

Everything Flows: Towards a Processual Philosophy of Biology Daniel J. Nicholson and John Dupré

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Symbiosis, Transient Biological Individuality, and Evolutionary Processes

Frédéric Bouchard

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Abstract and Keywords

Whereas individual organisms have acted as the paradigm case to make us think about biological individuality, multi-organism assemblages such as colonies and communities force us to reconsider how biological individuality can emerge. Symbiosis research has given philosophers of biology tools for rethinking the nature of biological individuality. This chapter discusses how the adaptations linked to symbiotic communities highlight a new research dilemma: should we think of a biological ontology focused on individuals and their traits (even if this means positing non-orthodox individuals with non-standard properties)? Or should we move beyond individuals and focus instead on intersecting evolutionary processes? While reasons are offered to favour the former option, it is explained why this dilemma highlights the question of the different temporal scales at which evolution occurs and how this forces us to consider the transient and intermittent biological individuals generated by evolution, as well as the significance of the processes that generate them.

Keywords: community evolution, emergence, individuality, process, symbiosis

1. Introduction

The debate about how to define biological individuality has a long tradition, both in philosophy and in biology. From the Greeks onward there has been a recognition that our intuitions about the metaphysical primacy of individual organisms is at best programmatic and at worse unjustified. Most common notions of individuality either fail for some paradigmatic individuals (e.g. we may

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assume that individuality demands some sort of autonomy, and yet a human baby is not autonomous) or apply to biological systems that, to many, do not seem to merit to be identified as individuals (e.g. an ant colony as an emergent individual, also known as a 'superorganism'). This philosophical problem has gained renewed currency in contemporary philosophy of biology in response to debates about group selection and whether groups exist with their own grouplevel properties (see Sober and Wilson 1998; Wilson and Sober 1989; and Okasha 2006 concerning group selection). Much theoretical work has been conducted to better buttress our metaphysical understanding of biological individuals and how they fit into various biological explanations (see e.g. Huneman 2014a and 2014b for how theoretical frameworks of weak and strong individuality fit into evolutionary and ecosystem biology; Pradeu 2012 for immunology; and Haber 2013 for a discussion of what he calls the problem of the paradigm and how it muddles our attempts to make sense of individuality). Although much of this work has focused on operational problems—that is, on questions such as 'How do individuals actually fit into scientific explanations?'many philosophers have been interested in the intersection between the metaphysical question concerning the nature of individuals in general (e.g. a chair as an individual) and how this issue is similar to and different from understanding biological individuals (e.g. Dupré 1993; O'Malley and Dupré 2007; Wilson 1999, 2004a, 2004b, 2008).

In this chapter I wish to address the issue of how to define biological individuals beyond common intuitions we have about individual organisms. I will argue that biological individuals are defined via the processes they are involved in. Processes make up the individuals. But if individuals are in some sense process-laden, couldn't **(p.187)** we dispense with individuals altogether and consider only processes in the same way? If the focus of biological individuality is the process that generates it (in this case, the process of natural selection), couldn't we forget about individuals and focus the explanation solely on processes? I will argue that doing so would prove too epistemically onerous because of the way evolutionary explanations are structured. Individuals and processes should be co-occurring in our explanations.

John Dupré in recent publications has toyed with this shift to a process-based ontology. Harking back to Heraclitus and Whitehead, Dupré writes:

Most philosophers, if asked what were the most basic constituents of their ontology, would probably name things and properties....There is, however, an alternative ontology, one generally attributed in antiquity to Heraclitus that takes things themselves to be only temporary manifestations of something more fundamental: change or process....I do want to claim that an ontology of processes is better suited to understanding the nature of life and the living.

