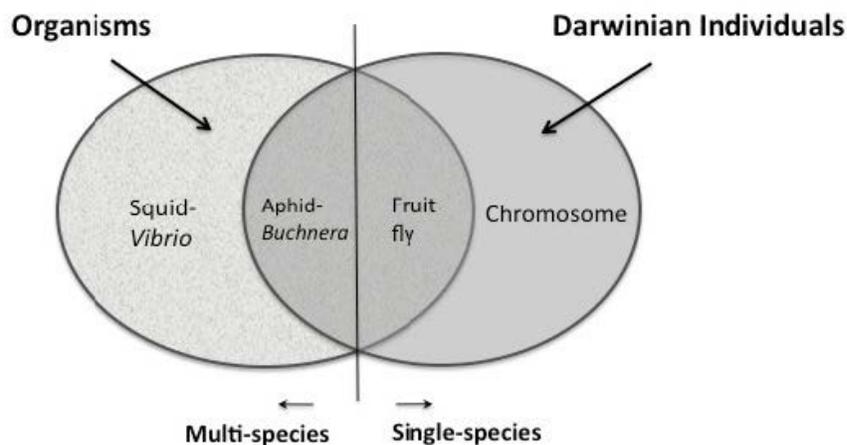


Figure 1: Godfrey-Smith's Different Biological Individuals. (Copied from Figure 4 of Godfrey-Smith, Peter, 2013, "Darwinian Individuals", in Frédéric Bouchard and Philippe Huneman (eds.) *From Groups to Individuals: Evolution and Emerging Individuality*, Cambridge, MA: MIT Press, pp.17–36.)

Godfrey-Smith's distinction between organisms and Darwinian individuals is another matter that Section 5 will return to and scrutinize in more detail. But here it is important to note Pradeu's (2016b) closely related distinction between Darwinian individuals and what he and some others call physiological individuals. According to Pradeu, each physiological individual is "a functionally integrated and cohesive metabolic whole, made of interdependent and interconnected parts" (Pradeu 2016b:807; see also Godfrey-Smith 2009:71).

More contentiously, Pradeu defends the view that an organism is a particular kind of physiological individual, being "a functionally integrated whole composed of heterogeneous components that are locally interconnected by strong biochemical interactions and controlled by constant systemic immune interactions of a constant average intensity" (Pradeu 2012:244). This takes the boundary established and maintained by the immune system as *the* boundary of the organism, an implication in tension with more expansive outlooks that would suggest there is more to the bases of physiological individuality than just immunological considerations. Nevertheless, on Pradeu's view organisms are inherently heterogeneous, given the collaborative nature of the microbial and macrobial worlds articulated in Challenge A. To put it slightly differently, the true organisms delineated by Pradeu's immunity criterion are holobionts constituted by a macrobial organism and all and only those microbes at least tolerated by its immune system. This criterion provides a way to individuate organisms *as holobionts*.

3.3 Conceptual Space and Pluralism

So minimally there are evolutionary individuals and there are physiological individuals, and organisms are typically thought of as exemplars of (but not strictly identical to) both. Godfrey-Smith's articulation of evolutionary individuals as *Darwinian* individuals has structured much recent and ongoing discussion—Pradeu's account of physiological individuals in terms of immunological identification less so. Both accounts respond to our second subsidiary question, which seeks the most useful distinctions between kinds of biological individuals. And they do so in ways that also allow for rich responses to our remaining subsidiary question, Conceptual Space: What is the best way to articulate the conceptual space surrounding the concept of biological individuals? In Section 4 we will take up that question in earnest by introducing a view that posits a particular type of relationship between evolutionary and physiological individuals. But to segue into that we first offer a brief comment on more radical forms that pluralism about biological individuals might take.

We have already seen that the emphasis on the collaborative nature of the interactions between biological individuals in Challenge A motivates Dupré's promiscuous individualism, a position that invites a radical form of pluralism that makes biological individuality seem a function of our epistemic, practical, and other proclivities, rather than of the structure of the biological world itself. Dupré's view here is a response to discoveries about the microbial world and views of its significance for re-thinking standard topics in the philosophy of biology.

Here he follows the intuition that if some kind *K* seems too diverse to characterize, it should be split into diverse sub-kinds and characterize each of those. In early philosophical work Jack Wilson (1999, 2000) also drew on this intuition, where *K* = biological individual, moving beyond that broad concept to characterize *genetic*, *functional*, *developmental*, and *evolutionary* individuals. Famously, the botanist John Harper invoked pluralism, where *K* = plant, by introducing the more particular kinds *ramet* and *genet* to replace talk of individuals or organisms. A ramet is what we might readily identify as an individual plant; a genet is a collection of ramets that propagate, as is often the case, through the clonal growth of a particular ramet. How many plants there are, in many cases, depends on whether we mean ramets or genets. For example, while each of the trees in an aspen grove that forms clonally is a ramet, collectively they typically form a single genet. A pluralist might prefer a description cast in terms of ramets and genets over any attempt to answer the question of how many plants or organisms, per se, there are in this case.

While this form of pluralism exemplified by these cases can be a useful device of disambiguation and help people avoid talking at cross-purposes, it propagates numerous categories that in our view are more limited than the categories *evolutionary individual* and *organism* for informing meaningful responses to Conceptual Space (see Barker 2013a).

Pluralism about biological individuals has also been motivated by the general idea that particular epistemic *practices*, rather than or additional to high-level biological theory, should drive one's ontological commitments (see Kovaka 2015, Chen 2016, Love 2018; for interplay of theory and experimental practice in this connection see Fagan 2016). Just as practices of the individuation of species might vary with the differential practices of (say) ciliatologists (Nanney 1999) and ornithologists, so too might the very individuating criteria for being a (relevant) biological individual differ according to the varying epistemic practices across the biological sciences. How radical the resulting form of pluralism is will depend in part on how fine-grained is one's view of the relevant practices, and how expansive is the range of those practices. For example, do we cluster all of the practices in developmental biology, or do we distinguish between those relevant to the experimental investigation of growth from those relevant to homology? Do we include biological individuals that are posited in community ecology and are constituted by organisms, other living things, and non-living things including soils, as Roberta Millstein (2018) has recently done when discussing the *land community* (see also Eliot 2011)? Whether this results in what Alan Love calls *strong individuality pluralism*, the

view that “for a given situation, individuality can be modeled correctly in more than one way” (2018:187), turns on answers to such questions.

4. The Organism-Centred View of Biological Individuals

Although we have seen that simply equating organisms with biological individuals or with living agents would be a mistake, some have thought a more nuanced sort of organism-centred view is defensible (see also Jagers op Akkerhuis 2010). We think that a particular organism-centred view affords some progress on the conceptual space dimension to The Focal Question. And minimally, as we shall see, it provides a way to usefully organize and discuss work in this area. On this organism-centred view, biological individuals include exactly:

- *organisms* (such as wasps and whales, and perhaps endosymbionts and slime molds)
- some *parts* of organisms (such as hearts, placentas and plasmids) and
- some *groups* made up of organisms (such as zebra lineages and colonies of bacteria).

The relevant parts and groups of organisms here will be precisely those that share the features that make something an individual in general: entities with three-dimensional spatial boundaries, which endure for some period of time, are composed of physical matter, bear properties, and participate in processes and events. Not all parts of organisms possess these—liquids such as blood and patches of skin don’t, for example—nor do all groups made up of organisms: temporary and dispersing groups don’t, nor does the collection of all the biological individuals in some arbitrarily delineated plot of soil.

So on this view, each and every biological individual is an organism, or a part of an organism, or a group of organisms. Although this aims to exhaustively cover the realm of biological individuals, note that these three sub-categories of biological individuals need not be mutually exclusive when we consider any particular biological individual. A given bacterium may both be an organism itself and be part of a different organism, such as a human whose gut it resides in and interacts with for some time. Likewise, some groups of organisms, such as the colonies of insects that are sometimes called “superorganisms”, may be *true* organisms rather than merely so-called organisms.

We call this an *organism-centred* view because each of its three parts references organisms (see also Pepper and Herron 2008, 622). It allows that many biological individuals—for example, hearts and some populations—are not themselves organisms. And it allows us to recognize a thing as a biological individual even when we are not sure whether it is an organism, or a part of an organism (e.g., an endosymbiont) or a group of organisms (e.g., a colony of eusocial insects).

Organism-centered views of biological individuals seem widely, if often implicitly, endorsed, even though confusing choices of terminology can conceal this. For instance, such a view may capture what truth lies behind proposals to extend the term ‘organism’

to both some parts and groups of organisms (e.g., Queller 1997; Okasha 2011). They also provide an interesting context in which to explore the basic metaphors we use to conceptualize organisms and the living world more generally, including those of organisms as a complex machines and life as a flowing stream (Nicholson 2018). To see how the organism-centred view captures something striking about organisms without running afoul of Challenges [A](#) and [B](#) from section 3.1, take those challenges in turn.

