

Biological Individuals

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How we should think about biological individuals and the roles they play in processes such as natural selection, speciation, and organismic development are lively topics of discussion in the philosophy of biology, discussion that has advanced significantly over the past ten years. Individual organisms have been central to philosophical reflection on such processes, but they are not the only type of biological individual or agent. For example, both genes and groups have been considered kinds of biological individual (e.g., as units of selection). And some propose that genomes are biological individuals or agents that code for organismal development. Focusing on organisms as one important kind of biological individual sheds substantial light on what biological individuals are. But to address broader questions about the biological world and how we think about it, we also need to reflect on the relations between organisms and other kinds of biological individuals.

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1. Introduction

An untutored but attentive survey of almost any part of the biological world reveals an incredibly diverse variety of individuals. At ground level we see ants, beetles, moles, marmots, alligators, ivies, mushrooms, algae blooms, and ostriches. Through magnification, we see or infer flagella-propelled protists, tRNA molecules, prions, and bacteria of many kinds. At larger or collective scales, we can find herds of zebra, sweeping and astonishing coral reefs, biofilms made up of many different species of organism, and even fungus complexes several hectares in area and with masses greater than an elephant's.

Each of these entities is a candidate biological individual, and each has been treated as such in the biosciences as they attempt to discover generalizations, provide explanations, and make predictions about the biological world. Amongst biological individuals, organisms are the most prominent in common sense. Their central place in discussions of biological individuals is reflected in sections 2-6 below, with sections 7-9 respectively going beyond organisms to groups, genes, and the evolution of individuality.

Given our everyday familiarity with organisms, it proves surprisingly difficult to specify exactly what it is to be an organism, let alone a biological individual. Intimate interplay between empirical data gathered by biologists, and the conceptual probing that both they and philosophers of biology offer, characterize explorations here. Consider two examples.

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 (J. Wilson 1999: 23–25). They used these 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, “members of the fungal kingdom should now be recognized as among the oldest and largest organisms on earth” (Smith, Bruhn, and Anderson 1992: 431). A number of other scientists have questioned whether this final claim about the organismal status of the humungous fungus is warranted, and some have argued 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 biological individuals. 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.

Consider a more elaborately described example (Turner 2000: ch.2). Despite rapidly becoming a thing of the past due to the climate changes associated with global warming, coral reefs are spectacular and beautiful parts of the living world. They consist 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, consisting of the polyps *and* deposits, as living things that can grow and die.

The reefs are at least biological individuals; 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. The dependence of the reefs on 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). And 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 (cf. also Combes 2001).

Again, knowing what to say about this striking claim turns in part on the empirical facts, but on more than just those. Polyps, zooxanthellae and reefs do not wear placards that state which is the better example of an organism. Knowing what to say about this case also turns on our conception of an organism. The interplay between our conception and empirical complexities both allows us to unpack our conceptions and informs how we might regiment them to better capture nuances of the biological world inaccessible to commonsense reflection alone.

The literature addressing these issues has recently grown rapidly. The selectivity this necessitates in our coverage here is guided by a central question: *what are biological individuals?* To address this and related issues, works whose influence is well-established and that are especially representative or instructive will be discussed in detail rather than giving briefer overviews of works whose influence is still emerging. And the following issues that may interest some readers will fall mostly outside of our purview: metaphysical issues about whether some or all biological individuals are physical objects (van Inwagen 1990) or processes (Whitehead 1929; Dupré 2012; cf. Barker 2013a) or something else, and about whether such individuals exist at all (Unger 1980; French 2016); epistemological issues about how to detect individuals, their features, and the relationships into which they enter (Hacking 1982; Godfrey-Smith 2016a); methodological issues about how we should make use of theoretical vs. experimental work (e.g., Quine 1948; Hull 1992; Chen 2016; Love and Brigandt 2017), historical work (e.g., Nyhart and Lidgard 2011; Lidgard and Nyhart 2017a), and work from non-biological sciences (e.g., French 2016; Patternote 2016) and other areas of philosophy (e.g., Chauvier 2016; Guay and Pradeu 2016a; Haber 2016; Lowe 2016), when studying philosophical dimensions of biological individuals; and ethical issues about whether biological individuals have moral status by virtue of being alive (Varner 1998).

2. The Problem of Biological Individuals

We call our focal question – what are biological individuals? – *The Problem of Biological Individuals* and treat the following questions as roughly equivalent to it:

- 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’?

These questions are similar to, but broader than, what Ellen Clarke (2010, 2012) calls *the problem of biological individuality*, where she focuses just on one type of biological individual, evolutionary individuals.

Responses to The Problem of Biological Individuals should clarify what relationship(s) hold between the category of biological individuals and the related categories of living thing, organism, physiological or evolutionary individual, and so on. For example, are biological individuals just organisms? Is there a nesting or some other hierarchical relationship between biological individuals and living agents? Explicit recognition of the need for the integration of philosophical and historical perspective on the problem of biological individuals (e.g., Lidgard and Nyhart 2017a, Lidgard and Nyhart 2017b, Nyhart and Lidgard 2011) is likely, in our view, to enhance the richness of responses to the problem (see also Guay and Pradeu 2016b).

The semantic decisions to be made about how the involved terms will be used should be assessed in part by the plausibility of the implications they hold for scientific methodology, evidence judgments, and prediction and explanation, as biologists themselves sometimes emphasize (Queller and Strassmann 2009, p.3152, Pepper and Herron 2008, p.625). To take a simple example, suppose someone proposes to equate evolutionary individuals (also called units of selection) with organisms. Measuring fitness values to help predict trait frequencies of populations of evolutionary individuals in the future would then involve counting just all the relevant organisms. This methodology will produce misleading predictions and evidence judgments about the course of natural selection, however, if groups (in some contexts) or genes (in other contexts) are also (even if infrequently) evolutionary individuals, as many have argued. Detecting the poor predictions or judgments would then tell against the initial equation between evolutionary individuals and organisms (see also Godfrey-Smith 2013, Clarke 2013, pp.413-418; cf. Kovaka 2015).

Taking *biological individual* as a quite general category that may subsume several kinds of biological individuals (e.g., evolutionary, developmental, living things, and others), we find it useful to distinguish two aspects of The Problem of Biological Individuals. The first concerns individuals in general—what it is that makes anything an individual of *any* kind (e.g., Strawson 1959; van Inwagen 1990; Chauvier 2016; French 2014; Lowe 2016; Wiggins 2016). The second aspect concerns biology in particular—what it is that makes an individual *biological* rather than, say, chemical or sociological.

Consider the first aspect of The Problem of Biological Individuals. When philosophers of biology discuss individuals they typically understand individuals to be distinct from other entities such as properties, processes, and events, even if certain (say) properties and processes are constitutive of some forms of individuality (cf. Dupre and O'Malley 2007). 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.

A further feature often associated with individuals is *agency*: minimally, a typical individual is a locus of causation, as are electrons in physics and molecules in chemistry (R.A. Wilson 2005). The sense in which biological individuals are agents is compatible with their playing a more passive role in biological processes, or with their functioning as products rather than as causes of the evolutionary processes in which they're involved. For instance, this notion of agency allows that some species and even larger clades (Doolittle 2017a) and perhaps whole ecosystems (Currie 2011; Eliot 2011; Leibold et al. 2014) are biological agents.

This deflationary notion of agency is weaker and less controversial than the notion of agency that Peter Godfrey-Smith (2009) has challenged through his critique of rationalizing and optimizing approaches to explanation within evolutionary biology, approaches exemplified by Dawkins' (1976 [1989]) classic appeal to selfish genes. In fact, the conception of agency that we draw on is compatible with recognizing that the vast majority of biological agents are not psychological agents at all. It remains an interesting question as to why the use of *cognitive metaphors* in describing biological agency is widespread, if not ubiquitous (R.A. Wilson 2005: ch.4–6; Godfrey-Smith 2009; Dennett 2012). 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; Kitcher 2001), and whether biological agency and reality can come in degrees (Child 1915; Conklin 2016; Sober 1991; Pepper and Herron 2008; Queller and Strassmann 2009; Godfrey-Smith 2009, 2013; Clarke 2012).

Consider now, in light of this, the second aspect of The Problem of Biological Individuals: with individuals understood as agents in our sense, what makes for distinctly *biological* individuals? We have already suggested that while there are many different kinds of biological individual, organisms have loomed large in how biologists and philosophers of biology have conceptualized biological individuals. Consider two recent challenges to this privileging of organisms in discussions of The Problem of Biological Individuals:

- 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 alive (Dupré and O'Malley 2009).

