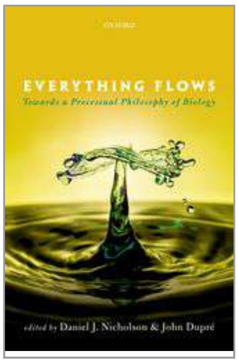

Everything Flows: Towards a Processual Philosophy of Biology
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From Organizations of Processes to Organisms and Other Biological Individuals

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Abstract and Keywords

The emphasis on the collaborative dimension of life overlooks the importance of biological individuals (conceived of as integrated, self-maintaining organizations) in the build-up of more complex collaborative networks in the course of evolution. This chapter proposes a process-based organizational ontology for biology, according to which the essential features of unicellular organismicality are captured by a self-maintaining organization of processes integrated by means of a special type of collaboration (realized through regulatory processes entailing an indispensable interdependence) between its constitutive and its interactive aspects. This ontology is then used to describe different types of collaborations among cells and to suggest the type that yields a multicellular organism. The proposed organizational framework enables us to critically assess hypercollaborative views of life, especially issues related to the distinction between biological individuals and organisms and between life and non-life, without however underestimating the central biological role of collaboration.

Keywords: biological individual, collaboration, functional integration, multicellular system, organism, organization, process, regulation, symbiosis

1. Introduction

Even though our world is continuously changing, contemporary thought is still dominated by a ‘substance-’ or ‘particle-based’ metaphysics, according to which static individuals composed by basic bits of matter constitute the world. Process philosophy opposes this view by suggesting that all things have to be conceived fundamentally as processes of various scales and complexity and with an inherent causal efficacy. Several thinkers (e.g. Christensen and Bickhard 2002; Ulanowicz 2009, 2013; Bickhard 2011a, 2011b; Dupré 2012) suggest that there are strong reasons for treating process as prior to substance in biology. Most of these suggestions are implicitly introduced as challenges to traditional assumptions. Issues of boundaries and individuation are among the first to be challenged. In a process ontology in biology, openness is the default. As Campbell (2009: 464) points out, the survival of a living system is due to the stability of its far-from-equilibrium processes as ‘a function of their being *necessarily open* processes’. Considering biological entities as open processes that participate in various causal networks and life as a hierarchy of such processes, Dupré and O’Malley (2012b: 225) have suggested that *collaboration* should be reconsidered as a central characteristic of life and its evolution.

The consideration of open processes as the basic ontological category implies that living systems are abstracted manifestations of the continuous underlying substratum of biological processes. Consequently, there are no definite answers to questions such as what the boundary of fungi or of molds is, or to questions like how many individuals we count in a field of crab grass, because the answers to these questions depend on the presupposed criteria of individuation and of boundaries—if there are any (Bickhard 2011a; Dupré 2012). It follows from this that there are various ways of dividing living systems into biological individuals —a position that Dupré (2012: 241) has called ‘promiscuous individualism’.

However, an excessive emphasis on collaboration, combined with promiscuous individualism, suggests something much stronger than the thesis that there is more **(p.200)** than one way to define a biological individual. Ultimately, all attempts at individuation may turn out to be completely futile, since, ‘overall, deep and extensive collaborations between biological entities blur—at the very least—any distinction between so-called individual organisms and these larger organismal groupings of which they are parts’ (ibid., 222). In light of these claims, the central contention of this chapter is that the emphasis on the collaborative and collective dimensions of the living world runs the risk of overlooking the importance of individual biological organizations as the very conditions of possibility for the subsequent build-up of more complex collaborations in the course of evolution.[1]

A process-based metaphysics implies that living systems (such as cells, multicellular systems, ecosystems, organisms) are just temporary phenomena—the products of the dynamics of some processes. Nevertheless, regardless of whether one takes these manifestations as classes of ‘topological knot persistences’ with respect to various kinds of dynamical properties (Bickhard 2011b) or, more simply, as transient intersections (i.e. causal loci) of multiple processes that operate on different timescales (Dupré 2012), such manifestations are processes that show some temporal stability. Consequently, what a process-based metaphysics indicates is that the becoming and persistence of such stabilities should be explicated rather than be taken for granted (Bickhard 2011b). Accordingly, my main aim is to propose *an organizational account of the various biological stabilities* that arise from the nexus of continuous change of biological processes. Once this is in place, the living realm can be described in a way that considers the diverse characters of different types of biological organizations as a result of different collaborative schemes, but without necessarily having to subscribe to the pluralism implied by promiscuous (biological) individualism.