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(Dupré 2014: 81)

This proposition is similar to discussions about the metaphysics of causality where Wesley Salmon (1984) among others suggested that causality is not about individual events but about continuous processes intersecting through time. Salmon's theory of causal process was geared towards providing a novel theory of explanation (a discussion of which is beyond the scope of this chapter). A better understanding of causal processes (instead of events) enabled Salmon to offer a Humean theory of scientific explanation where causality was both objective and contingent and allowed for indeterminism in the natural world (see Dowe 1992 for analysis). Salmon's account was influential in general philosophy of science but was also very influential for certain philosophers of biologynotably Brandon (1990), who imported Salmon's account of propensities into his understanding of evolutionary processes and individuals. Whereas Salmon (and Brandon in a different context) was interested in the continuous aspect of processes, in this chapter we will see how the debate between an individualbased ontology and a process-based ontology highlights the *transient* nature of biological organization and function. We can better understand biological individuals by paying closer attention to processes.

Bapteste and Dupré (2013) argue that, in our biological ontology, processes are prior to individuals but that individuals can remain in the scientific picture. While I agree with many of the points they make, in this chapter I emphasize why individuals *must* remain in the scientific picture, especially when adaptations are concerned. The upshot is that this will give us a better understanding of how evolution works on vastly different but intersecting temporal scales for entities with various levels of functional integration. In some sense I will argue that, for evolutionary explanations, there is no dilemma between individual-based and process-based ontologies: they are both part of the same picture.

To get there, I will need to reprise parts of arguments offered elsewhere (Bouchard 2009, 2010, 2011). Our focus shall be on the question of individuality that arises in certain cases of symbiosis. We shall see how a revised notion of biological individuality is necessary on the basis of actual biological cases that need better accounts of their ontological status. Specifically, I will discuss the case of the Hawaiian Bobtail squid and its interaction with *Vibrio fisheri* (here my exposition is based mainly on **(p.188)** McFall-Ngai and Montgomery 1990, Jones and Nishiguchi 2004, and Bouchard 2010). This will lead me to defend a definition of biological individuality that can apply to 'difficult' and exotic cases of associations of individual organisms (sometimes from different species) that generate emergent individuals (i.e. novel individuals that are caused by the interactions of underlying lower-level individuals).

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Wilson and Sober's notion of biological individuality in terms of functional integration and common fate (Wilson and Sober 1989) can offer a guide to the perplexed about individuality. To paraphrase their proposal, we get the following notion of biological individuality:

A biological individual is a functionally integrated entity whose integration is linked to the common fate of the system when faced with selective pressures from the environment.

I have argued elsewhere (Bouchard 2010, 2013) that this definition of biological individuality is fundamentally about how the process of natural selection generates and maintains biological individuals. The proposed definition of individuality is intended both as an operational definition that helps to make sense of certain scientific projects and as a metaphysical claim about what inhabits the universe independently of our needs and uses for certain types of scientific explanations. What I haven't discussed before, however, is the implication of this account for our assessment of the importance of processes in our understanding of nature.

At the end of the chapter I will argue that, although our metaphysical account could focus on processes and minimize the role that individuals play in explanations, this would be a pyrrhic victory, for it would be difficult to offer an operationally equivalent definition of these processes in an evolutionary explanation. Biological individuals may be temporary 'eddies in the constant flux of process' (Dupré 2015: 81), but viewing them as genuine individuals is necessary for evolutionary explanations nonetheless. In a naturalistic metaphysics, this may be an indication that individuals are real enough and should retain a prominent role in our explanations.

2. Beyond Replicators

Evolutionary theory allows for the explanation of the 'perfect' organs that organisms seem to have. They have traits that appear well suited to their circumstances. Dawkins (1976) codified adaptation as a relationship between 'replicators' (usually genes) and 'vehicles'—or, to use Hull's (1980) better coinage, 'interactors'—which, most of the time for Dawkins, are individual organisms.

You have variation among replicators, which translates into variation expressed by interactors. Interactors are differentially selected according to their properties by various selective pressures and, if these features are heritable, this will in turn translate into differential representation among replicators in the following generation. This differential representation will appear both among the interactors and among the replicators that generate them. In such an interplay, differential fitness or differential evolutionary success is in terms of

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survival and reproduction, or rather in terms of differential propensities to survive and reproduce (see Brandon 1990, 2008).