Challenge A to the historical privileging of organisms addresses the methodological question of how to study life. The challenge proposes that our studies focus not just on organisms but also on a variety of things that produce life through interactions. This methodological prescription is based on answers to other questions, e.g., about how life is generated. Although an organism-centered view and Challenge A directly address different questions, they in fact can be viewed as fitting together nicely. Both are based on rejecting the ideas that only organisms are biological individuals, that only organisms are alive, and that only things that are alive are biological individuals. The methodological reorientation that A proposes complements rather than challenges a nuanced organism-centered view of biological individuals.

Challenge B raises the question of which biological individuals are paradigmatic. There are many senses of ‘paradigmatic’, but it is difficult to think of a plausible sense here that results in a tension between this challenge and a nuanced organism-centered view of biological individuals. Such a view, after all, holds that the extension of ‘biological individual’ includes some (perhaps relatively many) groups above organisms, and some (perhaps relatively many) parts within organisms. Based on the number of traditionally excluded things this lets in, and on the differences between those and organisms themselves, an organism-centred view could allow that organisms are no longer paradigmatic biological individuals. It is simply that, conceptually or metaphysically, all biological individuals either are organisms or are importantly related to them on one of the two ways specified: mereologically, or by group membership. For this reason, understanding the nature of organisms and their relations is central to a full understanding biological individuals, even if organisms represent just a small fraction of the biological individuals there are, or are an idiosyncratic subset of biological individuals.

Figure 2 offers an initial summary of the organism-centred view of biological individuals described thus far (see also the figures in Pradeu 2016b). Over the following sections we will elaborate the initial visual summary offered by Figure 2. This will help clarify how we are complicating the picture taken from Godfrey-Smith in Figure 1 above, as we fill in the conceptual space that the organism-centred framework affords and further.

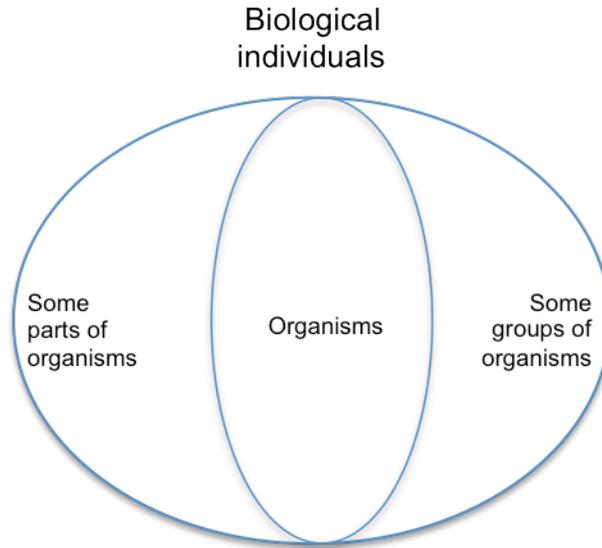


Figure 2: The Organism-Centred View of Biological Individuals

If the organism-centred view of biological individuals goes some way to framing the conceptual space that, in part, answers The Focal Question about biological individuals, then further development here rests very much on the concept of an organism. Missing so far from the emerging account of the conceptual space that biological individuals occupy is a more systematic treatment of the relationship between each of the primary kinds of biological individuals – evolutionary and physiological individuals – and other key features typically appealed to in characterizing them, including growth, reproduction, lineages, cohesion, metabolism, and control.

In section 5 we explore a view that offers a characterization of these key features as properties of *living things* in general (section 5.1), and then discuss two further conditions that distinguish mere living things from organisms. The first of these conditions—concerning reproductive lineages and intergenerational life cycles—has affinities with ongoing discussions of evolutionary individuals (section 5.2), while the second—concerning the kind of autonomy or agency that organisms have—has been emphasized in thinking about physiological individuals (section 5.3). We will then conclude section 5 with a summary of a view of organisms that draws on these three features and the implications of that view for a range of cases discussed in the literature on organisms and other biological individuals (section 5.4).

5. Organisms: Life, Reproduction, and Agency

Early in section 2 we saw that landmark works on the major transitions in the history of life and on evolutionary developmental biology each drew on the concepts of an organism and of living things. Although the reference to living things remains present in the traditions of work focused on physiological individuals, it has been backgrounded in work that has concentrated on evolutionary individuals, perhaps for the obvious reason

that many evolutionary individuals—including genes, groups of individuals, lineages, and clades—are not themselves alive. Yet since organisms are both evolutionary and physiological individuals, and they are paradigms of living things, neglect of the category of living things results in a limited answer to The Focal Question. We thus turn more explicitly to reflect on the significance of the fact that organisms are living things. Rather than attempting to define life (or living thing), or to provide necessary and sufficient conditions for these, we take as our starting point the promise of a general and influential view of biological kinds.

5.1 Living things as HPC Kinds

It is common to appeal to a list or cluster of properties—such as growth, reproduction, lineages, cohesion, metabolism, and control—in characterizing either life itself or organisms as living things or agents. Rather than pursuing the hapless project of attempting to parlay such a list or cluster into a set of singly necessary and jointly sufficient conditions (see also Cleland 2012), as some proponents of traditional conceptual analysis are wont to do, a more promising way to move from such an appeal is to try integrating this kind of list into an influential approach to biological kinds, the homeostatic property cluster (HPC) view (Boyd 1999a, 1999b; Griffiths 1997, 1999; R. Wilson 1999a, 2005:ch.3-4; Wilson, Barker, and Brigandt 2007). On this view, *living thing* is, like other biological kinds, an HPC kind, one constituted by the following three triads of, respectively, structural, functional, and relational properties. Living agents:

- have heterogeneous and specialized parts
- include a variety of internal mechanisms
- contain diverse organic molecules, including nucleic acids and proteins
- grow and develop
- reproduce
- self-repair
- have a metabolism
- bear environmental adaptations
- construct the niches that they occupy.

As with other HPC kinds in the biological sciences, this cluster of properties is reliably underwritten by specific causal mechanisms and constraints that *underlie* the cluster (Wilson, Barker, and Brigandt 2007:200). This underwriting gives definitive clusters their homeostatic character and ensures that the causal structure of the world plays a significant role in determining what is and what is not an HPC kind. Consequently, whether something is a living thing is determined in significant measure by how the mind-independent world is, rather than simply by our conventions and concepts for thinking about the world. This distinguishes the HPC view from Wittgensteinian family resemblance accounts of concepts and from subjective approaches to biological taxonomy such as pheneticism (Sokal and Sneath 1963; Sokal and Crovello 1970).

Supposing that organisms are living things so understood allows us to extend the visual summary we introduced in Section 4, with Figure 3 adding how the category *living thing*

relates to both *organism* and *biological individual*. Figure 3 shows that all organisms are living agents. But as the left-hand side of the boundary of the living agents category implies, some parts of organisms are alive without themselves being organisms (e.g., hearts); and as the right-hand side of that boundary implies, some groups of organisms may be alive without themselves being organisms (e.g., perhaps a coral reef).

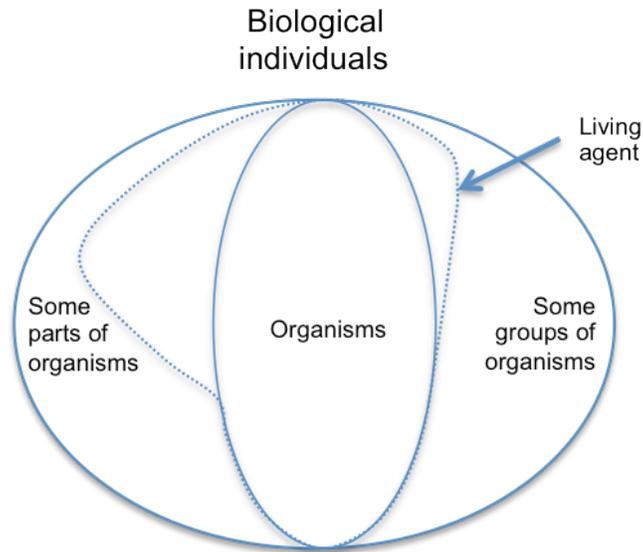


Figure 3: Living Things in an Organism-Centred View of Biological Individuals

So organisms are a kind of living thing or agent. But as we have seen, it would be a mistake simply to identify organisms with living agents. Biological individuals that are parts of organisms—cells and the organelles they contain (mitochondria and ribosomes), bodily organs (such as the heart or kidney) and even bodily systems (such as the digestive system or the circulatory system)—are decisive counter-examples.

5.2 Reproduction, Life Cycles, and Lineages

One feature of organisms that partially distinguishes them amongst living things is that they have *life cycles* that allow them to form reproductive lineages of a certain kind. The importance of life cycles for evolutionary change has been recognized both in the replicator-based view of evolutionary individuals (Dawkins 1989: ch.13) and in reproductively-centred accounts of Darwinian individuals (Godfrey-Smith 2009, 2016a). And the close relationship between being an individual organism and having a life cycle is widely accepted, being manifested in an extreme form by Griffiths and Gray's (1994) (less widely accepted) identification of individual organisms with their life cycles, within developmental systems theory.