I begin in section 2 by arguing that the main implications of the thesis of promiscuous individualism combined with an excessively collaborative view of life are a vague definition of organisms and a blurred position with respect to (a) the distinction between organisms and biological individuals, (b) the consideration of microbial communities as organisms, and (c) the distinction between life and non-life. In section 3 I outline a process-based organizational ontology for biology in which biological individuality is grounded on a special type of highly integrated far-from-equilibrium self-maintaining organization of self-generating and self-reinforcing processes. In section 4 I apply this ontology to describe different schemes of collaboration in multicellularity and to argue that the form of unicellular (organismal) integration is not exported to all types of multicellular collaboration. In section 5 I draw on the findings of sections 3 and 4 to critically revisit the implications presented in section 2. I offer some concluding remarks in section 6.

(p.201) 2. Some Implications of the Promiscuous Individualism Thesis Combined with a Hypercollaborative View of Life

Dupré (2012) has suggested that a process ontology is the most appropriate kind of ontology for thinking about life, organisms, and the organization of the biological world in general.[2] The main claim is that the biological realm consists of processes rather than things. The entities that we commonly represent or model as thing-like, such as organisms and other biological individuals, are just particular time slices of their life cycles, which Dupré takes to be a more basic reality (ibid., 2). Each one of those individuals is just an abstraction from the underlying causal nexus of biological processes. They are not necessarily bounded and, when they are, they can have different boundaries that result from the very dynamics of the related processes.

In a way, such ‘processual’ biological systems are inherently open (Campbell 2009), in that they are prone to *collaboration* (in a sense that entails both selfish/competitive and cooperative interactions) with other systems. Dupré argues that the omnipresence of collaboration between microbes (through lateral gene transfer) and between microbes and multicellular systems (through symbiosis) threatens the traditional view of an organism as a monogenomic biological individual and as the only, or even the central, unit of selection. Instead, one should consider biological entities as processes collaborating in various causal networks, and life as a hierarchy of such processes (Dupré 2012: 223, 225, 227).

Dupré also advocates a pluralism with respect to drawing individual boundaries; he argues that ‘drawing boundaries round biological objects is to an important extent a matter of human decision driven by particular human goals, practical or theoretical’ (ibid., 241). There are various ways of dividing living systems into organisms, according to the goals of the observer—a position Dupré calls ‘promiscuous individualism’ (ibid.). These ideas have several wider implications.

The first implication is that the position results in a rather vague definition of organisms, as well as in a blurred position with respect to the distinction between organisms and biological individuals. Dupré (ibid., ch. 13) stresses the inadequacy of the ‘monogenomic differentiated cell lineage’ (MDCL) view of organisms. In accordance with his thesis of promiscuous individualism, Dupré suggests that the correct answer to the question of what an organism is ‘requires seeing that there is a great variety of ways in which cells, sometimes genomically homogeneous, sometimes not, combine to form integrated biological wholes’ (ibid., 88). Some might say that this is not very informative, since there is no definite list of concrete criteria that the concept of an organism should satisfy. But this is exactly the reason why Dupré and O’Malley (2012a) urge that the classical concept of organism is a problematic biological **(p.202)** category. And although in several different cases Dupré suggests, and even favors, a ‘functional organism’ concept (see e.g. Dupré 2012: 124–5), he ultimately stays consistent with promiscuous individualism and does not provide a unique definition. For Dupré, ‘the omnipresence of symbiosis should be seen as undermining the project of dividing living systems unequivocally into unique organisms’ (ibid., 8). This is the reason why ‘what is an organism, and whether something is a part of an organism or not, are not questions that admit of definitive answers’ (ibid., 153). Due to extensive collaboration in the biological world, there are various ways to draw individual boundaries that reflect real biological aspects of the multiply symbiotic systems that make up the biological realm. This is not just an epistemic view. For Dupré, ‘ontological boundaries are relative to the issues with which we are concerned, which is a central part of the reason why there is no unique ontology’ (ibid., 97). The analogy with Dupré’s promiscuous realism makes this also an ontological view (see also Wilson 2012). Accordingly, since there are multiple biological individuals out there to classify, the question of how many biological individuals are out there neither has nor requires a definite answer. In all, Dupré’s definitions of an organism are so broad that there is no firm basis for distinguishing organisms from other biological individuals.