(p.189) In this view of evolution, the explanatory burden is on the replicator, for it is the only common denominator across generations. Interactors are explicitly defined in relation to replicators. The adaptive signal is about replicators, and the phenotype is at best the repeater or at worse the noise across generations. The distinction between interactor and replicator is a powerful explanatory factor, because it allows adaptive explanations via the tracking of changes in populations of interactors or replicators and the interaction (via heritability) of the two explanatory levels. Well-adapted interactors thrive; less well-adapted interactors do not. This allows replicators to thrive through the generations. If the environmental conditions are right, these small victories accumulate through the ages to form the adaptations that we observe in nature.

For simple organisms, this interplay between interactors and replicators seems explanatorily satisfactory. This assumes a strong link between the interactor population and the replicator population. But what if some biological systems decouple (to various degrees) interactor populations and replicator populations? I have argued (in Bouchard 2009, 2010, 2013) that this is what occurs in cases of symbiosis.

Take an adaptation—say, the ability to digest cellulose. In most simple organisms we assume that this feature of a given interactor is related to a given set of replicators. But if this ability emerges from the interaction of organisms of different species, the claim that replicator success explains interactor success (or vice versa, if you are not a gene centrist) relatively to a specific adaptive trait loses some of its explanatory appeal. In Bouchard 2014, I have explained, using the comparison between a termite whose cellulose digestion does not depend on another species (*Macrotermes michaelseni*) and one whose cellulose digestion does (*M. natalensis*), that traditional co-evolutionary accounts have difficulty comparing symbiotic communities with autonomous organisms. Moreover, the fact that the symbiont (in this case *Termitomyces*) is ecologically acquired raises the prospect that one will not always have neat intergenerational linkages between interactor populations and replicator populations in relation to a specific adaptation (in this case cellulose digestion).

If the bearers of adaptation (or, to use the term in Lloyd 2012, the 'manifestors' of adaptation) are complex multispecies assemblages, we should expect our description of the adaptive process to be complex as well. Multispecies assemblages put stress on the idea that replicator populations and interactor populations are always coupled. If that is the case, then one should expect individuality to become more complicated as well. Below I will briefly discuss an example I examined in more detail in Bouchard 2010, to show just how much the

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transiency of these interactions between species raises metaphysical and operational problems about individuality and processes.

3. Seeing the Light

The Hawaiian Bobtail squid (Euprymna scolopes) interacts with the bacteria Vibrio fischeri in a way that generates light (this phenomenon is called 'bioluminescence'). This interaction is the 'new' poster child of symbiosis research. McFall-Ngai has contributed a great deal to the detailed study of this symbiotic community; most of the description offered here is inspired by her work and that of other colleagues (see e.g. McFall-Ngai 1999, 2014; McFall-Ngai and Montgomery 1990; Jones and (p.190) Nishiguchi 2004). 'How does it glow' and, more importantly, 'Why does it glow?' or 'What is this bioluminescence good for?' are the traditional adaptationist questions. A plausible hypothesis is that bioluminescence allows Hawaiian Bobtail squids, through counterillumination, to avoid predation (see Jones and Nishiguchi 2004). A predator identifies its prey by the shadow the latter casts when swimming between the predator and the light above itself. If you glow and, moreover, if your glow matches other sources of illumination in the environment, you don't cast a shadow. That is to say, when the squid glows, it is unrecognizable as a prey to its predator.

Bioluminescence is obviously a wondrous trait demanding explanation, and natural selection seems to provide it. But things get murkier when one asks questions about the bearer of the adaptation. Who is the individual bearing the adaptation? For whom is the glowing good? What is it that glows? To answer these questions, one needs to understand how bioluminescence is triggered.

The Vibrio colonizes the apical surfaces of epithelial cells at each squid generation. The Vibrio then reproduces inside individual squids. When it achieves high enough density, quorum sensing triggers a chemical reaction that generates light. This light is oriented by the squid thanks to developmental changes (a lens-like structure) that are initiated by the colonization itself. In other words, the bacteria both trigger developmental changes in the squid and produce the light that these changes take advantage of. Each day, the squid flushes out much of the Vibrio, bacteria density falls, and bioluminescence is temporally 'turned off'. The remaining Vibrio then starts reproducing again inside the squid, until a high enough density is achieved once more. Quorum sensing triggers the bioluminescence and, as a result, the confused predator keeps looking unsuccessfully for the squid prey. The squid alone cannot glow, and the *Vibrio*, although it could reproduce to high enough densities sans squid and generate quorum sensing and bioluminescence, does not actually generate bioluminescence in the wild outside the squid. Bioluminescence is a transient, intermittent, yet recurrent state of a *community*. What glows is a temporary assemblage of species interacting in the right way.