Put most generally, a life cycle is an intergenerationally replicable series of events or stages through which a living thing passes (Bonner 1993). These events or stages constitute a *cycle* in that they begin and end with the same event, such as the formation of

a fertilized egg in sexually reproducing organisms, or the creation of a fissioned cell in clonally reproducing organisms. *Development* is the global name for the processes that causally mediate between these events or stages in a life cycle, with *reproduction* marking the transition to the creation of a new individual, the offspring of one or more parental organisms. Although Richard Dawkins's suspicion "that the essential, defining feature of an individual organism *is* that it is a unit that begins and ends with a single-celled bottleneck" (1989:264) has proven hyperbolic, the more cautious view that the "two phenomena, bottlenecked life cycles and discrete organisms, go hand in hand" (p.264) expresses a view that has been widely held.

It has long been recognized that some organisms, such as flukes, have life cycles that take them literally through one or more host organisms, and that many insects undergo significant metamorphic changes in bodily form through their life cycle. But such sophistications to life cycles are only the tip of the iceberg here. While the stages themselves often form standard sequences within particular species, there can be tremendous variation across species and phyla in what a given organism's life cycle consists in, as others have emphasized (Buss 1987), including in recent discussions of complex life cycles (Godfrey-Smith 2016b, 2016d, Griesemer 2016, Herron 2016, O'Malley 2016; cf Gerber 2018).

In the life cycles with which we are most immediately familiar, processes that mark the end of one life cycle and the beginning of another of the same kind of organism—processes such as material bottlenecking, sexual reproduction, and multiplication—temporally coalesce. In the life cycles of other organisms, such as ferns and scyphozoan jellyfish, these processes are sometimes dispersed, function differently, or are absent (Godfrey-Smith 2016b, 2016a). Such cases call for a corresponding sophistication of accounts of reproduction and, as James Griesemer says, these complexities in life cycles may "complicate relations between processes of development and reproduction to such an extent that even the meaning of 'organism' begins to break down" (Griesemer 2016:804).

Maureen O'Malley (2016) has drawn attention to other cases that pose more radical challenges to the standard ways of thinking of life cycles themselves. An example is the asexually reproducing, multicellular protist *Volvox carteri* (green algae), whose "sexual phase of the life cycle is nonreproductive because there is no multiplication" (O'Malley 2016:838). This kind of sexual recombination occurring between members of asexually reproducing generations takes on a striking form in ciliates, such as *Tetrahymena*, whose micronucleus provides germ-line isolation. Whether O'Malley's concept of *multigenerational individuals* can be squared with extensions of standard views of reproduction and life cycles remains subject to further exploration (see also Nanney 1999 on *Tetrahymena* and the species concept).

Although there is a relationship between having a life cycle and reproducing, simply reproducing is *not* the distinctive feature here, as a number of others have recognized (e.g., Griesemer 2014, Godfrey-Smith 2013, O'Malley 2016, R. Wilson 2005). Organisms and perhaps other biological individuals typically reproduce through material

overlap (Griesemer 2000), or via bottlenecks requiring material minimalization of the organism and mark the transition between generations (Godfrey-Smith 2009:ch.5). These kinds of constraints on biological reproduction go hand in hand with growth and development as part of the intergeneration life cycle of biological individuals. Intergenerational life cycles, in turn, make it possible for organisms to form reproductive *lineages* of living things. Reproduction not only structures such lineages. It also structures the lineages of non-living biological individuals, whether they be smaller than the organisms they are parts of (such as genes) or groups of those organisms (such as populations) that feature centrally in discussions of evolutionary individuals.

Although reproduction itself has sometimes been conceptualized as part of the organismic life cycle, we should think about this more carefully in articulating the role of reproduction in intergenerational life cycles that characterize organisms in general. For there are many species in which only a small minority of organisms get to reproduce, with reproductive skew being a widespread feature of the world of organisms. Meanwhile it seems clear that all of these organisms, however much or little they reproduce, still possess a life cycle. Note that even the *capacity* to reproduce is not a universal feature of organismic life cycles. This is not only because the capacity itself may not be replicated, but also because there are organisms *designed* by natural selection to be non-reproductive, with sterile castes in the so-called *social insects*—species of ants, bees, wasps, along with the phylogenetically distinct termites—being perhaps the best-known examples.

In such species, a few individuals do most if not all of the direct reproductive labor (e.g., queens), and many others are rendered reproductively sterile throughout all or much of their life (e.g., worker castes). So there are reasons to include neither reproduction nor the capacity to reproduce as part of the generic life cycle of organisms. What is true, however, is that all organisms have life cycles that allow them to form reproductive lineages. They do so sometimes through the reproductive activity of members of the lineage to which they belong, even if not every member of that lineage reproduces or even can reproduce. Like viruses, individual members of sterile castes of insects rely on the reproductive machinery *of others* in order for descendant members of those castes to be reproduced in future generations.

This is an example of what Godfrey-Smith (2009:ch.5) calls *scaffolded reproducers*, “entities which get reproduced as part of the reproduction of some larger unit” and whose “reproduction is dependent on an elaborate scaffolding of some kind that is external to them” (p.88). These contrast with what he calls *simple reproducers*, a paradigm of which is a bacterial cell, being “the lowest-level entities that can reproduce largely ‘under their own steam’” (p.88). Both simple and scaffolded reproducers can be parts of what Godfrey-Smith calls *collective reproducers*, which are “reproducing entities with parts that themselves have the capacity to reproduce ... largely through their own [the parts’] resources rather than through the coordinated activity of the whole” (p.87). Both groups of organisms and multicellular organisms exemplify collective reproduction, and Godfrey-Smith’s discussion of the continuous dimensional space that characterizes collective reproducers, and Darwinian individuals more generally, has been influential. In

order to vividly convey one important suggestion in this discussion—that individuality consisting in three continuous variables, including reproductive specialization, itself has a continuous nature—we reproduce one of his depictions of such a space as Figure 4 below.

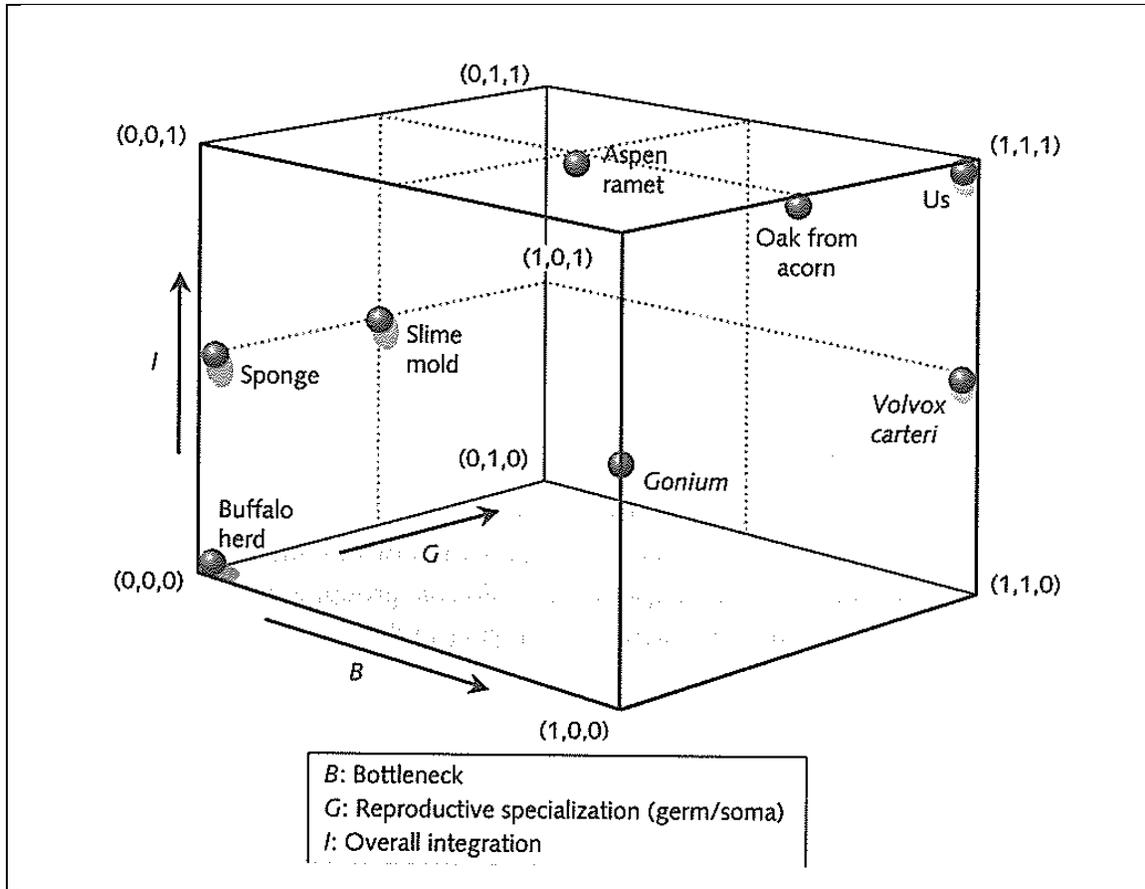


Figure 4. Godfrey-Smith's Dimensional Space for Collective Reproduction. (Copied from Figure 5.1 in Godfrey-Smith, Peter, 2009, *Darwinian Populations and Natural Selection*, New York: Oxford University Press.)