A second implication is the consideration of microbial communities as multicellular organisms. This is also implicitly related to the inadequacy of the MDCL point of view of organisms. O’Malley and Dupré (2007) argue that the

MDCL conception prevents us from identifying microbial communities as *bona fide* organisms due to the polygenomic character of such communities. Moreover, for Dupré and O’Malley biofilms are much more than simple aggregations of individuals; they are self-organizing entities that operate as functional units. This being the case, they suggest that the only reason for not considering microbial communities as multicellular organisms is that the classic understanding of multicellularity is exclusively based on knowledge of multicellular eukaryotes.

A third implication is the blurring between life and non-life, mainly due to the highly important role of collaboration in life and its definition. Dupré and O’Malley (2012b) see a tension between two widely discussed criteria for life: replicating lineages and metabolic self-sustainability. They suggest that this tension can be overcome once we decide to see life as occurring at the intersection of lineage formation and the (collaborative dimension) of metabolic processes. In this respect, biological entities such as viruses, prions, and plasmids, which are problematic under other frameworks and ontologies for life, should be considered alive when actively collaborating in various metabolic processes. This blurs the distinction between life and non-life and also drops the commitment to an exclusively cellular view of life (ibid., 227–8).

These conceptual and theoretical implications are crucial for our understanding of the living. My goal in this chapter is to clarify these issues by adopting an organizational perspective with respect to the diverse characters of the biological realm. Specifically, I intend to show that a process-based organizational ontology in biology can offer clearer and more explicit alternatives to all these issues, in a way that avoids the problems of pluralism without ignoring or undermining the collaborative nature of the biological realm.

(p.203) 3. A Process-Based Organizational Ontology for Biology

3.1. Simple self-maintenance

The basic assumption in the study of complex systems is that a certain part of the world (usually, a set of elements and their interrelations) constitutes a system, and that the rest is the environment. As discussed in section 2, promiscuous individualism rejects the possibility of individuating a system in a single, unique way. The identity of the system (the relevant inside–outside dichotomy) would always be a matter of a particular point of view. However, there are systems that draw their own distinctions from the environment; they create their own identity. There should then be a way to explain the formation of this identity so that it may be not entirely dependent on the relativist position of an observer.[3] The adoption of an organizational perspective, which focuses on the current causal relations between the processes constituting a system, is suggested as the basis for specifying the identity of a system in such a way

(Bickhard 2000; 2004; Moreno and Barandiaran 2004). Let us elaborate more on this.

Processes exist in relation to other processes, in an organization of processes (Bickhard 2009, 2011a, 2011b; Campbell 2009).[4] Among them, there are some that work together so that they constitute *cohesive systems*, that is, systems that persist and manifest *a form of stability* in the sense of a spatio-temporal integrity —unlike the case of a quantity of gas (Campbell 2009).[5] Some organizations of processes manage to maintain such cohesion in appropriate *far-from-equilibrium* conditions.[6] A well-discussed example is that of a candle flame (Bickhard 2000). The microscopic reactions of combustion generate the flame (a macroscopic pattern), which contributes to the maintenance of the conditions for its own existence by constraining[7] the surroundings (temperature, wax, oxygen) and turning them into appropriate boundary conditions required for its own maintenance. As long as the combustion feeds back to its boundary conditions, the whole organization is self-reinforced and the flame will stably persist. Through its dynamics, the flame manages to maintain its **(p.204)** own process of burning. It is in this respect that we can account for the generation of an *identity* as the consequence of a set of far-from-equilibrium processes—which are stably maintained, given certain boundary conditions—and not entirely as a result of an observer's description. A candle flame is a form of self-constitution of the very identity of the system: a cohesive organization of processes that, given adequate initial and boundary conditions, contributes to its own maintenance. Such an organization of processes constitutes a *self-maintaining system*.[8]