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As I have argued in more detail in Bouchard 2010, the question of individuality is not trivial in this case: how many individuals and how many types of individuals are there? Using Wilson and Sober's notion of individuality (which is based on functional integration and common fate), I offered a few possible scenarios (ibid., 632):

(a) Considering that the squid can survive without the bacteria, do we have 1 squid and a multitude (10^9) of *V. fischeri* = 1 billion and 1 individuals?

(b) Considering that the bioluminescence, because of the quorum sensing, is a collective property of the bacteria, do we have 1 squid + 1 *Vibrio* superorganism = 2 individuals?

(c) Considering that the symbiotic community has its own additional survival potential (i.e. its own emergent common fate), should we say that we have 1 squid + 1 billion *Vibrio* + 1 *Vibrio* superorganism + an emergent squid/colony superorganism = 1 billion and 3 individuals?

These scenarios highlight that, because functional integration and common fate can be achieved at various levels of organization, one can have overlapping individuals operating at different temporal scales and with different levels of transiency and **(p.191)** continuity. In the following section I will examine this issue in more detail, to see how individual-based and process-based ontologies fare in relation to it.

4. Transient and Intermittent Individuals

Traditional intuitions about biological individuality are tailored to account for the common individual organisms that we encounter as human beings and that conform to our perceived experiences of our own individuality: animals. And yet, as we have seen, many biological systems at levels of organization below and above animals form systems that deserve to be understood as genuine emergent biological individuals. Such emergent individuals force us to consider accounts of biological individuality that depend less on structure—on the basis of the common origin of the parts of the system, which in many respects is how we conceive of organisms as the expression of shared DNA and as belonging to a single lineage—and more on the functional integration of parts in a larger functional whole. How does this functional integration obtain, and how is it maintained? Via the process of natural selection and adaptation.¹ An adaptation is a trait that *functions* in a way that increases the fitness of its bearer. To be functionally integrated is to have one's parts work in a way that maintains the system as a cohesive whole, as an adaptation bearer. Here my understanding of functional integration is inspired by McShea and Venit's (2002) discussion of *connectedness* between zooids in a colony.² Functional integration is a matter of degree. But because the parts, in this account, do not have to be related, they will not have commensurable differential reproductive success.³

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In the specific case of symbiosis that we have discussed here, there is reproduction at the *Vibrio* level, and at the squid level, but not at the community level. And yet the community is the bearer of the adaptation (i.e. bioluminescence) that results from the temporary but repeated ecological interaction between organisms of different species. The squid-*Vibrio* assemblage persists better with the bioluminescence than without it. But it would be inaccurate to say that this assemblage reproduces. There is repetition of this association and its emergent properties, which has lead me to argue that, instead of focusing on differential reproductive success of individual organisms, one should focus on the differential persistence of lineages (broadly construed).

(p.192) The lack of reproduction should not jettison the possibility of an evolutionary explanation. From clonal species favouring growth over reproduction to associations of organisms from same or different species forming emergent individuals, the biological world is rife with systems for which evolutionary success is more about increasing the potential for 'survival' (or 'persistence', to be more precise) than about generating more copies of itself. Survival is related to the 'common fate' identified by Wilson and Sober as a necessary property of biological individuals, and this common fate is made possible via the functional integration of the parts. Individuals have always been understood in relation to their integration as wholes. For our purposes here, the point is that biological individuals are defined by the functional integration of their parts (or by their connectedness, in accordance with McShea and Venit 2002) and by the common fate of the whole system. In the case of biological individuals, both of these features are the result of the process of evolution through natural selection: functional integration is the result of adaptive processes; and the common fate is success (or failure) when faced with pressures from the environment (i.e. selective pressures).