- B. Far from being *paradigmatic* biological individuals, organisms may be marginal or unusual special cases of biological individuals (Haber 2013).

We next introduce a framework for addressing the The Problem of Biological Individuals, heeding what is uncontroversial in these challenges to the privileging of organisms. The framework is also useful for considering much of the recent work on biological individuals (see sections 4-6).

3. Organism-Centred Views of Biological Individuals

Although simply equating organisms with biological individuals or with living agents would be a mistake (Pradeu 2016a, Pradeu 2016b), a more nuanced sort of organism-centred view is, we think, defensible (cf. Jagers op Akkerhuis 2010). On this 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 populations and aggregates of bacteria).

We call this an *organism-centred* view because each of its three parts references organisms (cf. 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 recent proposals to extend the term ‘organism’ to both some parts and groups of organisms (e.g., Queller 1997; Okasha 2011). In section 7 we turn to more explicitly consider certain groups of organisms, such as superorganisms, and in section 8 certain parts of organisms, such as genes, that have sometimes themselves been conceptualized as biological individuals or agents.

To see how this organism-centred view captures something striking about organisms without running afoul of challenges [A](#) and [B](#), take those challenges in turn. [A](#)’s challenge to 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 an 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 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 1 offers an initial summary of the organism-centred view of biological individuals described thus far (cf. also the figures in Pradeu 2016b). Figure 1a indicates how such a view in one sense *shrinks* the importance of organisms, by showing how organisms are just one among potentially many other types of biological individual. Figure 1b adds depiction of the further claim that even non-organism biological individuals will either be parts of organisms or groups of organisms, thereby *enlarging* the importance of organisms in another sense. Sections 4-6 below will take up ongoing issues in the literature, and our discussions there will allow us to further elaborate the initial visual summary offered by Figure 1.

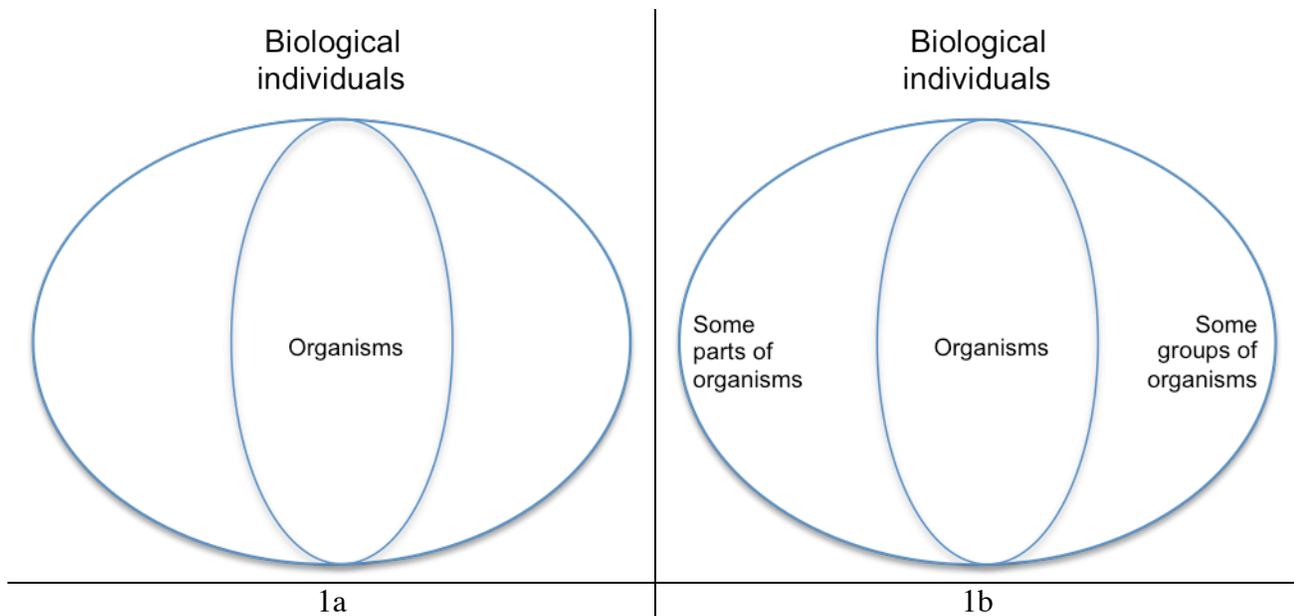


Figure 1: An Organism-Centred View of Biological Individuals. Each biological individual is an organism, a part of an organism, or a group of organisms. Note that these alternatives are not

mutually exclusive. For example, a particular 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; in addition, some groups of organisms, such as “superorganisms”, may also be organisms.

Minimally, elaborating this view involves specifying which *parts* and which *groups* of organisms are biological individuals and which are not. Elaboration should also provide an account of what an organism is. To proceed, it is useful first to reflect on the related diversity or heterogeneity of the living world.

4. Biological Heterogeneity

In this section we make two points about the *variety* of biological individuals that we emphasized at the outset. The first is that this diversity exemplifies a key difference between biological categories and many other categories. The second is to explain the basic contrast between pluralist and monist responses to the heterogeneity distinctive of biological categories and to illustrate how they can be viewed as complementary.

To begin with the first point, consider that biological categories other than just *organism* also feature striking diversity. The categories *evolutionary individual*, *developmental individual*, and taxonomic categories such as *Homo sapiens*, are also, for instance, highly internally diverse. Such diversity has been labeled *intrinsic heterogeneity* because it seems part-and-parcel—as well as distinctive—of those categories or kinds and how they are theorized in the biological sciences (R.A. Wilson 2005: ch.3).

Intrinsic heterogeneity is manifest most clearly in the centrality of *population thinking* in evolutionary biology. Natural selection acts on variation within a population of individuals. As Elliott Sober influentially argued (1980), in the physical sciences and in pre-Darwinian biology variation was understood as deviation from a natural or normal state, whereas in the post-Darwinian era, and especially through the Modern Synthesis, researchers came to view variation as prodigious and itself crucial to the underlying causal mechanisms at the heart of biological stasis and change. Rather than being explained away, variation goes all the way down and itself plays an explanatory role.

Intrinsic biological heterogeneity isn't restricted to *evolutionary* biology. The geophysicist Walter Elsasser drew this out long ago in his *Atom and Organism* (1966), with his contrast between physical and biological kinds (see also Elsasser 1975, 1998). Roughly, the chief idea is that if you've seen one electron (or quark or boson) you've seen them all. Although there are differences between instances of any two individuals (in accord with Leibniz's Law), these are differences that do not matter for physical kinds. Physicists and chemists abstract away from such differences, treating any instance like any other. This is not so in the biological sciences. If you've seen one tiger (or vertebrate or coral reef) you have *not* seen them all, for there are differences between instances of any of these biological kinds that remain significant—in some cases, central—for the articulation of biological knowledge.

We find intrinsic heterogeneity throughout the biological sciences. In ecology, heterogeneity is manifest in mechanisms of competition and cooperation between species. In developmental cell biology, it is manifest in the diversification of cell types in accord with cellular environment and the timing of their movement and cell division. In genetics, we see so many different sorts of genes that we struggle to say what ‘gene’ should mean. Biological heterogeneity complicates attempts to more precisely specify what it is to be an organism or a biological individual.

This moves us to the second point of this section: there is much convergence between pluralist and monist responses to biological heterogeneity, despite their different starting responses to biological heterogeneity.

Pluralists often respond to the difficulty that intrinsic heterogeneity presents for characterizing some kind K by moving on to characterize finer-grained, more determinate kinds (Barker in press): if K seems too diverse to characterize, split it into diverse sub-kinds and characterize each of those. Jack Wilson has done this where K = biological individual, as he moves beyond this to characterize *genetic*, *functional*, and *developmental* individuals (1999, 2000). And famously, John Harper invoked pluralism where K = plant, by introducing the more particular kinds *ramet* and *genet* as replacements for 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.