At this point, the crucial question is whether the ontology of such organization of processes is sufficient for biology and, as Moreno and Barandiaran (2004) put it, whether self-maintenance is enough for the formation of a genuine in–out dichotomy. As Campbell (2009) points out, a candle flame is a system that contributes to the persistence of the conditions upon which it depends, but the constitutive complexity that enables the candle flame to self-maintain is not internal to the flame itself. There is no doubt that the candle flame is a complex of processes—a complex that actively contributes to its own persistence. However, its persistence is much more dependent on the environmental conditions (the candle and the atmosphere) than on the flame itself, to the extent that the flame cannot do anything to maintain its organization in the face of an abrupt shifting of the conditions of its environment (e.g. running out of wax, suffering a decrease in oxygen availability). As the flame is a cohesive organization of processes that persists far from thermodynamic equilibrium, its openness to the environment is an ontological feature of the system, and not only of our apprehension of it. However, the high degree of explicit and immediate dependence of the flame on its boundary conditions makes this openness so direct that, as pointed out by Bickhard (2011a), there is actually no boundary at which the flame can be isolated, for instance. The flame and its environment are so intertwined that they cannot be distinguished from each other. There is no genuine in–out dichotomy.

3.2. Minimal recursive self-maintenance and biological individuality

Nevertheless, one might still suggest that the (minimal) self-maintenance exhibited by the candle flame could be sufficient for defining biological individuality. It has been argued in detail in various studies that this is not the case (Moreno and Ruiz-Mirazo 2009; Mossio and Moreno 2010; Arnellos and Moreno 2012; Moreno and Mossio 2015). The main argument is that functions begin with biology.[9] As I will try briefly to explain, simple self-maintenance is a necessary but not a sufficient condition for grounding functions in the organization of a system. In principle, a self-maintaining system contributes to the existence of its organization. So the reply to the question ‘Why does the flame exist?’ is: ‘Because it contributes (in the way described above) to its maintenance.’ In other words, the flame plays a direct causal role in the dynamics responsible for its maintenance. The conditions of existence of **(p. 205)** the flame are the norms of its activity, and what the flame does is relevant for its existence. Therefore one can say that self-maintaining systems exhibit a minimal organizational closure (Mossio and Moreno 2010). It is in this sense that Christensen and Bickhard (2002) suggest that any such contribution (e.g. of the flame to its own maintenance) *serves* a function relative to the organization of the processes whose existence it contributes to maintaining. But, despite the intuitive meaning of such an assertion, what is the explanatory (added) value of ascribing functions to the candle flame? In the case of a candle flame, as in all physical dissipative systems, there is a single type of constraints—the macroscopic pattern of organization, in other words the flame—that constrains its surroundings by turning them into appropriate boundary conditions for its maintenance. It doesn’t matter how materially complex the system is, or how many constraints we can indicate; what matters is that in simple self-maintenance (i.e. at the level of minimal organizational closure) all constraints are of the same type, thereby producing the same effect.[10] So, if there is no way to distinguish between different contributions to a self-maintaining organization, it makes no sense to ascribe functions to these very contributions.

If we want to speak of functions in a system, *differentiation* (both in terms of the processes of the system and in terms of their specific contribution to its global far-from-equilibrium self-maintaining dynamics) seems to be crucial (Mossio et al. 2009). For this reason, we need to move to higher levels of organizational complexity than the one of minimal organizational closure, which involves only cyclic processes and reactions. But what would the characteristics of such an organization be? As it has been suggested elsewhere (Moreno and Ruiz-Mirazo 2009; Arnellos and Moreno 2012), functional differentiation could emerge in a scenario where a set of different types of constraints come together in a mutually reinforcing manner, thereby establishing a more robust type of self-maintaining dynamics.

An example of such a system would be a prebiotically plausible case of cellular proto-metabolism, where the self-maintenance of the system's organization of processes is a consequence of the interplay between different types of constraints. In this scenario certain processes selectively constrain the low-level microscopic behaviour of different networks of processes in such a way as to enable them to generate more stable macroscopic patterns, which in turn constrain (also selectively) another collection of processes, leading to the production of another macroscopic constraint, and so on—provided that all of them, together, end up depending on one another and the whole organization of processes closes itself recursively.[11] In such an organization of processes, diverse constraints (e.g. the cell membrane and the enzymes) mutually enable their continuous regeneration. By internally synthesizing (at least part of) its own constraints, the system becomes capable of performing a **(p.206)** diversified modulation of its own self-maintaining dynamics. And it is in this organizational context that different constraints can be taken to make *distinguishable contributions* to the global self-maintenance of the system, thereby mutually enabling their continuous regeneration and thus serving a function relative to the specific organization of processes (a form of *functional interdependence*). In principle, this is the basic or core type of organizational closure realized by biological systems: a type of robust self-maintenance.