This example and the treatment offered here evoke other traditional metaphysical problems about individuality that will concern us for the remainder of this chapter. First, it becomes obvious that individuality is a matter of degree: if functional integration is the principle of individuality, then we must accept that there are degrees of individuality. Functional integration and common fate are never absolute, in part because evolutionary success is never absolute and depends to a large extent on the external environment in which the individual operates. A hostile environment may weaken the functional integration of an individual, while other environmental conditions may strengthen the functional relationships between the parts of a system. Our strong intuition that animals are paradigmatic individuals may be vindicated by the fact that the functional integration or connectedness of their parts is higher in most conditions than, say, that of a herd of bisons (see Clarke 2010 and Godfrey-Smith 2009 for a defence of this idea). This is not a novel result, but focusing on multispecies associations makes this issue more salient. Looking at the functional integration of the parts of an individual organism, one also recognizes that the degree to

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which a part is functionally integrated into the whole will vary from one part to another: my heart is more functionally integrated to me as a whole (and to my fate) than my toes are. Functional integration is a question of degree among the parts themselves.

This should not be surprising, given that the environment dictates the conditions of emergence and persistence of a system, and this environment will put varying stress on different parts of a given individual. This raises a second classic ontological problem for biological individuality: identity through time.⁴ If we accept that individuality is about functional integration and that functional integration is a question of degree, we must also accept that an individual's degree of individuality may fluctuate over time. How do we conceive of the permanence of individuals with fluctuating degrees of functional integration? A functional (**p.193**) account of individuality based on evolutionary processes has to take into account the transiency of biological individuals.

At one level, it is trivial to say that individuals are transient. Our lifespans are transient compared to the permanence of Mount Everest or even to that of a protected artefact in a museum. But focusing on fluctuating functional integration raises the spectre that individuals are not only *transient* but also *intermittent*, because some of the parts appear and disappear on vastly different temporal scales.

One symbiont may not go through intergenerational change, while another symbiont may have much shorter generational time and therefore see much more intergenerational change. This leads us to a view of individuality where the parts of a given individual are not synchronized. Parts of the same whole (in the case of multispecies individuals) do not belong to the same temporal scales. While the squid may persist for X years, the individual *Vibrio* may survive less than a day, and yet be part of a colony that surpasses the lifespan of the squid temporarily hosting it.

If functional integration obtains via evolutionary processes, it is the interactions between species that become the locus of individuality: the individual that is the bioluminescent *Vibrio*-squid community *exists only when* both species interact in the right way. This integrated ecological interaction obtains once a day. But how are we to make sense of the periods in which the *Vibrio* density is not high enough (after the daily purge)? How are we to interpret the succession of bioluminescent events? How are we to understand the relation between a single squid individual and a single *Vibrio* colony, when the former interacts with the latter periodically but intermittently and the latter is formed by ever-changing individual *Vibrio* bacteria? Do we have a single, temporally discontinuous, functional individual, or a succession of very short-lived (transient) distinct *Vibrio*-squid emergent individuals?

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Take an individual squid—call it Bob—and an individual *Vibrio* colony—call it Kala. Bob and Kala are well integrated individuals persisting over similar temporal scales. But how is Kala formed and maintained? The answer is: via the succession and aggregation (accomplished in the right way) of myriads of individual *Vibrio* bacteria (i.e. Vib, Viba, Vibo, etc). Once a day, Bob and Kala form an emergent functional individual (the glowing squid–*Vibrio* community). How many emergent individuals are there?

(1) Do we have a single individual appearing and disappearing once a day (i.e. the same KaBo blinking in and out of existence every time quorum sensing is achieved)?

OR

(2) Do we have a succession of communities leading to distinct multispecies individuals (i.e. KaBo, BoKa, etc.)?

Integrating a process-based approach to biological explanations, one can see why the former should be favoured. If we are to focus on functional integration, it seems perverse to multiply individuals when, after all, it is a given set of intersecting processes that leads to the periodic blinking of Kabo in and out existence.