5.3 Autonomy and Agency

A second feature sometimes invoked in distinguishing organisms from other living things is that they have some distinctive kind of autonomy or agency. This builds on the thought that organisms are not simply living things or agents but *have a life of their own*: they are able to exercise some sort and degree of control over themselves and subsequently are relatively free with respect to relevant other things, including relevant other agents and environments. We might express this in terms of both the organism's relative autonomy from its external environment and its control over the activity of its components or internal parts (Wilson 2005:62-65). Organisms have a distinctive kind of agency because of the integrity with which such autonomy and control imbues them.

This appeal to autonomy and agency has a long history in thinking about what is distinctive about the biological world, particularly when the focus has been on physiological individuals. For example, in the first volume of his *Principles of Biology* (1866), Herbert Spencer argued at length that the capacity of an organism to “continuously adjust its *internal* relations to *external* relations, so as to maintain the equilibrium of its functions” (p.207, our emphasis) is one of the key features that sets it apart as biological. Likewise when Julian Huxley later proposed three conditions of minimal organismality, one of these concerned integration of *internal* functions and a second concerned independence from *external* forces (Huxley 1912, p.28). Like Spencer, Huxley saw these internal and external matters as causally linked within organisms, and as together achieving equilibria in distinctive ways. Huxley thought this was due especially to the parts of organisms being both more heterogeneous and functionally integrated with each other than we see in the non-biological context external to such individuals. We will return to contemporary cousins of this idea in section 6.

Pradeu’s (2012) view of immunological control as marking the boundary of the biological individual is one way of specifying this idea of autonomy or agency. Likewise for Godfrey-Smith’s continuous dimension of *integration*, which summarizes features such as “the extent of division of labor, the mutual dependence (loss of autonomy) of parts, and the maintenance of a boundary between a collective and what is outside of it” (2009:93). Generalizing these ideas, any organism is a *locus of control* in ways that neither non-living things nor obligately-dependent living things (such as organs) are. Or as others have said, the high level of functional integration (or cohesion, e.g., see Collier 2004) possessed by *parts* of organisms (Okasha 2011: 59; Pradeu 2012: 243–244) imbues the *whole* organisms they constitute with both capacities to act and largely shared fates to which those capacities contribute (Sober 1991: 291). In some sense, this is why any organism has a life *to lead*, rather than simply being alive.

Organismal agency is stronger than the deflationary kind of agency that Wilson characterizes in terms of being “a source of differential action, a thing from which and through which causes operate” (R. Wilson 2005:6-7). On that deflationary notion of agency, more unwieldy entities such as species (Ghiselin 1974; Hull 1976, 1978) and larger clades (Doolittle 2017a) and whole ecosystems (Currie 2011; Eliot 2011; Leibold et al. 2004) may sometimes qualify as agents. On the stronger organismal notion of agency, those more inclusive entities would be agents in only a metaphorical sense. Organismal agency is, however, weaker and less controversial than the appeal to agency that Godfrey-Smith (2009:ch.7, 2015) has identified and challenged through his critique of rationalizing and optimizing approaches to explanation within evolutionary biology. Those approaches are exemplified by Dawkins’s (1976 [1989]) classic appeal to selfish genes (see also Moreno and Mossio 2015).

It remains an interesting question as to why the use of *cognitive metaphors* in describing biological agency is widespread, if not ubiquitous (R. Wilson 2005:74-79; Godfrey-Smith 2009:142-145; Dennett 2011; Nicholson 2018, Okasha 2018). Related issues that likewise are worth pursuing elsewhere include whether the agency of some biological individuals is determined partially by their context or relations to other things, or by our

values or conventions (Butler 2009; Keller 2002), and whether biological agency and reality can come in degrees (Child 1915; Conklin 1916; Sober 1991; Pepper and Herron 2008; Queller and Strassmann 2009; Godfrey-Smith 2009, 2013; Clarke 2012).

5.4 The Tripartite View of Organisms

One view drawing together these thoughts about organisms is what one of us has called the *tripartite view of organisms* (R. Wilson 2005:ch.3-4). Here we can set aside the issue of whether this view is true and merely use it as a tool to help frame widely discussed thoughts about organisms in a way that makes direct contact with a range of concrete examples. The tripartite view holds that any organism is physically continuous and bounded and:

- a) is a living thing (individual, agent) during at least some of its existence,
- b) which belongs to a reproductive lineage, some of whose members have the potential to possess an intergenerational life cycle, and which
- c) has a distinctive kind of autonomy or agency.

The most under-developed part of the tripartite view has been (c), and it has remained unclear whether the kinds of articulations of autonomy or agency summarized above are sufficient to flesh out this part of the view robustly, or whether (c) should be altogether replaced, particularly in light of the development of ideas about collaborations and dependencies between living things often thought of as separate organisms.

For putting these thoughts about organisms in contact with a range of examples, consider how well the three parts of the tripartite view, (a) – (c), capture and explain much about our (at times) mixed judgments about the organismal status of twenty-two biological and non-biological individuals that have featured in recent discussions of organisms, evolutionary individuals, and physiological individuals:

<i>bodily organs, systems</i>	satisfy (a) but not (b); (c) very limited, if satisfied at all.
<i>obligate parasites</i>	satisfy (a)–(b), though the extent to which (c) is satisfied varies; see also viruses on (a) and (c) below.
<i>mitochondria</i>	were once organisms (Margulis 1993) but are no longer such: special case of obligate parasites that have given up (b) in addition to (c) over evolutionary time.
<i>genes, or DNA fragments</i>	at least some satisfy (c), and a variant of (b), but do not satisfy (a).
<i>developmental systems</i>	do not satisfy (a)–(c); may be parts of organisms, or have organisms as parts, but are not organisms.
<i>single cells</i>	as unicellular organisms, satisfy (a)–(c), but in multicellular organisms, fail to satisfy (b) and (c).
<i>viruses</i>	satisfy (b); satisfaction of (a) borderline and of (c) questionable in many cases because of the sort of dependence on other organisms.
<i>plants</i>	satisfy all of (a)–(c)

<i>vertebrates + their environments</i>	not themselves organisms because not living things, even though they contain an organism as a proper part; see also parasite-host systems.
<i>parasite-host systems</i>	satisfy (a) and (b), but so too do their constituent parts; this makes us reluctant to see them as satisfying (c), and so reluctant to count them as organisms.
<i>first/last living thing</i>	if in a lineage, can satisfy (a)–(c); if not, doesn't satisfy (b).
<i>individual sterile termites</i>	satisfy (b) despite their sterility, as well as (a) and (c), and so are organisms.
<i>a group of sterile bees</i>	do not satisfy (a), and so are not organisms, even if they satisfy (b) and (c).
<i>colonies of organisms</i>	satisfy (b), and in key cases (e.g., social insects), (c); if but only if they satisfy (a), this would justify the view that they are a kind of organism, superorganisms.
<i>higher level entities (e.g., groups, species)</i>	do not satisfy (a) and even satisfaction of (b) and (c) are likely to be contentious: they are lineage-based, biological individuals that are not living things.
<i>Gaia</i>	does not satisfy (b); defenders of Gaia hypothesis (Lovelock 1979 [1995], Doolittle 2017b) suggest that Earth satisfies (c) and, less obviously, (a).
<i>autocatalytic chemical reactions</i>	do not satisfy (b), and even though they share some of the properties in (a), do not satisfy (a).
<i>artificial life critters</i>	may satisfy a variant of (b) and perhaps even (c), but fail to satisfy (a) due to the simulational nature of the entities and their environments.
<i>humungous fungus</i>	satisfies (a)–(c), and so is an organism, but that status is jeopardized if there is lack of physical continuity and boundedness.
<i>coral reefs</i>	may satisfy (a) and (c), but not (b), and so are like Earth on the Gaia hypothesis.
<i>Adult vestimentiferan tubeworm + its symbiont gut bacteria</i>	may satisfy (a), but probably not (b) because worm and bacteria “do not reproduce as a unit” (Godfrey-Smith 2015, p.10122); there is a good case for (c) because the bacteria entirely overtake digestion from the adult worm.
<i>Hawaiian bobtail squid + its symbiont Vibrio bacteria</i>	may satisfy (a), but probably not (b) for the same reason as the tubeworm-plus-bacteria; in addition, there is a weaker case for (c) here than in the tubeworm case.