Do systems of processes that exhibit this type of organizational closure achieve a 'genuine' in–out dichotomy? The appearance of cellular systems at large that build their own boundary with the environment introduces the level of organizational complexity necessary for a clear distinction between the inside and the outside of a system. In the organizational framework we have discussed so far, such systems should be considered *biological individuals*.[12] We can distinguish two aspects: (a) the organization of processes of the system and its environment;[13] and (b) the constitutive processes that occur within the system's physical boundary, including those of its construction and maintenance, together with the interactive processes of the system that occur outside of it. The constitutive processes are organized so that they constrain the flow of matter and energy between the environment and the system, and especially the interactive processes, in such a way that certain relations of the system to the environment hold in order for the identity of the system (as an organization of processes) to be both defined and maintained. Therefore, *the ontological requirement for biological individuality (a clear far-from-equilibrium in-out dichotomy) is an organization of processes that achieves closure on the basis of two kinds of process: constitutive and interactive.*

What is of importance for our discussion is whether this type of self-maintenance of a system of processes is sufficient to describe *the organizational complexity of present-day biological systems*. In cases of cellular proto-metabolism, a plausible scenario is that the constraining of interactions was presumably happening in the form of simple homeostatic reactions implemented via feedback relations through the dynamics of the constitutive processes (see e.g. Ruiz-Mirazo and Mavelli 2008). The constitutive processes would not only produce and maintain part of the semi-permeable membrane of these cells, but also modulate it so that it would be able to mediate different relations of the system to the environment. This kind of process stability would require mutual dependence between different constraints capable of compensating against a range of perturbations by virtue of the plasticity of their dynamics and the resulting global constitutive organization. This kind of biological individuals would overcome certain variations. However, the nature of the interactive processes would not be different from the mere physico-chemical reactions happening all the time across the membrane of all cells. As pointed out by Moreno and Mossio (2015), this type of (constitutive) stability would be limited, since it wouldn't allow the exploration of other regimes of closure by the system (provided that there **(p. 207)** are available ones). Such an organization of processes can't actively change its environment in such a way as to use it again for its viability, nor can it leave its environment for another one. For these systems, the environment is just a source of indistinguishable perturbations. Organizations of processes that manage to maintain cohesion within a small range of changes of very local conditions can be said to exhibit *limited recursive self-maintenance.*

3.3. Recursive self-maintenance and the organismality of unicellular organizations

All present-day unicellular organizations have the capacity to adapt to their environments to some extent by switching between different regimes of closure (achieved by their organizations of processes) so as to contribute to their self-maintenance, and thereby to their self-reproduction, in response to some changes in the conditions they detect in the environment.[14] A typical, well-discussed example is the bacterium *Escherichia coli* and its capacity for chemotactic interactions (Campbell 1974). When the bacterium is close to a sugar gradient, it will swim up this gradient—instead of the usual tumbling movement within periods of not encountering increasing concentrations. Swimming and tumbling are two different interactions that are both *functional* in the sense that they contribute to the bacterium's self-maintenance in different conditions, and the bacterium can usually *switch* between them accordingly. The effects of these interactions—materialized as changes produced at the system–environment interface (e.g. more sugar)—become inputs for the coordination of interactions, and consequently for the modulation of the maintenance of the whole bacterial organization. This is an organization that manages to maintain its cohesion in substantially different environments. It achieves self-maintenance across a (relatively) wide range of changes of environmental conditions; in other words, it exhibits *(genuine) recursive self-maintenance* (Bickhard 2004; Campbell 2009).