Monistic responses to intrinsic heterogeneity typically retain a focus on more general or course-grained categories. But it is often overlooked that this focus is usually compatible with, even complementary to, the pluralistic focus on finer-grained categories (Brigandt 2009, Barker in press). Monists can quite happily recognize as correct, useful, or legitimate, multiple categories that result from splitting K , while still attempting to elucidate K as an important umbrella or genus category, or even a less neatly related category. Splitting the category *tools* into *hammers*, *saws*, and others doesn’t thereby impugn *tools* as a category. (For readers seeking more on pluralism and monism here, see Barker 2013a; Chen 2016; Clark 2010, 2013; Dupré 2007; Dupré and O’Malley 2010; Guay and Pradeu 2016b; Haber 2016a; Lidgard and Nyhart 2017a, pp.18-23; Pradeu 2016a, b; J. Wilson 1999; R.A. Wilson 2005.)

The dialectic between Peter Godfrey-Smith and Mark Ereshefsky and Makmiller Pedroso over Godfrey-Smith’s “bottleneck condition” illustrates our point about the complementarity of pluralism and monism here. Ereshefsky and Pedroso (2013) interpret Godfrey-Smith (2009) as implying a certain necessary condition on being what he calls a *non-marginal evolutionary individual*: to qualify, a thing must be the product of a significant genetic bottleneck event. A genetic bottleneck event is a narrowing between

generations. 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.

Ereshefsky and Pedroso propose that *biofilms* are a counterexample to this necessary condition on being a non-marginal evolutionary individual: biofilms are non-marginal evolutionary individuals despite not satisfying the bottleneck condition. Ellen Clarke (2013) has also argued against the necessity of the bottleneck condition.

A pluralist might accept this as a counterexample, then consequently move from *non-marginal evolutionary individual* to two even more fine-grained concepts, one associated with genetic bottlenecks and the other with cases like biofilms. But an ecumenical monist can simply recognize the multiple realizability of non-marginal evolutionary individuals, a point that Clarke (2013) has elaborated on. This is an attractive option when there is some good theoretical reason for retaining the initial concept. Godfrey-Smith had argued for the bottleneck condition on the basis that non-marginal individuals are the kinds of things that form populations in which selection can produce evolutionary novelty. Production of such novelty is important enough, he contends, that whatever mechanism enables this should count as a constitutive factor (one satisfied to degrees) of being a non-marginal evolutionary individual.

We can agree with both this *and* Ereshefsky and Pedroso's insistence that bottlenecks are not the only novelty-creating mechanism. They are not the only such mechanism because biofilms enjoy novelty creation by *lateral gene transfer* rather than bottlenecks.

What is right about pluralism here is that there are at least *two* distinct mechanisms rather than one. What is right about monism is that the two mechanisms play the *same* theoretically important role—helping generate evolutionary novelty. This role helps distinguish the concept of non-marginal evolutionary individual that the monist retains as theoretically important, while encouraging pluralist exploration of distinct mechanisms.

In Section 5 we elaborate on a view of organisms called *The Tripartite View of Organisms* (R.A. Wilson 2005, ch.3-4) that extends our framework for discussing biological individuals. This view of organisms helps to clarify points that pluralists and monists find important, while framing these in complementary ways. It draws on the more general *Homeostatic Property Cluster* (HPC) view of kinds (Boyd 1999a, b; Griffiths 1997, 1999; R.A. Wilson 1999), which has been widely discussed with respect to biological species (Ereshefsky 2007; Ereshefsky and Matthen 2005), but also introduced in accounts of higher taxa (Assis and Brigandt 2009), homology (Rieppel 2005a, 2005b, 2007), and cell types (Wilson, Barker, and Brigandt 2007). Accepting that the take-home message of Elsasser's point about biological heterogeneity is that heterogeneity should be captured rather than overcome within one's metaphysics, the HPC view responds with naturalistic humility: when empirical work repeatedly reveals intrinsic heterogeneity, change your philosophy of kinds to accommodate this.

5. The Tripartite View of Organisms and HPC Kinds

At the core of The Tripartite View is the explicit claim that organisms are a type of *living thing* (or individual or agent), and the implicit claim that this kind is central to the biological sciences. Organisms are additionally distinguished from other living agents by two further properties: belonging to a certain sort of reproductive lineage, and having a certain type of autonomy. In summary, 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, which
- b. belongs to a reproductive lineage, some of whose members have the potential to possess an intergenerational life cycle, and which
- c. has minimal functional autonomy of the relevant kind.

To explicate the view further, consider each of these three features in turn.

Like other biological kinds, *living agent* is an HPC kind and so we give ‘living agent’ an HPC definition. By ‘definition’ we mean something more interesting than do some authors who are cynical about definitions of ‘living agent’ (e.g., Cleland 2012). We mean a summary of a fuller theory about the nature of living agency. Empirical facts and findings continually inform such a definition and to see what a good definition might look like consider the following structural, functional, and relational properties possessed by living things. 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.

The fundamental, general feature of HPC views of kinds concerns how an HPC kind term is defined by appeal to a cluster of properties rather than any one property. No one property in the definitive cluster need be possessed by any individual belonging to the kind, but each individual must have one of the n -tuple of properties in the cluster that is sufficient for belonging to the HPC kind. What features or implications of the HPC view of kinds are important for understanding its application to the case of living things?

First, defining a kind term by reference to a property *cluster*, rather than a single property, as HPC views do, acknowledges a complexity to the structure of entities that fall under the biological kind *living thing*. While the view allows that there may (though needn’t) be some properties in the defining cluster that all living things share (e.g., metabolism), it resists the idea that even these properties are profitably thought of as essential to the kind.

Second, implying that no one of the properties in a given definitive cluster is strictly necessary for an individual to belong to the corresponding HPC kind recognizes the intrinsic heterogeneity of entities subsumed under *living thing*. For instance, this accommodates biological individuals that don't reproduce (e.g., sterile organisms), or that stop growing, or that malfunction so as to lose the capacity for self-repair as living things, and so on.

Third, the HPC view leaves open that there is much of interest happening outside the coinstantiation of properties that form a definitive cluster; the view isn't just about the cluster. Rather, coinstantiation of properties in the cluster is reliably underwritten by specific causal mechanisms and constraints that *underlie* the cluster (Wilson, Barker, and Brigandt 2007, p.200). This underwriting gives definitive clusters their homeostatic character, and ensures 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 categories for thinking about the world, thus distinguishing 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).

Suppose that organisms are living agents, and that we accept the HPC view of living agency. This tells us something significant about what organisms are. But as Section 3 suggested, it would be a mistake simply to identify organisms with living agents. Doing so would have problematic implications, chief among them being the false claim that *only* organisms are living agents.

The view that *only* organisms are living things appears subject to a range of decisive counter-examples: entities that form parts of organisms. These include cells and the organelles they contain (such as mitochondria and ribosomes), bodily organs (such as the heart or kidney), and perhaps even bodily systems (such as the digestive system or the circulatory system). Such entities have the structural, functional, and relational properties specified in the HPC definition given above, but they are not themselves organisms. Closest to our commonsense thought is the second of these, where we readily speak of an organ that is available to be transplanted, from a dead person to living recipient, as living or alive. Cells are conceptualized in much the same way, with certain diseases leading to the death of particular cells, or treatments of those diseases as succeeding just when they preserve the life of those cells. This is not simply a matter of how we speak or think about such parts of organisms, but of medical practice and legal policy, each imbued with normative, action-guiding consequences that turn on the status of these biological entities as living things.

This allows us to add to the visual summary we introduced with Figure 1 in Section 3. Figure 2a shows where the earlier summary left off, while Figure 2b adds how the category *living agent* relates to both *organism* and *biological individual*. (Please bear with the irregular geometry of the added line, which will allow us below to properly make further additions.) In Figure 2b we see 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 complex).