Table 1: Putting the Tripartite View of Organisms to Work

6. Finding Evolutionary Individuals in Conceptual Space

The discussion in sections 4 and 5 reflects the distinctive standing of organisms as physiological individuals, rather than simply being one kind of evolutionary individual amongst others. But it remains true that they are *also* evolutionary individuals and there is more to be said on recent thinking about this kind of biological individual. In this section, we focus on three authors whose work on evolutionary individuals has been influential and that considered together provides a thread through some of the ongoing debates here. In section 6.1, we elaborate further on Peter Godfrey-Smith's conceptualization of evolutionary individuals as Darwinian individuals; in section 6.2 we turn to the empirically-driven work of Joan Strassmann and David Queller on conflict and cooperation in evolutionary individuals; and in section 6.3 we examine Ellen Clarke's integrative philosophical work on the role of policing and demarcating mechanisms in defining evolutionary individuals.

6.1 Locating Particular Darwinian Individuals

Having seen how the category of living things fits into an organism-centred view of biological individuals, we can now readily add Godfrey-Smith's articulation of evolutionary individuals as Darwinian individuals to our running summary diagram. Although organisms such as finches are Darwinian individuals, so too are some parts of organisms (such as chromosomes) and some groups of organisms (such as a colony of eusocial insects), although neither is an organism. Figure 5 expresses these complexities to the conceptual space afforded by the organism-centred view.

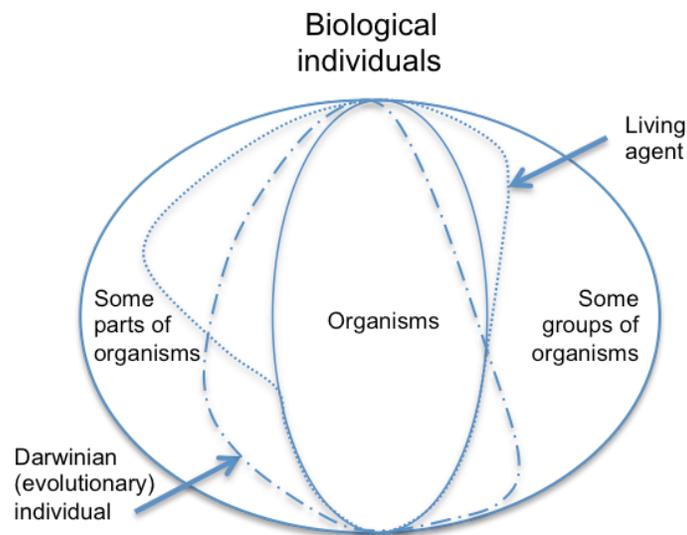


Figure 5: How Darwinian Individuals Figure in the Organism-Centred View of Biological Individuals

Figure 5 incorporates three other clarifications. The first concerns how the category of Darwinian individuals relates to that of living agent. Some *parts* of organisms that are not themselves organisms, such as some viruses, are both living agents and Darwinian individuals. But other parts of some organisms, such as hearts, lie within the living agent

category and *outside* the Darwinian individual category. At least some hearts are alive, but none reproduce or relate to reproducers in the manner needed for being a Darwinian individual, even though the separate genes that combine to code for heart construction may reproduce as needed. (For a good summary discussion of the complex issue of how different sorts of reproduction relate to evolution by selection, see Godfrey-Smith 2013.) Conversely, some other parts of organisms, such as the heart construction genes, are not living agents despite being Darwinian individuals.

A similar pattern is found when shifting to *groups* of organisms in Figure 5. Some groups, for instance some honey bee colonies, are Darwinian individuals even though they are not literally living agents; individual bees within a colony are each alive, but as can be inferred from discussion of living agency in Section 5, it is only in a metaphorical sense that the whole colony itself should be called a living agent. The converse type of case — a group of organisms that is a living agent but not a Darwinian individual — is more difficult to find. A coral reef may be an example. As we saw earlier, coral reefs don't feature the type of reproduction-involving life cycles that are characteristic of organisms. Some of the same facts about reproduction may disqualify them from being Darwinian individuals. Yet perhaps a case can be made for saying that some reefs are living agents.

The second additional clarification found in Figure 5 is more straightforward: there are biological individuals other than just Darwinian individuals. Many higher taxa are examples. Even the most optimistic of clade selectionists will probably agree that a relatively very inclusive and diverse taxon such *Bryophyta*, consisting of about 10,000 moss species, is not a Darwinian individual. Neither is such a taxon a living agent nor an organism. Yet assuming as some authors do that monophyletic clades are a type of biological individual, *Bryophyta* will nonetheless count as a biological individual because it is a monophyletic clade (De Luna, Newton, and Mishler 2003). (In Section 8 we return to the idea that some taxa are individuals.) *Bryophyta* thus belongs in the far right of Figure 5, outside all categories depicted except the umbrella category of biological individual. In addition to such groups of organisms that belong outside all but the umbrella category, there are many parts of organisms that also belong outside. A typical lysosome, for instance, is a biological individual without itself being alive, being an organism, or being a Darwinian individual. Hence it belongs to the far left in Figure 5.

The third and last clarification in Figure 5 returns us to more complicated issues. As the top-right side of the border for the Darwinian individuals category crosses into the organism category's area, it implies that some living organisms are not Darwinian individuals. We already saw in Section 3 (especially Figure 1) that Godfrey-Smith (2013), in addition to others, has discussed the example of the compound organism formed by two things: a Hawaiian bobtail squid plus its colony of *Vibrio fischeri* bacteria. Such authors judge this entity to be an organism because (using our terms) it seems to be a living thing, and to have minimal functional autonomy, the latter being due to the intricate integration between squid and bacteria (see Nyholm and McFall-Ngai 2004, and Bouchard 2010). But in our list of 22 examples in Section 5, we noted that this compound entity may not have the sort of life cycle needed to count as an organism on the tripartite

view. (Likewise for the preceding example in our list, the adult vestimentiferan tubeworm plus its symbiont gut bacteria.)

This may turn out to be mistaken, but it points to a potential tension in referring (as Godfrey-Smith does) to these as examples of things that are not Darwinian individuals but are organisms. If they do not enjoy a type of life cycle that features reproduction by them or their kind, this is a reason to leave them *out* of the category organism, not just out of the category Darwinian individual. Yet if we end up judging that their life cycle features the right sort of reproduction among at least some members, then that speaks in favour of their being *both* Darwinian individuals and organisms. The issue will turn partly on how exactly we distinguish different sorts of reproduction, and which sorts are required for evolution by natural selection, topics that have recently become more intensely debated (e.g., Godfrey-Smith 2015, 2016b, d; Griesemer 2014, 2016; O'Malley 2016).

Figure 6 further updates our running visual summary of the organism-centred view of biological individuals, with Figure 6a numbering some of the examples just discussed in Table 1, and Figure 6b locating those examples in the overall picture from Figure 5.

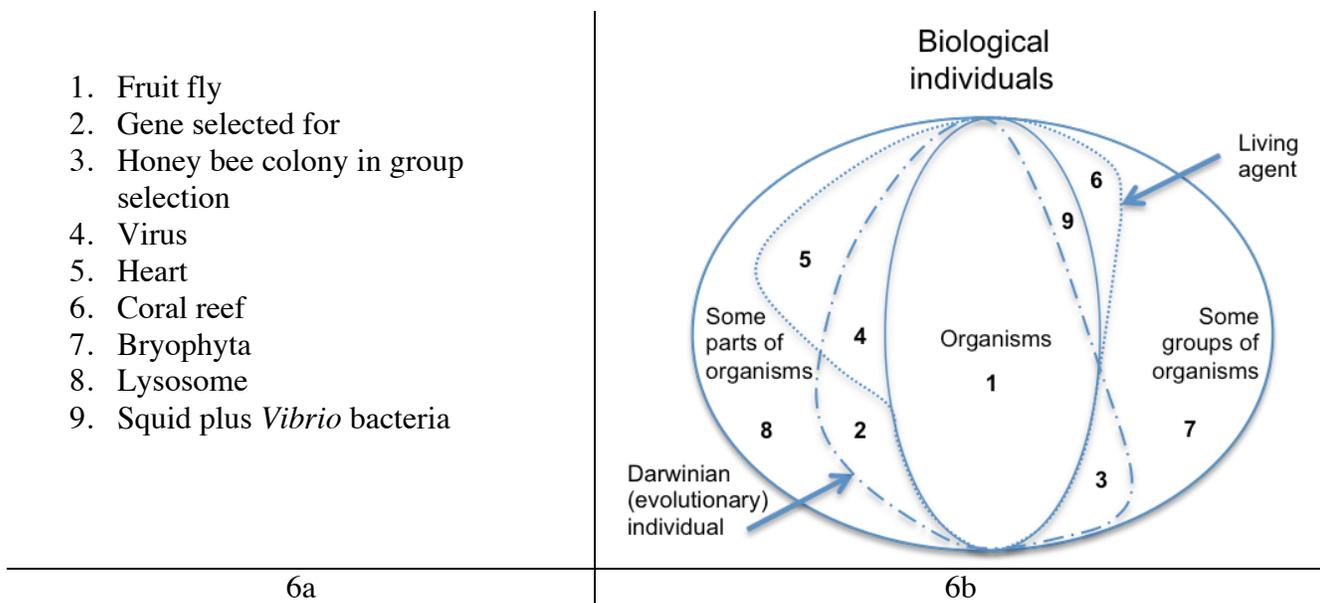


Figure 6: Identifying and Classifying Types of Biological Individuals

6.2. Conflict and Cooperation in Evolutionary Individuals

At the end of section 1 we suggested that in answering The Focal Question about biological individuals there is (and needs to be) an intimate interplay between the interpretation of empirical data and conceptual probing. David Queller and Joan

Strassmann (2009; see also Strassman and Queller 2010) provide one agenda for the empirical study of what they call “the evolution of organismality”, equating organism and individual here (see also Queller and Strssmann 2016). Queller and Strassmann begin from the claim that the definitive feature of organisms is the combination of high cooperation and low conflict between their parts (see also Folse and Roughgarden 2010 on organisms). Queller and Strassmann note both that these things are matters of degree and that one can vary independently of the other, and they use these parameters to define a two-dimensional space that represents a variety of biological individuals, as Figure 7 illustrates.