While individuals may exist by virtue of their functional integration, it is the continuity of process intersections that leads to their identity through time, even if their degree of individuality fluctuates.

(p.194) Note that the issue is not novel or especially applicable to my account and examples: Hull famously defined species as spatio-temporally located individuals, and yet the individual organisms constituting the species are a succession of transient parts. Even in cases where one gets overlapping generations, one has the succession of distinct individual parts. The additional difficulty with multispecies associations is that in most cases the parts spend much of their lifespan outside of the emergent individual. For complex emergent individuals, the functional integration is not only transient; it is intermittent. The issue is whether this intermittency disaggregates the whole into a succession of distinct wholes or merely reflects a fluctuation of integration that leads to fluctuation in the degree of shared individuality of the whole. A squid+Vibrio is, both literally and figuratively, a flickering individual.

I suggest that, when we are faced with such transient and intermittent individuals, a process perspective allows us to identify (i.e. specify the identity of) an individual through time, however discontinuous that individual may be. Shouldn't we, then, entertain the possibility that, in the biological world, processes and not individuals are primitive, and that individuals can be demoted in our explanations? This is how Bapteste and Dupré (2013: 380) propose to

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redefine not only the microbial world but biology in general: 'We understand living things to be most fundamentally the consequences of numerous interweaving (occasionally nested) processes. Although it is common to describe the domain of biology as consisting of things, for example organisms, cells, genes, and so on, we understand even these as ultimately processual.'

The appeal of processual explanations is evident in evolutionary biology: adaptation unfolds over time, traditionally across generations of individual organisms. At first glance, a process-based ontology seems to be compatible with such a view of life—a view that life unfolds over many generations. The real question is whether the centrality of process should displace individuals altogether. Here the answer depends on whether you demand that individuality reveals a substance (in an Aristotelian sense) or whether you allow that individuals can be defined as the result of processes in interaction.

Bapteste and Dupré (2013: 381) write: 'For these reasons, the ontology we aim to describe is an ontology of processes. A processual ontology should characterize entities in terms of how they emerge, are maintained and are stabilized.' Although they offer compelling reasons for thinking of processes as a necessary condition for biological interactions (and for associated explanations), they do not explain why a process-based ontology could truly overshadow an individual-based ontology. They offer good reasons for entertaining a processbased ontology, but it is less clear what role is left for individuals to play: the reader may infer that Bapteste and Dupré prescribe forgetting about individuals. To frame this in a language that has probably never been used to characterize Dupré's work, on one reading Bapteste and Dupré are reductionists ('individuals are ultimately about processes'), but on another they are eliminativists ('individuals hinder our explanations, we should forget about them, and focus on processes instead'). Based as it is on Dupré's well-established promiscuous realism, the first reading is probably closer to the intended project.

Ellen Clarke diagnoses the importance of individuals in our evolutionary explanations:

(p.195) It is hard to overemphasize the importance of individuals within the Modern Synthesis. They are central to the inner logic of evolution by natural selection, according to which evolution occurs because of the differential survival and reproduction of individuals. Even in its most abstract minimal formulations, the action of a selection process requires that there be a multiplicity of objects that are sufficiently separate from one another that they can be differentially deleted or copied.

(Clarke 2010: 313)

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Arguably, evolutionary explanations are individual-based. Rightfully highlighting the centrality of process does nothing to reduce the dependency of process on individuals. The explanandum in the case of bioluminescence was the trait that seemed to confer an adaptive advantage to an individual. What would the explanandum and the explanans be if we got rid of entities and of their relative success?

Cases such as the symbiosis discussed here show how much processes need to be taken seriously, both in our scientific explanations and in our metaphysics; but they also show how processes underpin a revised notion of individuality instead of displacing or minimizing individuals.⁵

5. Conclusions

Historically, biological ontology has focused on individual organisms, their parts (organs and cells), and the aggregation of individuals (groups, species, etc.). In the second half of the twentieth century, the development of molecular biology tied to a neo-Darwinian account of evolutionary processes raised the possibility that the core level of organization may be the gene (or a gene complex), its parts (e.g. nucleotides), and the aggregation of genes and their expression (from genomes to cells, to organisms, and to species). With developments in metagenomics and a better understanding of symbiotic associations, we are now entertaining the possibility of multispecies assemblages that form emergent individuals. In this chapter I have discussed some of the implications of such developments for our understanding of evolution and individuality.