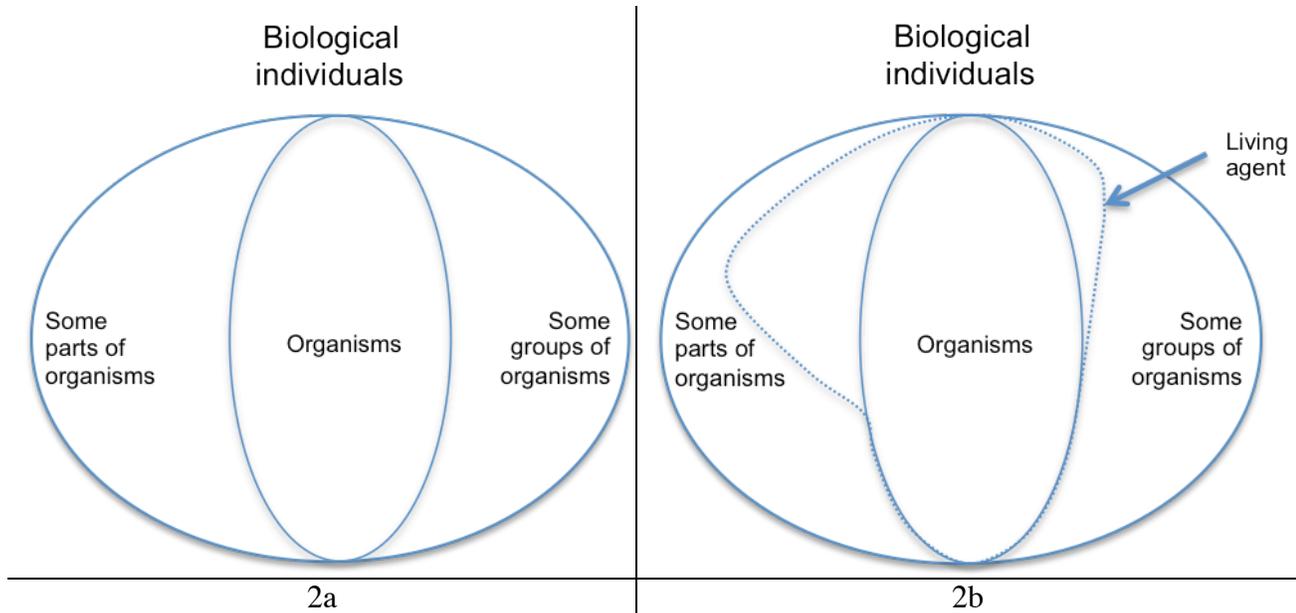


Figure 2: How Living Agents Figure in an Organism-Centred View of Biological Individuals

So organisms are a kind of living thing. The next distinguishing feature of organisms according to The Tripartite View, something that helps separate organisms from other living things, is that they have *life cycles* that allow them to form reproductive lineages of a certain kind. 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. A. Wilson 2005).

A life cycle is an intergenerationally replicable series of events or stages through which a living agent 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. And while the stages themselves often form standard sequences, there can be tremendous variation across phyla in what a given organism's life cycle consists in, as others have emphasized (Buss 1987; Godfrey-Smith 2009, O'Malley 2016). Some organisms, such as flukes, have life cycles that take them literally through one or more host organisms, and many insects undergo significant metamorphic changes in bodily form through their life cycle.

Intergenerational life cycles make it possible for organisms to form reproductive *lineages* of living things. Such reproductive lineages are one of the most impressive and causally potent features of the biological world. Although reproduction itself has sometimes been thought of as part of an organism's 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. Yet 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 example.

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 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 (R. A. Wilson 2005).

On The Tripartite View, the third distinguishing feature of organisms is that they have a minimal level of functional *autonomy* of the relevant kind. This builds on the intuition 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 view Pradeu's (2012) view of the immune system serving to mark the boundary of the biological individual as specifying and arguing for a particular way of understanding functional autonomy that comports with this notion of self and agency.

Judgments about which contrast classes are relevant, and whether freedom with respect to those is sufficient in a case for the minimal functional autonomy required to be an organism, are likely shaped partially by our norms. Barker and Velasco (2013) have uncovered roles played by such norms in judgments about evolutionary categories, while Slater 2017 has documented norms at work in classification of planets and animal taxa. In the case of organismic autonomy, Godfrey-Smith 2013 has discussed "exclusion principles" that may count as or reflect such norms. This still allows that being an organism remains in many cases a relatively natural matter, and that rationality constrains whatever normative elements there must be (see Slater 2017 on analogous rationality). Putting the minimal functional autonomy condition differently, 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 1994) 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.

The Tripartite View serves as a good framework for discussing issues about biological individuals because it has the resources to capture and explain much about our (at times) mixed judgments about the organismal status of certain biological and non-biological individuals. In order to see what the Tripartite View implies about a range of putative biological individuals, consider 22 such individuals:

1. *bodily organs, systems*: satisfy (a) but not (b); (c) very limited, if satisfied at all.
2. *obligate parasites*: satisfy (a)–(b), though the extent to which (c) is satisfied varies; cf. viruses on (a) and (c) below.
3. *mitochondria*: 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.
4. *genes, or DNA fragments*: at least some satisfy (c), and a variant of (b), but don't satisfy (a).
5. *developmental systems*: do not satisfy (a)–(c); may be parts of organisms, or have organisms as parts, but are not organisms.
6. *single cells*: as unicellular organisms, satisfy (a)–(c), but in multicellular organisms, fail to satisfy (b) and (c).
7. *viruses*: satisfy (b); satisfaction of (a) borderline and of (c) questionable in many cases because of the sort of dependence on other organisms.
8. *plants*: satisfy all of (a)–(c)
9. *vertebrates + their environments*: not themselves organisms because not living things, even though they contain an organism as a proper part; see also parasite-host systems.
10. *parasite-host systems*: 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.
11. *first/last living thing*: if in a lineage, can satisfy (a)–(c); if not, doesn't satisfy (b).
12. *individual sterile termites*: satisfy (b) despite their sterility, as well as (a) and (c), and so are organisms.
13. *a group of sterile bees*: do not satisfy (a), and so are not organisms, even if they satisfy (b) and (c).
14. *colonies of organisms*: 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.
15. *higher level entities (e.g., groups, species)*: 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.
16. *Gaia*: does not satisfy (b); defenders of Gaia hypothesis (Lovelock 1979 [1995], Doolittle 2017b) suggest that Earth satisfies (c) and, less obviously, (a).

17. *autocatalytic chemical reactions*: do not satisfy (b), and even though they share some of the properties in (a), do not satisfy (a).
18. *artificial life critters*: 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.
19. *humungous fungus*: satisfies (a)–(c), and so is an organism, but that status is jeopardized if there is lack of physical continuity and boundedness.
20. *coral reefs*: may satisfy (a) and (c), but not (b), and so are like Earth on the Gaia hypothesis.
21. *Adult vestimentiferan tubeworm plus its symbiont gut bacteria*: 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.
22. *Hawaiian bobtail squid plus its symbiont Vibrio bacteria*: may satisfy (a), but probably not (b) for the same reason as the tubeworm-plus-bacteria; there is a case for (c) because the bacteria are so important to the squid’s capture of prey, but we may have to rely on norms when deciding whether this functional integration regarding prey-capture bestows the degree or kind of autonomy associated with the digestive integration in the tubeworm-plus-gut bacteria case.

At least the last three of those biological individuals, 20 – 22, are examples of *holobionts*, a concept central to what an interdisciplinary team of scientists, philosophers, and historians recently called a “nascent area” of debate (Theis et al. 2016). In addition to attracting some scientists (e.g., Zilber-Rosenberg and Rosenberg 2008; Bordenstein and Theis 2015; Bosch and Miller 2016; Douglas and Werren 2016), this concept has sparked philosophical work that, although just emerging, has the potential for significant future influence, as evidenced by a recent special issue of the journal *Biology & Philosophy* (volume 31, issue 6), most of whose papers—Chiu and Eberl (2016), Gilbert & Tauber (2016), Queller and Strassmann (2016), and Skillings (2016)—focus on holobionts.

To summarize, we have seen that biological individuals include organisms and non-organisms. The Tripartite View of Organisms shows how insights from both pluralism and monism can be combined. And if the minimal organism-centred view of biological individuals introduced in [Section 3](#) is correct, The Tripartite View also helps frame discussions of both biological individuals that are organisms and those that are not.

Pairing the organism-centred view and The Tripartite View of Organisms also provides a vantage point on much of the literature on biological individuals. In Section 6, we illustrate this by reviewing and connecting three recent discussions. The first discussion is of Peter Godfrey-Smith’s Darwinian individuals; the second is of Ellen Clark’s view of the multiple realizability of “biological individuals”; and the third is of David Queller and Joan Strassmann’s empirical proposals about the study of the evolution of organismality. While these discussions have sometimes been understood as decentring The Problem of Biological Individuals from a default concentration on organisms, each in fact shows important affinities with the widespread organism-centred view clarified here (see also Queller and Strassman 2016 on multi-species organisms).