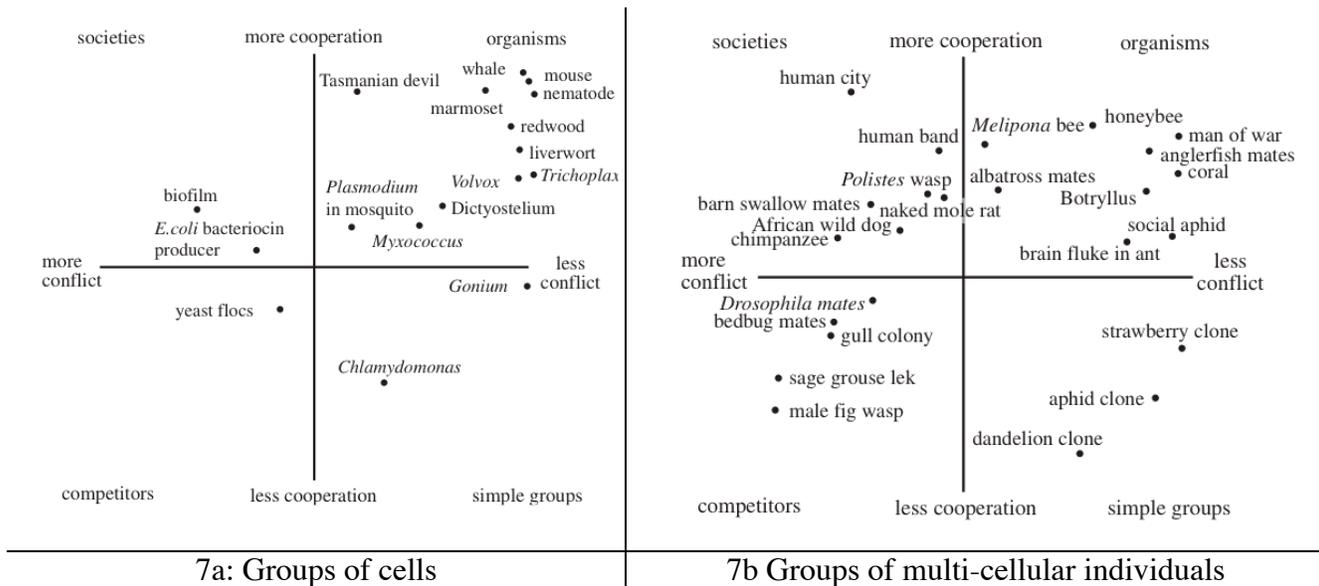


Figure 7: Varying Degrees of Conflict and Cooperation

(From copies of Figures 1 and 2 in Queller, David C. and Joan E. Strassmann, 2009, “Beyond Society: The Evolution of Organismality”, *Philosophical Transactions of the Royal Society*, 364: 3143–3155.)

To capture these ideas, it is useful to think of the feature that Queller and Strassmann believe is definitive of organisms as the *internal ratio*: internal cooperation/internal conflict. The higher this ratio is, the higher the degree of what they call organismality. Figure 7a indicates that, relative to other groups of cells, a mouse will have a relatively large internal ratio, while a yeast floc will have a relatively small internal ratio. Queller and Strassmann’s agenda to study the evolution of organismality would then be an agenda to study the evolution of relatively high internal ratios. But our discussion of ongoing work on autonomy and agency in section 5.3 indicates that some researchers would suggest supplementing this. Explicitly, the internal ratio considers only internal

matters, leaving out both external relations and the interaction between these and internal relations. Two added concepts can help remedy this.

One is an *immediate environmental ratio*: cooperation between things outside the candidate organism/conflict between things outside the candidate organism. Outside of the typical organism's boundaries, in its immediate environment, this ratio will be much lower than the organism's internal ratio. Indeed, such differences between the internal relations and those outside are probably lurking as unappreciated assumptions behind the concept of organism that Queller and Strassmann seek.

To capture those *differences*, one can turn to a type of *meta ratio*: internal ratio/immediate environment ratio. If the Spencer-Huxley emphasis on the interaction and relations between both internal and external that we met in section 5.3 is apt, then the meta-ratio does a better job than the internal ratio alone. The empirical agenda — what should be quantified, measured, compared, predicted — should then be updated to reflect this. The aim would be uncovering the evolution of relatively high meta ratios, not just high internal ratios. The development of such concepts may prove useful in fleshing out more details of what Godfrey-Smith (borrowing a term of Huxley's) calls the “movement of individuality” (2013:33). This refers to the ways in which new kinds of organisms evolve slowly, over geological time scales, from recurring collaborations between different types of Darwinian individuals. Such partnerships sometimes lead to new examples of paradigm organisms, but other times falter or stall at the mere collaboration stage with no new organisms at all.

In “the movement of individuality” over evolutionary time there is a sort of to-and-fro between the category *organism* and the category *Darwinian individual*. Further details on such processes could help advance recent discussions — motivated largely by empirical findings on the deep dependence relations between microbes and their hosts — about how to apply or revise our concepts of biological individuals when accommodating the importance of phenomena such as endosymbiosis and lateral gene transfer. We have seen how the work of Dupré and O'Malley, with its consistent emphasis on collaboration, the microbial world, and the importance of metabolism (Dupré and O'Malley 2007; Dupré and O'Malley 2009; O'Malley, Simpson and Roger 2013; O'Malley 2015), has suggested some radical rethinking about organisms, metagenomics, and the basic metaphors we use for conceptualizing life (Dupré 2012, Nicholson 2018, Nicolson and Dupré 2018). While the concepts of the holobiont and hologenome have been drawn on here, there is less consensus in the literature on the utility of these concepts than there is about Godfrey-Smith's concept of Darwinian individuals.

6.3 Policing, Demarcating, and Multiple Realizability

In effect, Queller and Strassmann have proposed a view of evolutionary individuals that is exclusively focused on the regulation of the parts of an evolutionary individual as a means to avoiding subversion from within. In a series of papers (Clarke 2010, 2012, 2013, 2016a, 2016b), Ellen Clarke has developed a more integrative view of evolutionary individuality that incorporates this regulative dimension, though like Strassman and

Queller she also has simply identified evolutionary individuals with organisms (e.g., 2013:413). Despite this equation and talking of biological individuals in general, Clarke's interest is very much on what we have been calling evolutionary individuals and individuality.

Clarke (2010) canvassed thirteen criteria that researchers have had good reason to draw on while characterizing biological individuals, and she issued a plea for some resolution between these competing criteria. In Clarke (2012), she focused on plant individuality, arguing that one should focus on the *mechanisms* that are causally responsible for constraining either sources of heritable variation (such as niche construction, bottlenecks, and polyploidy) or fitness differences mediated via the interactivity or the plant's parts (such as investment in root connections and the synchronization of flowering) (2012:351, 356). This trajectory to a more integrative view of biological individuality continues in Clarke (2013), which we will concentrate on here, where Clarke offers a specification of evolutionary individuals that departs from Godfrey-Smith's in various ways and that aims to provide something more like traditional necessary and sufficient conditions for being an evolutionary individual.

Clarke argues that a thing is (to use the term we have used) an evolutionary individual if and only if it possesses what she calls *policing* and *demarcating* mechanisms (2013:427). A policing mechanism "is any mechanism that inhibits the capacity of an object to undergo within-object selection" (2013:421), typically by decreasing the genetic variation between *parts* of an object. This decreases the chance that the object's parts will undergo selection that disrupts the integration of those parts. There is a sense in which demarcating mechanisms operate in just the opposite way. Rather than working to constrain or limit selective processes amongst an individual's parts, a demarcating mechanism "increases or maintains the capacity of an object to undergo between-object selection" (2013:424), doing so by promoting the variation (between objects) that fuels selection.