The goal here was not (and could not be) to offer an exhaustive account of this new biological ontology, but rather to examine one key implication of this story: if biological individuals emerge through a progressive functional integration that arises from and is maintained by selective processes, this entails that biological individuality is a matter of degree: a degree that increases or decreases over time. Being an individual is not a binary affair. If being an individual is not an absolute and if 'weak' individuals are as important to evolutionary explanation as 'strong' individuals (i.e. strongly integrated individuals with a clear common fate), then why not shift the focus away from individuals altogether in favour of focusing on the processes that generate them?

One must not forget what was the explanandum in the first place: adaptive traits. How do we explain bioluminescence? How do we explain the ability to digest cellulose? These traits are what forced us to consider these complex explanations in the first place. It is easier to make sense of these adaptive traits if they are properties of an individual **(p.196)** (whatever its level of organization: gene, organism, population, or species) that faces a selective environment (two individuals interact, generating a new individual with emergent traits) than if they are merely a causal nexus of intersecting processes (the squid process interacting with the *Vibrio* process generating a

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bioluminescence process). Or, to be more precise, we know how to think about competing individuals with differential evolutionary success, but it is less clear how we should think of competing bundles of processes and what would count as evolutionary success for these bundles. We have to wonder about whether a process-based ontology (in its eliminativist form, and possibly in its reductionist form) can accommodate Darwinian explanations of adaptations in any shape or form. Adaptation has always been both a process and a result (i.e. the trait; see Brandon 1990); but, more importantly, adaptations *as the traits/properties of individuals* were the original explanandum of evolutionary theory. Any thorough attempt to introduce a process-based ontology will have to accommodate this fact or to demonstrate the explanatory benefit of minimizing the role that individuals play in our explanations.

The appeal of a revival of a process-based ontology for the biological world must not overshadow the potential cost of making Darwinian explanations incompatible with said ontology. If adaptations remain wondrous features of the natural world, and if such features are to be explained in a Darwinian framework (however broadly construed), then the bearers of adaptation will be individuals (at some level of organization or another). Adaptations explain the thriving of some entities that bear them, and these traits emerge and unfold through a process of adaptation to natural selection. Natural selection and adaptation are the processes, but individuals remain in the picture as the entities generated and transformed through these processes. Notable proponents of a processbased ontology, such as Bapteste and Dupré, are right to indicate the severe blind spots of substance-based ontologies, especially in microbiology. But new adherents of a process ontology for biology should not take Bapteste and Dupré further than what they intended: from a process-based ontology it does not follow that there is an explanatory gain from getting rid of individuals altogether. If adaptations are a genuine question (and they are), processes are necessary to our biological explanations, but they are not sufficient. Individuals will need to remain in the picture as well.

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Notes:

 $(^1)$ The reader may compare this account of functional integration to the one offered in chapter 10.

(²) 'Connectedness. The assumption here is that connectedness reflects the degree to which lower-level entities can share resources and function in a coordinated fashion, and therefore the degree to which the colony operates as a unified whole. Connectedness can take a variety of forms, including physical attachment; sharing of a gut, coelom, vascular system, or nervous system (as in some colonial invertebrates); and behavioral interactions mediated by pheromones, sound, or physical contact (as in social insects and vertebrates)' (McShea and Venit 2002: 311).

(³) This was my reason for proposing a different understanding of evolutionary success in terms of differential persistence. I have argued extensively elsewhere (Bouchard 2004, 2008, 2011, 2014) that, by understanding evolutionary success in terms of differential persistence instead of differential reproduction, one can account for many species and associations of species that cannot be readily accommodated in reproduction accounts.

(⁴) On the issue of diachronic identity, see also chapters 1, 2, 4, 5, 6, 7, 11, and 18.

 $(^{5})$ The implications of symbiosis for biological ontology are also considered in chapters 1, 5, 10, and 15.

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