6. Vantage Points on the Literature

6.1 Peter Godfrey-Smith and Darwinian Individuals

Since Peter Godfrey-Smith published his influential 2009 book focused on the nature of evolution and natural selection, he has further examined what his views about natural selection imply about one subset of biological individuals. He calls this subset ‘Darwinian individuals’ – a subset that we and others sometimes call ‘evolutionary individuals’ – and contrasts the individuals it contains with other types of biological individuals such as organisms. Although in recent work he has acknowledged a special role for organisms at the intersection of biological individuals and cognition (Godfrey-Smith 2016c), his earlier focus on ‘Darwinian individuals’ (both the ‘minimal’ and ‘paradigm’ sorts, as he calls them) has had most influence in the literature on biological individuals.

Good conceptualizations of subsets or categories of biological individuals often (not always, e.g., see Chen 2016; Fagan 2016) have one or a combination of biological theories in their foundation. While evolutionary theory may not be foundational in thinking about all biological individuals, as Thomas Pradeu has argued (2010, 2012), it is foundational when thinking about Darwinian individuals. On Godfrey-Smith’s view of evolution and natural selection, what evolves are ‘Darwinian populations’. Building on views of selection such as Richard Lewontin’s (e.g., 1970), these are 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. These conditions, in conjunction with others, suffice for a collection to undergo evolution by natural selection. In such a Darwinian population, the members are Darwinian individuals (Godfrey-Smith 2013, p.19). There is then a sense in which the nature of the category *Darwinian individual* is parasitic on, or otherwise bound up with, the nature of evolution by natural selection. (The natures of other kinds of biological individuals are bound up with the natures of other biological processes.) So one way to determine what counts as a Darwinian individual is to look at cases of evolving populations, to see which features of its members typically help secure the three conditions just listed.

Upon doing this, at least three features of population members jump out as important. 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. (But see Section 5’s discussion of life cycles for complications that the Tripartite View of Organisms accommodates.) 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, pp.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 long 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.

To see how this account of Darwinian individuals fits within the broader organism-centered view of biological individuals, we should note, as Godfrey-Smith and others do, that although organisms such as finches often count as Darwinian individuals, so too do some parts of organisms and some groups of organisms. Some genes, for instance, satisfy the conditions of Darwinian individuals, including the three conditions stated in the preceding paragraph. Some groups satisfy them as well. (Some authors relax the necessary conditions so that types of interaction and processes may count as Darwinian individuals, e.g., Doolittle and Booth 2017; cf Bouchard 2010.) We can acknowledge such non-organism Darwinian individuals by adding to the running visual summary of the organism-centred view of biological individuals.

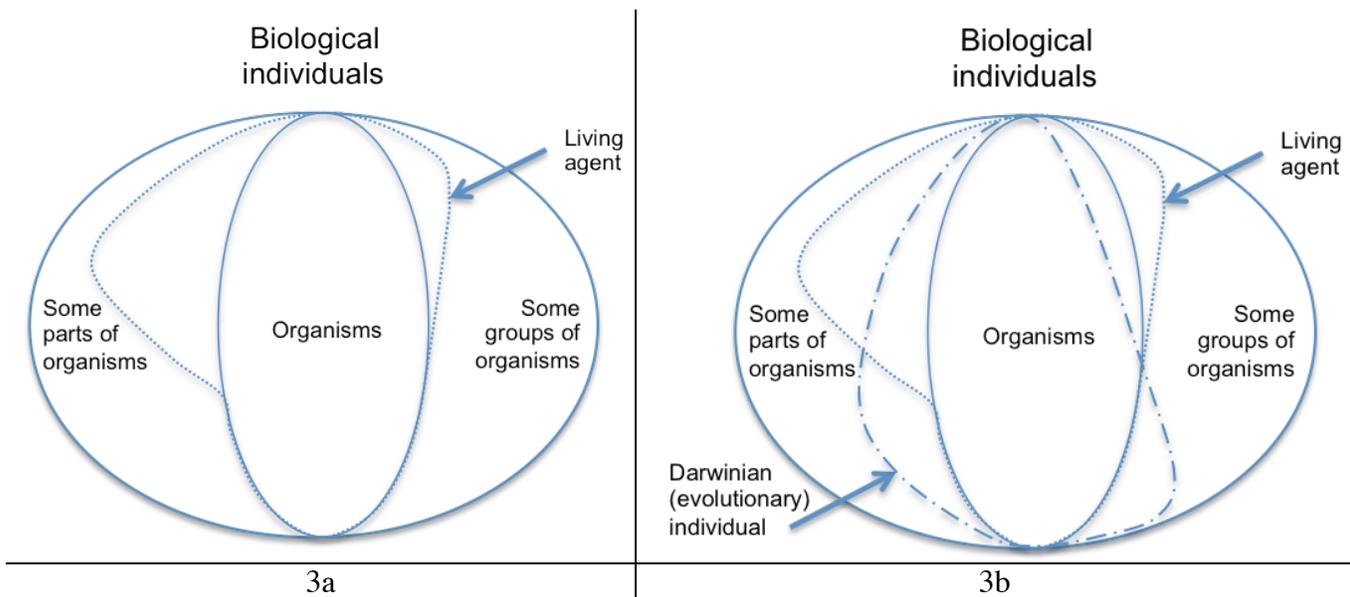


Figure 3: How Darwinian Individuals Figure in the Organism-Centred View of Biological Individuals

Figure 3a is identical to Figure 2b, reminding us where the running visual got to in Section 5. Figure 3b begins to clarify the place of Godfrey-Smith's Darwinian individuals. We see that some of these individuals, such as fruit flies in an evolving fruit fly population, are organisms. But as part of the area representing Darwinian individuals extends beyond the left-hand boundary of the organism category, we see, as Godfrey-Smith does, that some Darwinian individuals are parts of organisms rather than organisms themselves (e.g., genes that are selected for). And the extension of the area for Darwinian individuals beyond the right-hand boundary of the organism category indicates that some groups of organisms are themselves Darwinian individuals without being organisms (e.g., a honey bee colony involved in group selection).

Figure 3b includes three other clarifications. One concerns how the category of Darwinian individuals relates to living agents. 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 probably none reproduce 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 3b. 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 additional to the particular bees. 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. We saw that coral reefs don't feature the type of reproduction-involving life cycles that are characteristic of organisms, and 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 3b 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 or 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 (Efrain, Newton, and Mishler 2003). (In Section 7 we return to the idea that some taxa are individuals.) *Bryophyta* thus belongs in the far right of Figure 3b, 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 3b.

The third and last clarification in Figure 3b 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. Godfrey-Smith (2013) and others have 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 of the adult vestimentiferan tubeworm plus its symbiont gut bacteria.)

This may turn out to be mistaken, but it points to a potential tension in calling these 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, which have recently become hot topics in the literature (e.g., Godfrey-Smith 2015, 2016b, d; Griesemer 2014, 2016; O'Malley 2016).

Figure 4 further updates our running visual summary of the organism-centred view of biological individuals, with Figure 4a numbering some of the examples just discussed, and Figure 4b locating those examples in the overall picture from Figure 3b. (Of course, other synoptic viewpoints are possible as well and could emphasize categories and relations between them differently than Figure 4 does.)