Clarke (2013:429) says that it is *what* these two sorts of mechanisms do that is important, not *how* the mechanisms do this in various ways. In other words, it is only the *functions* of the mechanisms that Clarke thinks are definitive, not the various *material* ways those functions are realized. As Clarke repeatedly stresses, this implies the multiple realizability of evolutionary individuals. This is to embrace the heterogeneity of the living world in one of the ways an organism-centred view of biological individuals does but without urging a pluralism so extreme as to lose sight of important commonalities across cases.

More distinctive of Clarke's view is that it (quite deliberately) exemplifies what Beckett Sterner has called a "thoroughgoing functionalism about individuality" (Sterner 2015:610) in the criteria that it homes in on, abstracting away from specific realizations of the functional roles of policing and demarcation. It thus contrasts with many other views of evolutionary individuals that are at least partly more materialist in claiming that because particular material realizations of mechanisms are so much more important than others, *those* realizations are essential to evolutionary individuals. Clarke notes, for

example, how Dawkins, Maynard-Smith, and Bonner imply that certain material bottlenecks are essential ways for policing to be realized in evolutionary individuals (Clarke 2013:418-419), how Ratcliffe and Kirk instead make material germ-soma separation essential (Clarke 2013:420), and how one might instead appeal to the essentiality of other material realizers of policing (Clarke 2013:422-423). Clarke's functionalism does not prioritize any of these material realizers over others; it is policing by whatever means, and demarcation by whatever means, that matters.

For this reason, Clarke has rejected the idea that the "bottleneck condition" is strictly necessary for being any kind of evolutionary individual, a condition she takes Godfrey-Smith (2009) to imply. Doing so marks the potential for agreement with Ereshefsky and Pedroso (2013, 2015), authors who defend the idea that multispecies *biofilms* are evolutionary individuals. A genetic bottleneck event is a narrowing between generations that is familiar amongst the metazoans of common sense, including our own species. Any human individual, for instance, is typically the product of such a bottleneck in developing from a single cell (a zygote) in which maternal and paternal genetic material is combined.

If we think of such bottlenecks as a mechanism for facilitating evolutionary novelty, as all three sets of authors here do, then we can look to identify alternative mechanisms, such as lateral gene transfer in the case of biofilms, that serve that function in contexts where the usual material bottlenecks are not present. This suggests one way of harnessing the insights of both pluralistic and monistic views of biological individuals, and Clarke uses her functionalism as a way to unify otherwise apparently discordant views.

This makes all the more interesting a way in which Clarke's view disagrees with those who have defended the idea that biofilms are evolutionary individuals (Clarke 2016a). On one hand, she operates with an inclusive, functionalist perspective on biological individuals. On the other hand, she finds that many of the important claims that underpin ascriptions of multicellularity to biofilms—such as that they are physiologically unified systems or contain cells that interact synergistically—are either not verifiable (e.g., they have higher-level adaptations) or are false (e.g., they display heritable variation in fitness). While Clarke's functionalism means that she remains open to Doolittle's (2013) suggestion that there may be some non-genetic form of heritability in biofilms, she takes the empirical evidence here to be indecisive (Clarke 2016a:202).

7. Groups as Biological Individuals: Superorganisms, Trait Groups, Species, Clades

Despite disagreements about how best to exactly characterize evolutionary individuals, and thus evolution by natural selection, many authors largely agree with the Lewontin-type gloss of evolution by natural selection that Section 3.2 summarized and exemplified by describing a finch population. And finches count as organisms on most views. Lewontin-type accounts have been long recognized to be individual-neutral in that things other than organisms can satisfy the conditions that enable the populations they form to

evolve by selection, something that preceding sections have already hinted at. In principle, selection can act on a large variety of entities, stretching from the very small (e.g., single base pairs) through to the very large (e.g., clades). But as a matter of fact the bulk of discussion that moves beyond preoccupation with organisms has focused on two such agents: groups “above” and genes “below” (Sober and Wilson 1998; Okasha 2007; Godfrey-Smith 2009; Haber 2013). Here we will concentrate on groups as biological individuals, providing a partial review of the levels of selection debate that served to motivate much of the initial work on biological individuals.

The term ‘group’ itself refers to collections of individuals of very different scales and kinds, ranging from temporary dyads of individuals (such as two crickets sharing a ride on a leaf, Sober and Wilson 1998), through to organisms that live together with a social division of reproductive labour (such as social insects), and higher-level taxonomic groups whose members are largely separated in space and time (such as planktotrophic mollusks, Jablonski 1986, 1987). Darwin himself appealed to group selection between “tribes” in explaining how moral traits involving self-sacrifice could evolve in human societies that differed with respect to such traits. But he offered no substantive discussion of the differences between these kinds of groups and the relevance of each for natural selection. It has only been with the revival of group selection, largely through the work of David Sloan Wilson (1975, 1977, 1980, 1983, 1989, 1997a,b) and his frequent collaborator Elliott Sober (Wilson and Sober 1989; Sober and Wilson 1994, 1998) that this question has received heightened attention (Lloyd 2005; Lloyd et al. 2005; Okasha 2007; Waters 2005; R. Wilson 2007).

One fundamental distinction here is between two sorts of groups. One is *superorganisms*, which are groups sometimes viewed as organisms as we saw above. The other is *trait groups*, which possess few of the characteristics that organisms have but nonetheless might be thought to function as organisms do vis-à-vis natural selection. Paradigm examples of superorganisms are colonies of social insects, e.g., *Hymenoptera* such as ants, wasps, and bees, together with the taxonomically distinct termites. Indeed, the term ‘superorganism’ was introduced by the entomologist William Morton Wheeler in his 1920 essay “Termitodoxa, or Biology and Society”, although he had talked of ant colonies as organisms as early as his 1911 essay “The Ant-Colony as an Organism”. Even though evolutionary considerations were often in the background in appeals to the concept of a superorganism, the concept has had a metaphorical life of its own in characterizing the intricacy of certain social structures of a small number of species.

By contrast, D.S. Wilson (1975) introduced the term ‘trait group’ specifically to name a type of group that he thought was pervasive in nature, and that could be a unit of selection just as individual organisms were. Thus, trait group selection came to represent a form of “new group selection”, contrasted with forms of group selection that were likely much more limited in their efficacy and prevalence.

The intuitive idea behind a trait group is that demes can feature evolutionarily relevant structure wherein organisms belonging to one part of the deme are subject to causal influences that do not extend to the deme as a whole. A population of such *structured*

demes would then function as a metapopulation, with natural selection operating between the trait groups that make up that metapopulation. Sober and Wilson have defined a trait group as “a set of individuals that influence each other's fitness with respect to a certain trait but not the fitness of those outside the group” (1998: 92; Basl 2011 raises important problems for this definition; also see McLoone 2015). This builds on D.S. Wilson's earlier talk (e.g., 1980: 20–24) of trait groups exerting a “sphere of influence”.

On this view of what a group is, how long a group persists is not necessarily relevant to its status as a group. What is crucial, rather, is that group members interact in some evolutionarily significant way, such as caterpillars feeding on the same leaf might. It is also strictly irrelevant whether the members of such groups are conspecifics, and this is one reason why D.S. Wilson has used the notion of a trait group to discuss the evolutionary dynamics of multispecies communities (e.g., D.S. Wilson 1980: ch.5–6). While we might describe such groups as evolutionary individuals or as individual units of selection, it should be clear that trait groups in general are not organisms because they are not themselves living things. They are made up of living things.

Kim Sterelny (1996) has invoked the distinction between superorganisms and trait groups to argue that group selection is a much less significant force in directing evolution than proponents of group selection have thought. The idea is that superorganismic group selection is real but found only in special cases, while examples we might describe as instances of trait group selection are better described as cases of genic or individual selection *relativized to a particular environment, where part of that environment is composed of other individual organisms*. In effect, this argues that Wilson and Sober have failed to identify a new form of group selection (trait group selection) since at best they have offered a way to *redescribe* how natural selection operates on individuals and genes. Together with skepticism about the notion of a trait group (Sober 2011), this amounts to denying the significance of trait groups for natural selection.

Sterelny's view that we can redescribe trait group selection without positing groups as the units of selection is an instance of a position that has been called *model pluralism* about the levels of selection, since it implies that there is a plurality of models that evolutionary biologists might adopt (R. Wilson 2003, 2005:ch.10). This view has gained much support, being defended in influential papers by Dugatkin and Reeve (1994) as “broad-sense individualism” and by Kerr and Godfrey-Smith (2002).

Paleobiologists and paleontologists have also explored higher-level selection with a focus on species and clade selection (Grantham 1995; and see Doolittle 2017a). Clades are monophyletic groups of organisms or species, groups defined by an ancestor and all of and only its descendants. Steven Stanley and Stephen Jay Gould have been two of the most prominent defenders of the idea that there are large-scale patterns of evolutionary change that are due to species or clade selection, and both have done so in part by explicitly developing an extended analogy between individual organisms and species (e.g., Stanley 1979: 189; Gould 2002: 703–744). Amongst putative examples of clade selection are the evolution of planktotrophic mollusks in the late Cretaceous (being selected for greater geographic dispersal and so longevity, Jablonski 1986, 1987), the

evolution of larger body size in males (selected via population density and geographic range, Brown and Maurer 1987, 1989), and the evolution of flowering plants (selected via vector-mediated pollen dispersal, Stanley 1981:90–91).