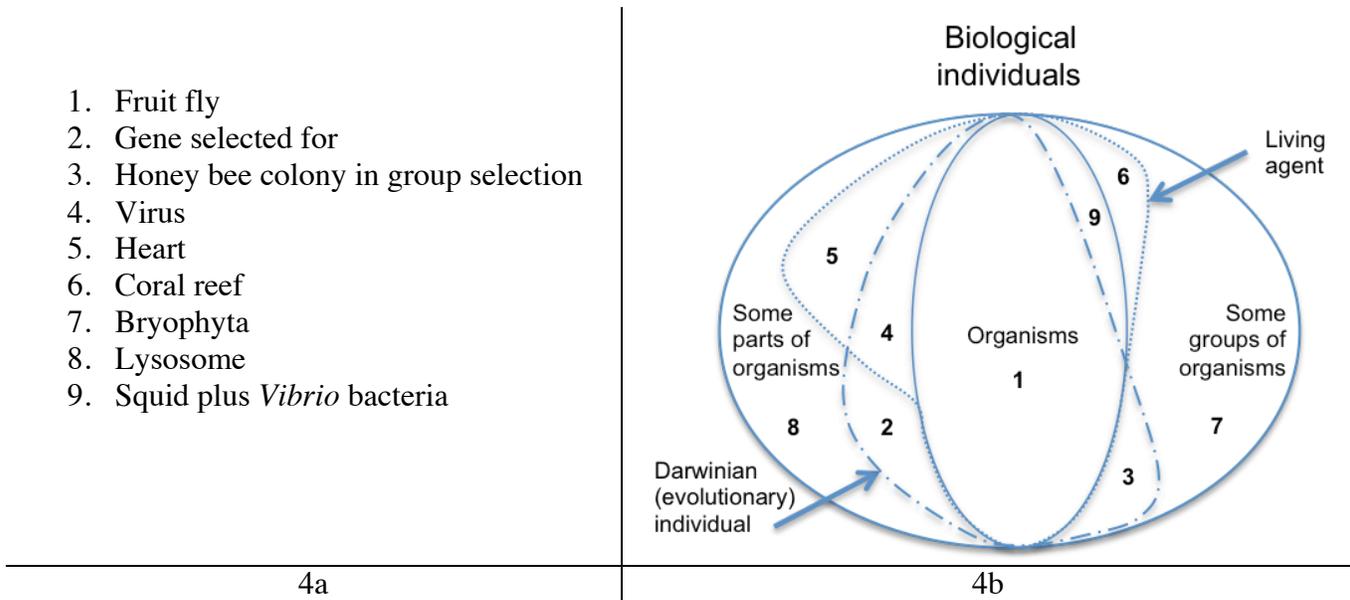


Figure 4: Identifying and Classifying Types of Biological Individuals

6.2 Ellen Clarke and Multiply Realizable Functions of Darwinian Individuals

In preceding sections we have seen how the organism-centred view of biological individuals fits with and helps organize proposals from various authors about various biological individuals. Part of this was seeing how there is less conflict than might be

expected between that view and others, but there is also less friction and more complementarity than usually appreciated *between other extant proposals*. Here we'll use our vantage point to summarize Ellen Clarke's views and compare them with those of Godfrey-Smith, views that researchers (e.g., Sterner 2015) have supposed are in significant disagreement.

Although Clarke's (2013) paper in *The Journal of Philosophy* is titled "The Multiple Realizability of Biological Individuals", Clarke explicitly restricts her focus to what we are calling Darwinian or evolutionary individuals, a focus that persists in her more recent work (e.g., Clarke 2016). This is no substantive disagreement, rather just a terminological difference, albeit one that occasionally seeds potential confusion (e.g., "Bigger than organs, but smaller than populations, 'biological individuals' are in some ways the most obvious of biological particulars", 2016, p.893). Clarke's focus on Darwinian individuals does, however, suggest that she is taking up exactly Godfrey-Smith's issue of specifying what it is to be the particular kind of biological individual that makes up populations undergoing natural selection in Lewontin's sense.

Clarke argues that a thing is (to use our term) an evolutionary individual if and only if it possesses both *policing* and *demarcating* mechanisms (2013, p.427). Policing mechanisms inhibit the capacity of an object to undergo *within*-object selection, typically by decreasing the 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 at the within-object level, they work at the higher *between*-object level, maintaining or increasing the capacity of those objects to undergo selection. They do this by promoting the variation (between objects) that fuels selection.

Clarke (2013, p.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 Darwinian individuals. This is to embrace the heterogeneity of the living world in one of the ways an organism-centred view of biological individuals does – without urging a pluralism so extreme as to lose sight of important commonalities across cases. This was highlighted in Section 4's discussion of the debate between Godfrey-Smith and Ereshefsky and Pedroso over the role of bottlenecks in evolutionary individuals.

A more distinctive aspect of Clarke's view is that it is deliberately *purely* functionalist. It thus contrasts with many other views of Darwinian individuals that are at least partly materialist in claiming that because particular material realizations of mechanisms are so much more important than others, *those* realizations are essential to Darwinian individuals. Clarke notes, for example, how Dawkins, Maynard-Smith, and Bonner imply that certain material genetic bottlenecks are essential ways for policing to be realized in Darwinian individuals (Clarke 2013, pp.418-419), how Ratcliffe and Kirk instead make material germ-some separation essential (Clarke 2013, p.420), and how one might instead

appeal to the essentiality of other material realizers of policing (Clarke 2013, pp.422-423). Clarke's pure functionalism does not prioritize any of these material realizers over others; it is policing by whatever means, and demarcation by whatever means, that matters.

Here our chief aim is to show that there is less disagreement than has been supposed between the views of Clarke and Godfrey-Smith. (This can prime us to spot such complementarity elsewhere in literatures on biological individuals.) The key to seeing things this way lies in charitably interpreting each author as answering subtly different though related questions. What makes these questions different is how they vary in specificity, and the range of cases each covers. Consider the following three questions:

Question I. Across all conceivable cases of a populations undergoing natural selection, *what is it for a thing to have*, in very general terms, the capacity to participate in a selection process as a member of a population undergoing selection?

Question II. How should we further specify the answer given to Question I, so that we clarify not just what it is to have the capacity to participate in a selection process, but also *the kinds of mechanisms that give* a thing the capacity described?

Question III. Narrowing down from the focus in Questions I and II on all conceivable cases of selection, to a focus now on the *actual* selection processes that have occurred on our planet and those that are *likely* to occur in the future, what are the *most important material realizations* of the kinds of mechanisms described in the answer to Question II?

When Godfrey-Smith draws on Lewontin's account of natural selection to argue that a Darwinian individual is a reproducing bearer of traits that vary in fitness within the population, we can understand him as answering Question I – that's what it is to have the capacity the question asks about. Clarke can then agree with that answer to Question I, and be understood as then taking up the more specific Question II – she argues that two kinds of mechanisms give things the capacity described in Godfrey-Smith's answer to Question I. Finally, when Godfrey-Smith gives an account of "paradigm" Darwinian individuals, we can see him as getting more specific still, in the way Question III encourages: he implies that particular material realizers of mechanisms have been, and will probably continue to be, important on our planet. This leaves open the conceivability of different realizers being more important in selection process that may happen elsewhere.

We thus see there are many tasks within the literature on Darwinian individuals, let alone on biological individuals more generally, a point that Love and Brigandt (2017) have also underscored and which can be gleaned by comparing the wide range of vantage points represented in Guay and Pradeu's (2016b) recent collection of papers on individuals across the sciences. Labour on these tasks can be fruitfully divided, and the organization of and coordination between researchers working on biological individuals then becomes

important. For instance, as an answer to Question II, Clarke's view can be seen as helping to guide work on the task of answering Question III, where both these questions are related to, but still upstream from, the further task of choosing between evolutionary models, let alone more applied tasks such as formulating operational criteria that field biologists could use to more accurately and exactly count individuals when measuring fitness. Rather than criticize the upstream views for failing to address the downstream tasks (see Sterner 2015; Kovaka 2015), it may pay to focus efforts on distinguishing various tasks and better coordinating the work that corresponds to each.

Taking the views of Clarke and Godfrey-Smith as more complementary than some have relieves neither view from challenges, such as the implications of Godfrey-Smith's view of Darwinian individuals, addressing Question I, that we have posed. (For other criticisms of his views on Darwinian individuals, see Dennett 2011, Queller 2011, Sterelny 2011, and Sterner 2015). For Clarke's view, even when interpreted as modestly addressing just Question II, there is a concern that her functionalism does not adequately respect the biological heterogeneity that we have attempted to accommodate within the organism-centred view of biological individuals. Although Clarke allows many ways for the functions of policing and demarcating to be realized, she insists, as a traditional essentialist might, that each is strictly necessary for being a Darwinian individual. But as Sober's comprehensive examples of selection imply (1991), it is possible for an individual to be a *Darwinian* individual within a particular selection process in virtue of the operation of just *one* of the two kinds of mechanisms.

6.3. Queller and Strassman on the Empirical Study of the Evolution of Organismality

Switching from a focus on what is possible in principle for Darwinian individuals to what makes for such individuality in most familiar cases of natural selection puts Clarke's emphasis on *both* policing and demarcating in historically interesting company. Recall that policing mechanisms are an *internal* (within-object) matter, while demarcating mechanisms pertain to an object's *external* relations. While addressing what our framework would call 'organisms' in his 1866 book *Principles of Biology, Volume I*, 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, in 1912, 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.

The organism-centered view of biological individuals incorporates these ideas when unpacking living agency (which appeals to heterogeneous and specialized parts) and minimal functional autonomy (which implies degrees of internal coordination and external freedom). It is then not surprising that when Clarke characterizes the more

specific category that picks out things with the capacity to form populations undergoing selection, she is compelled to underscore more specific kinds of internal and external mechanisms: policing and demarcating kinds with respect to natural selection. To further accommodate the insights of Spencer and Huxley, her view could be developed with an eye to the reinforcing *interactions between* these two types of mechanisms (also see Sterner 2015), and distinctive relations arising from them.

This sort of development has the potential to enrich current empirical agendas. Earlier sections in this entry have suggested that this type of enriching connection between conceptual and empirical work is important in the study of biological individuals. To exemplify this now in more detail, and thereby further clarify the forms that these important connections can take more generally, we will focus next on David Queller and Joan Strassmann’s (2009) agenda for empirical study of the evolution of organismality.

These researchers begin from the claim that the definitive feature of organisms is the combination of high cooperation between, and low conflict within, their parts. Using graphs, with degree of internal cooperation as one axis and degree of internal conflict as the other, Queller and Strassmann also clarify both that these things are matters of degree and that one can vary independently of the other.

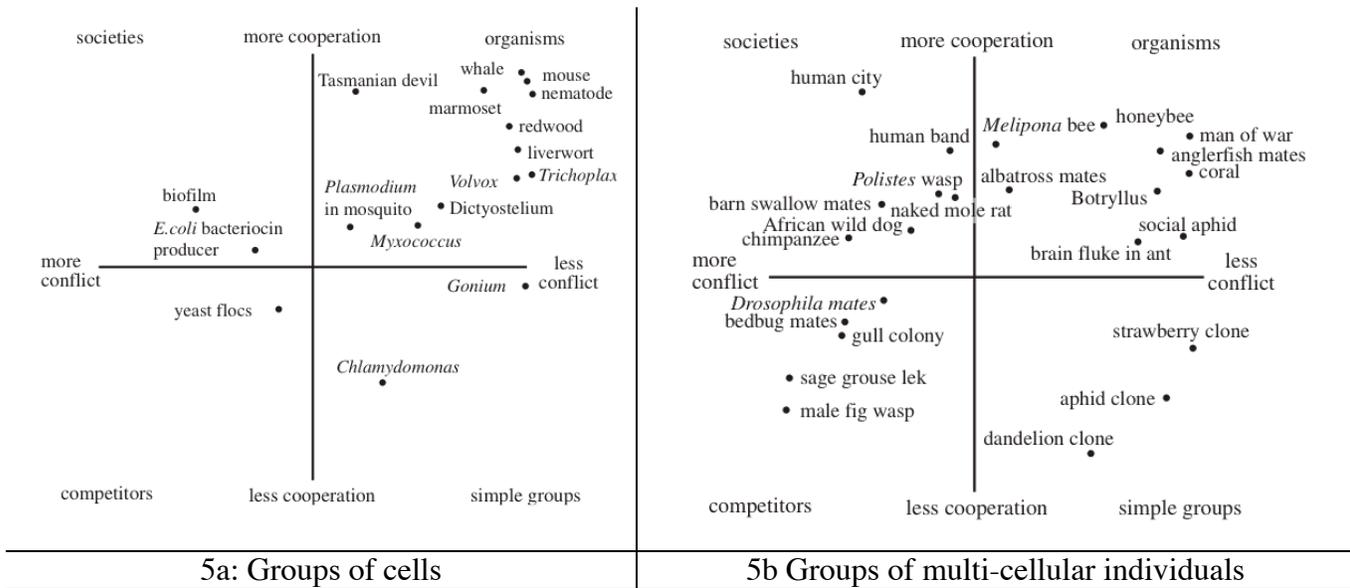


Figure 5: Varying Degrees of Conflict and Cooperation.

(From Figures 1 and 2 in Queller and Strassmann 2009)

Here low conflict does not simply entail high cooperation. For example, clones of dandelions and non-social aphids exhibit low conflict, but also low cooperation.

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 organismality. Figure 5a indicates that, relative to other groups of cells, a mouse will have a relatively large internal ratio, while a yeast floc 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 the lessons from Spencer and Huxley suggest we should supplement 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 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.

This could be seen as one way of studying the evolution of what was called *minimal functional autonomy* in The Tripartite View of Organisms. And if something like that view is correct, the agenda for studying the evolution of organismality should be expanded even further, to accommodate the roles of living agency and life cycles involving reproduction. As researchers move ahead with part of that agenda, we should begin to glimpse previously unappreciated details about how organisms and Darwinian individuals relate to each other. We might, for instance, begin fleshing out more details of what Godfrey-Smith calls (in borrowing a term of Huxley's) the "movement of individuality". 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 (Godfrey-Smith 2013, p.33).

Over evolutionary time there is then, Godfrey-Smith notes, 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 (e.g.,

Bouchard 2010; Doolittle and Booth 2017; Dupré and O'Malley 2007; Dupré and O'Malley 2009; O'Malley, Simpson and Roger 2013; O'Malley 2015; Pradeu 2012).

There remain issues about biological individuals other than organisms to consider. The next two sections consider two such biological individuals in more detail, groups and genes respectively. In each case we focus primarily on just one debate that the kind of individual has been central to: debate about the role of groups with respect to the levels of selection, and debate over the place of genes in understanding organismic development and evolution.

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 6.1 summarized and exemplified by describing a finch population. And finches count as organisms on most views. But many biologists and philosophers have also long seen that Lewontin-type accounts are substrate-neutral in a sense. 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).

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, 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.A. 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 (cf. 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.A. Wilson 2003, 2005: ch.10). This view has gained much support, being defended in influential papers by Dugatkin and Reeve (1994) and by Kerr and Godfrey-Smith (2002).

While pluralistic in name, the effect of model pluralism has often been to reinforce the status of individual and genic selection at the expense of group selection. For example, Dugatkin and Reeve call model pluralism "broad-sense individualism", characterizing this as the view that "most evolution arises from selfish reproductive competition among individuals within a breeding population" (1994: 107). And entomologists Andrew Bourke and Nigel Franks summarize their discussion of this topic by saying that "colony-level, group, individual, and kin selection are all aspects of gene selection" (1995: 67). As with Dawkins's appeal to shifts in perspective between two views of a Necker cube as a way to explain the relationship between the selfish gene view and traditional organismic views of natural selection, here pluralism-in-the-abstract often amounts to a sort of fundamentalism-in-the-particular-case. Model pluralism may sometimes best be seen as the pluralism you have when you're not having pluralism, a sort of "Clayton's pluralism".

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 2004). 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, and in part as a way to express the idea that species were treated within systematics and evolutionary biology not as kinds but instead as spatiotemporally restricted *lineages*, with individual organisms as their physical parts. The species-as-individuals thesis was 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) is a question that remains open.

8. Genes: Shifting Views of Developmental Agency

Genes themselves have been thought of as biological individuals of particular significance not only in the process of natural selection, but also as developmental individuals in the construction of organisms. This has led researchers to ask how genes have been and should be conceptualized, what kinds of properties genes are thought to have, and what causal roles have been ascribed to them in inheritance and development (Griffiths and Stotz 2013a, 2013b). We will focus on two metaphors that have played an important role here—the much-discussed *informational metaphor* and what has been called the *cognitive metaphor* (R.A. Wilson 2005: ch.2). We will also discuss a related challenge to the standard view of genetic agency that has been issued by developmental systems theory (Griffiths and Gray 1994, 2001).

The ideas that genes carry information about phenotypic traits, that they encode for proteins, and that they contain a blueprint for organismic development, are all widely accepted in the biological sciences and in broader representations of what genes do. Yet it is more recently that these ideas have been recognized as forming part of a cluster of claims that make up an informational metaphor for characterizing genetic agency, with the status of that metaphor a continuing topic of debate. This information metaphor

predates the discovery of the structure of DNA by Watson and Crick in 1953, having its roots in the cybernetic tradition led by the physicists Norbert Wiener and Erwin Schrödinger in the 1940s and '50s. The metaphor also subsumes talk of genetic programming, instructions, and recipes. Evelyn Fox Keller (2000) has argued that this blending of computational and coding metaphors was productive for geneticists because it allowed the development of a notion of genetic action in absence of detailed knowledge of the biochemical structures and mechanisms in which such action was ultimately realized. In our view, the informational metaphor has also contributed to a misleading view of the kinds of individuals or agents that genes are. This is so to the extent that the metaphor has implied that genes are self-contained and autonomous agents in their own right, agents whose intrinsic properties hold the secret to understanding a wide range of phenomena in the biological world.