One of the chief threads to the continuing debate over species and clade selection parallels that over trait group selection and model pluralism. Are species or clades themselves really the agents of selection, the units that are being selected, or do they simply tag along for the ride, with selection operating exclusively on component things such as organisms and genes? Elisabeth Vrba (1986, 1989; and see Vrba and Gould 1986), for example, has distinguished between species *sorting* and species *selection*, arguing that while a sorting of species may be the product of evolution by natural selection (see Barker and Wilson 2010), this outcome is typically brought about not by species selection but by individual selection.

Although we have concentrated on groups and the levels at which natural selection operates in this section, it would be an oversight to remain silent on an idea about species that has become influential in the literature: that species themselves are individuals. Historians have discussed the extent to which past biologists such as Buffon (via his *sterility criterion* of species), and philosophers such as Hegel (through his conception of concrete universals), helped generate and facilitate this view (Stamos 2003). But the species-as-individuals thesis did not flower until Ghiselin (1974) argued for it and quickly converted David Hull (1976, 1978) to the idea (see also Ghiselin 1997). Levels of selection considerations were only a periodic and small part of the motivation for the thesis. Rather the thesis developed as part of a response to the perceived failure of essentialism about species (Barker 2013b, Sober 1980), reflecting the way in which species were treated within systematics and evolutionary biology not as kinds but instead as spatiotemporally restricted *lineages*, with individual organisms as their physical parts (Ereshefsky 1992, Wilson 1999a, 1999b).

The species-as-individuals thesis was originally presented and seen as making a radical break with previous views of the ontological status of species, as it implied that biologists and philosophers alike had misidentified the basic ontological category to which species belonged. But over time, both as its proponents have clarified what the thesis implied (e.g., gravitating to talk of historical entities rather than individuals) and as more sophisticated options for defenders of the view that species are kinds were developed (e.g., the HPC view of kinds discussed in section 5), this radical edge to the thesis has diminished. A now widely accepted insight clarified in the process is that in the case of many species, organisms belong to them (as parts or members) by virtue of their interactions and their extrinsic rather than intrinsic properties (Barker 2010; cf. Devitt 2008). Whether this combats (or instead exemplifies) what the historian James Elwick has recently called “resilient essentialisms” (Elwick 2017; cf. Hull 1965) remains contentious.

Finally here, Mariscal and Doolittle (2018) have recently adapted a version of this view to suggest that all of life, i.e., the Last Universal Common Ancestor and all of its descendants, is a biological individual in the sense in which Ghiselin and Hull argued that

species were. They take life to be “a monophyletic clade that originated with a last universal common ancestor, and includes all of its descendants.” (2018: abstract). Complementing this is their adaption of Ereshefsky’s eliminative pluralism about living things as a kind, arguing that we should be eliminativists about living things as some kind of natural kind. We suspect that discussion of this radical proposal could be profitably informed by reflection on the older literature on species here (R.Wilson 1999b, Barker in press).

8. The Evolution of Biological Individuality

We noted in section 3.1 that much of the impetus for thinking about biological individuals stemmed from work on the evolution of individuality (Dawkins 1982; Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1999), a topic that continues to be of lively interest (Okasha 2011; Calcott and Sterelny 2011, Bourrat 2015, Clarke 2016b, O’Malley and Powell 2016, Queller and Strassman 2016, Herron 2017, Sterner 2017). The starting point here, also seen in section 3.1, is the idea that the history of life is the history of the construction of more complicated biological individuals from simpler individuals, with natural selection (operating at one or more levels) facilitating the transitions between these individuals. Underlying these ideas is the assumption that many or all biological individuals are hierarchically organized: earlier individuals provide the material basis for later individuals. For example, prokaryotes, which are single-celled organisms without a nucleus, form the material basis for single-celled eukaryotes, which are organisms that do have a nucleus; in turn, single-celled eukaryotes serve as the material basis for multicellular eukaryotes.

The evolution of biological individuals from prokaryotes to single-celled eukaryotes around 2 billion years ago, and from those to multicellular eukaryotes in the last 600–800 million years, are established facts. In addition, there appear to be no counter-examples to this evolutionary trend. Yet speculation and controversy surround almost everything else that has been said about these evolutionary transitions. Consider three such issues on which there is a sort of default position in the literature that remains subject to ongoing philosophical and empirical interrogation.

First, it is common to view the evolution of individuality itself as the evolution of complexity. There are, however, questions both about how complexity itself should be measured or conceived and about what empirical evidence we actually have for viewing the complexity of individuals as increasing over evolutionary time (McShea 1991). Do we consider the number of cell types that an organism has (Bonner 1988), the types of hierarchical organization it manifests (Maynard Smith 1988), or some more taxa-specific criterion, such as the information required to specify the diversity of limb-pair types (Cisne 1974)? Fossils constitute a principal source for the criteria that have been proposed here. Yet different kinds of organisms leave fossils with distinct kinds of features, and some kinds of organisms are more likely to leave fossils than are others.

One natural suggestion is that there may well be different kinds of hierarchies for the evolution of individuality, since kinds of individuals can differ from one another in more

than one way. Daniel McShea (2001a, b; McShea and Changizi 2003) has proposed a structural hierarchy that is based on two components, the number of levels of nestedness and the degree to which the highest individual in the nesting is individuated or developed. McShea provides an overarching framework in which we can view eukaryotic cells as evolving from differentiated aggregations of prokaryotic cells that have intermediate parts; multicellular eukaryotes as evolving from differentiated aggregations of single-celled eukaryotes; and colonial eukaryotes as evolving from differentiated aggregations of multicellular eukaryotes.

By contrast, Maynard Smith and Szathmáry (1995) focus on differences in how genetic information is transmitted across generations, proposing eight major transitions in the history of life. These start with the transition from replicating molecules to compartmentalized populations of such molecules, and end with the transition from primate societies to human societies. While Maynard Smith and Szathmáry are interested in individuality and complexity, their eight transitions do not form a continuous, non-overlapping hierarchy. Their discussion is focused primarily on exploring the processes governing each of the particular transitions they propose in terms of changes in replicative control. O'Malley and Powell (2016) have recently argued that not only does this perspective omit critical events – such as the acquisition of mitochondria and plastids, in what those authors prefer to think of as turns rather than transitions in the evolution of living things – but also that we need a “supplementary perspective that is less hierarchical, less focused on multicellular events, less replication oriented, and in particular, more metabolic” (2016:175).

Second, it is common to view the trend from prokaryotes to multicellular eukaryotes as resulting from some type of directional bias, one that makes the trend a tendency supported by underlying mechanisms and constraints. Perhaps the tendency is underwritten by thermodynamic, energetic considerations, by facts about the generative entrenchment of developmental systems (Griffiths and Gray 2001), or by evolutionary advantages of increases in size (McShea 1998). But in supposing that there is some type of directional bias, each of these hypotheses might be thought committed to the sort of Panglossianism about adaptation that Gould and Lewontin (1978) are famous for critiquing, or (more subtly) to a view of evolutionary change as progressive or inevitable in some way. Gould has used his discussion of the Burgess Shale (Gould 1989) to challenge such views of evolution, arguing that the disparity of the fossils in that shale indicates that living things are significantly *less* different from one another than they once were. Gould argues that the range of biological individuals we see now on the planet is largely the result of highly contingent extinction events, and we should be wary of immediately assuming that observed trends or patterns are adaptive (or other) tendencies.

Third, many authors have recognized that whatever trends or tendencies there are in the evolution of individuals, there have also been changes over evolutionary time in the social relations between individuals (e.g., Frank 1998), and in the sorts of shared resources that are available to the biological individuals that Douglas Erwin has recently discussed while drawing on the economic concepts of *public goods* and *club goods* (Erwin 2015, McInerney and Erwin 2017). Yet how we should integrate sociality into

our view of the evolution of biological individuals remains under-theorized (for a recent exception, see Birch 2017). And however limited fossil evidence for individual structures and ecological niches may be, such evidence for the kinds and extent of sociality is significantly more sparse. Much of the work to be done here seems distinctly philosophical in that it concerns how we think about what sociality is. Should we consider the simple aggregation of organisms to be a basic form of sociality? Does sociality essentially involve some form of cooperation, and if not, what is the relationship between “prosocial” sociality and antagonistic forms of sociality (e.g., competition or predation)? Although the “evolution of sociality” has been taken up by animal biologists (especially by primatologists) and evolutionary anthropologists (where it is often viewed game-theoretically), this has served to reinforce a view of sociality that seems somewhat narrow, e.g., the view is not clearly applicable to structurally simpler organisms. Perhaps we need to take seriously the idea that sociality is not a relatively recent addition to multicellular life but a more sweeping feature of many if not all biological individuals, and that the evolution of individuality is to be understood in tandem with the idea of changing, shared, public and club goods, making for a more dynamic and cyclical view of the history of life.

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