The informational metaphor has done this partly through its interactions with appeals to *cognitive metaphors*, the metaphorical attribution of cognitive states and traits to biological entities that do not literally possess those states and traits. When we describe a laptop computer as thinking what to do next or as not wanting to be cooperative, we make use of the cognitive metaphor, something that Daniel Dennett (1987) calls *adopting the intentional stance*. Reliance on such cognitive metaphors is widespread in the biological sciences, ranging from our attributions of knowledge and recognition to cells in the immune system, through to the attribution of goals and desires to Mother Nature in describing how natural selection operates (cf. Godfrey-Smith 2009: 9–11, 36–39).

The cognitive metaphor enters talk of genes in several ways. First, the metaphor of the selfish gene, introduced and made popular by Richard Dawkins (1982, 1989), conceptualizes genes as having interests (their own replication and preservation), and engaging in means to satisfy those interests (strategies). Having interests and adopting strategies are both properties that only agents with a psychology can literally possess, and so the cognitive metaphor serves to extend this sort of cognitive agency to biological agents, such as genes. Second, explanations of molecular and intra-cellular processing in general have made use of the cognitive metaphor, and accounts of the operation of genes have been no exception. Genes execute instructions, recognize binding sites, and try to maximize their replication in future generations. The interaction between the informational and cognitive metaphors is apparent not only in such examples, but might be thought required insofar as the informational metaphor itself presupposes the cognitive metaphor, as some have in effect argued is the case in cognitive science (Horst 1996).

One reason why the web of informational and cognitive metaphors has been productive within genetics is that their extensive, fruitful entwinement with literal descriptions has made it difficult to say just where the boundary is between literal and metaphorical description. Genes are sequences of DNA that serve as templates for the production of amino acids, which in turn constitute the proteins that are the basic building blocks of biological structures and processes. Given this and the correspondence between specific nucleotide triplets and specific amino acids, it is very natural to talk of genes as coding for protein synthesis, and even for organismic traits. While some have been critical of the role of these metaphors in directing our thought about both natural selection and

organismic development (Griffiths 2001; Sarkar 1996; Moss 2003), others have sought to defend much of the orthodoxy here (Maynard Smith 2000).

One of the chief criticisms of the reliance on the informational metaphor has been that it distorts the role of genes in developmental biology and in our understanding of how evolution operates. This criticism has been articulated by proponents of *developmental systems theory* (DST), a loose-knit cluster of historians, philosophers, psychologists, and biologists who view themselves as redressing an imbalanced view of organismic development (Oyama, Griffiths, and Gray 2001). According to DST, genes are simply one type of developmental resource for the building of organismic bodies, and to view them as coding for organismic traits or, in toto, as serving as “master molecules” for the construction of whole organisms, is to inflate their actual role in ways that are misleading. The psychologist Susan Oyama's 1985 book *The Ontogeny of Information* is widely viewed as a founding document for DST (see also Oyama 2000b), and there have been healthy interactions between explorations in DST, reinterpretations of the history of biology (Amundson 2005; Keller 2000, 2001), the development of niche construction theory at the interface of ecology and evolutionary theory (Odling-Smee, Laland, and Feldman 2003), and the rise of evolutionary developmental biology in contemporary biology (Maienschein and Laubichler 2006; Neumann-Held and Rehmann-Sutter 2005; Müller and Newman 2003; Robert 2004).

The positive vision that has emerged from such interactions is something like this. Organismic development is not simply the unfolding of a genetic program but an active process in which organisms construct themselves through the recruitment and deployment of a range of developmental resources. These form developmental *systems*, and it is these systems that are the fundamental units for understanding development. Because development is systematic, developmental causes are typically context-sensitive and contingent on what is “going on” in the system more generally, not just on the intrinsic properties of some particular developmental resource. Development itself is a constructive process in that organismic traits are built from the full range of resources that constitute particular developmental systems, rather than simply being “passed down” through their encodings in particular developmental resources, genes. Developmental resources can be found at various scales beyond that of the gene, ranging from nuclear but non-genetic resources, such as the methyl groups in chromatin marking, through to other cellular resources, such as actin fibres and other cytoskeletal structures, and to organismal-level resources, such as the *Buchnera* bacteria that are transmitted as digestive resources in aphid development.

Thus, DST involves broadening the conception of what the causal agents for organismic development are. But since there seems no barrier within DST to viewing developmental resources as forming part of an organism's environment, it also returns us to a question about organisms raised earlier: where do individuals begin and end? Consider animal-built structures, such as nests and burrows. These often form a crucial part of the environment for the birth and development of offspring, and their particular properties often have a differential impact on the survival of those offspring. Such environmental resources seem no less (than genes) a crucial, causal part of what particular organisms

need to develop, even if multiple organisms share them. If that is so, then developmental systems can extend beyond the bodily boundary of the organism whose development they are crucial for. However, they are not simply an extended phenotype (Dawkins 1982) of some gene or genes, for they form an active causal role in the creation of the very thing that possesses such a phenotype, the organism. As such they are akin to the extended cognitive systems defended by proponents of the extended mind thesis in the philosophy of mind (R.A. Wilson 2004; Clark 2008; Wilson and Clark 2009).

9. The Evolution of Biological Individuality

However we understand the concept of an organism (sections 2-6), and whatever we think of the status of both groups (section 7) and genes (section 8) as biological individuals, biological individuality is a dynamic phenomenon that has changed over time. What biological individuals there are has changed over the 3.8 billion or so years of life on planet Earth, and the evolution of individuality itself has become a major topic of discussion in the last twenty years or so (Dawkins 1982; Buss 1987; Maynard Smith and Szathmary 1995; Michod 1999; Okasha 2011; Calcott and Sterelny 2011, Clarke 2016, Queller and Strassman 2016, Sterner 2017).

The starting point here 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. For instance, one does not find examples of (say) prokaryotes appearing from eukaryotes. 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. Also their discussion is focused primarily on exploring the processes governing each of the particular transitions they propose in terms of changes in replicative control.

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, 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). But how we should integrate sociality into our view of the evolution of biological individuals remains under-theorized. 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.

10. Concluding Thoughts and Future Study

Philosophical discussions of various biological individuals, including organisms, groups of organisms, and parts of organisms (such as genes), have flourished for more than twenty years. Although one should heed the pluralist warning that what may be claimed about biological individuals per se holds true of only some particular type of biological individual, we have also suggested that an organism-centred view of biological individuals provides a useful way to recognize some core structure to the world of heterogeneous biological individuals.

We concluded section 1 by bracketing out some metaphysical, epistemological, and ethical issues about biological topics, directing readers accordingly to some of the relevant literature here beyond the purview of this article. We conclude the article as a whole with one topic for future study with less anchorage in the ongoing debates that we have reviewed but that has the potential to encourage a healthy interchange between the literature on biological individuals and discussions in the social sciences. This is the topic of *human variation* and our attempts to understand it.

This topic reflects the centrality of the issue of heterogeneity when understanding what biological individuals are, taking us from the living world in general to the small part of it that human beings occupy. While variation is crucial to the process of natural selection in general, and there are many techniques (both mathematical and biological) for understanding it, a particular set of concepts and ideas has been used in understanding human variation in particular. Historically, we have conceptualized our own variation in terms of there being sorts or kinds of people, whether those be defined in racial, ethnic, geographic, cultural, genetic, phenotypic, economic, or other terms. Such conceptions share some distinctive features: they are often hierarchical, are often associated with positive status or negative stigma, and have often involved an explicit or implicit appeal to both norms and ideals of what it means to be human.

Since our own species is not simply the purview of the biological sciences but of much of medicine, the social sciences, and the humanities as well, more systematic reflection on this aspect of biological individuality will likely draw from, and in turn be relevant to, a wide range of disciplinary approaches to understanding human beings. Philosophers of

biology and biologists themselves are especially well placed to make a significant contribution to this issue, as the following questions suggest. What does the widely recognized “death of essentialism” within evolutionary biology imply about the study of human variation (Hull 1986)? In what ways does the study of genetic variation within our species constrain or even dictate how we should think about human variation more generally (Lewontin 1982)? Are there significant continuities between historically influential ways of classifying and categorizing people—in racial terms, or on the scale of feeble-mindedness (as imbeciles, idiots, and morons) prominent in eugenics—and contemporary views of health, human functioning, disability and disease (R.A. Wilson 2018)?

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