What are the organizational characteristics of such systems of processes? Given that the appropriate physico-chemical conditions are not always immediately available, robust self-constitution (reproduction and maintenance) involves not only the control of metabolic processes (for instance through modulation of the metabolic organization—e.g. the lac operon mechanism) but also the control of the production, maintenance, and modulation of boundary conditions through the regulation of the system's interaction with the environment.[15] We have mentioned the capacity of *E. coli* to switch between different interactions (swimming and tumbling). It would be rational to assume that 'switching' between different sets of self-maintaining processes needs some sort of infrastructure that can make the relevant shifts in relation to the detected environmental input. As a matter of fact, in *E. coli*, the operation of the two-component signal transduction (TCST) subsystem of processes relates the metabolic regime with the two types of motility-based interaction in a way that **(p.208)** modifies boundary conditions so that metabolic maintenance is ensured.[16] We can leave aside the physico-chemical details of the processes involved; but the organizational characteristics of the TCST are important. As all types of functions in biological systems, the TCST can be considered a set of constraints that act in the bacterium. But, contrary to the metabolic constraints (e.g. enzymes) operating on basic thermodynamic processes, the TCST operates by coordinating the action of other functional constraints. Specifically, the operation of the TCST results in the coordination between membrane receptors and motor mechanisms. And, although this coordination is generally mediated by metabolic pathways of the bacterium, the whole process is organized so as to operate over the basic metabolic functioning of the bacterium, and with dynamics that exhibit a degree of *decoupling* from those of the basic metabolic organization; otherwise the maintenance of the bacterial organization could be disrupted.[17] So, in the organizational framework we are considering, we could say that switching in *E. coli* is organized on the basis of 'second-order' constraints that operate on constitutive constraints while being decoupled from them. Importantly, as suggested by Bich et al. (2015), in such organizations we already find all that is required for ascribing *regulatory functionality* to the set of processes that control the activation of its various self-maintaining processes according to environmental changes. In this respect, the TCST operates as a *regulatory subsystem that functionally coordinates the bacterium's interaction with the environment.*[18]

Chemotaxis can thus be considered a form of higher-order control of bacterial metabolism. Accordingly, a chemotactic interaction (and its regulation) is functional as long as the selected action (tumbling or swimming) satisfies the endogenously generated *norm* associated with the maintenance of the bacterial organization, namely that the constitutive processes must occur as they do in order for the bacterium itself to exist (Barandiaran and Moreno 2008). The nature of chemotaxis as well as of other motility-based interactions performed by such organizations is different from the nature of the interactions performed by limited, recursively self-maintaining organizations. Chemotaxis is more than a mere physical interaction, as the biological individual's own viability is affected by it. Chemotaxis is a functional action on the environment, in the sense that it is performed outside the system's own boundaries and it actively modifies the conditions of the system–environment relation in such a way that the whole bacterial organization can use the new conditions for its own maintenance and, consequently, for its reproduction. The environment is no longer simply a source of indistinguishable perturbations. On the contrary, the cell itself (its identity) determines what is relevant for its maintenance. In this way the interactive dimension of the organization can be viewed as a function of its constitutive normativity.

(p.209) From an organizational perspective, the endogenously produced regulation that dynamically coordinates the constitutive with the interactive processes entails a particular form of functional integration that seems to characterize all present-day cells.[19] Extant unicellular entities are organized on the basis of functional coordination, which in turn requires multiple sets of functional interdependence. This form of integration entails that cellular organizations show a functional and reciprocal relationship between interactive processes (and the regulatory subsystem that coordinates them) and the overall constitutive organization that supports this subsystem materially and energetically. This form of integration requires a type of closure and mutual interdependence between constitution and interaction that is realized via the endogenous production of regulation for both self-construction and self-maintenance, through functional interactions with the environment. This form of integration is characteristic of unicellular, (genuinely) recursively self-maintaining organizations; in other words, it is characteristic of a basically autonomous biological organization (Ruiz-Mirazo and Moreno 2004). An ontological consequence of this form of integration is that, ultimately, in such a biological individual *the confluence between metabolism and reproduction is organized in such a way that it is not really possible to separate the individual's 'being' from its 'doing'*. It is in this respect that such a unicellular organization is considered an *organism* (Ruiz-Mirazo et al. 2000; Arnellos and Moreno 2016).

4. Collaboration and Multicellular Systems

As argued in section 3, different types of collaboration among processes result in different types of self-maintaining organizations. One of the conceptual challenges of multicellularity is that the organizational variety of the diverse types of cellular associations is hidden under their common capacity for adaptation. All types of multicellular (MC) collaborations appear to exhibit the same form of integration among their unicellular constituents. Indeed, all MC collaborations manage to generate and maintain relatively cohesive forms of integrated organization. This integration—the various functional interactions between the cells—enhances the overall adaptive capacity of MC associations, as they can occupy new niches and increase the possibilities of survival of the constituent units, as well as of the association as a whole. Thus, considering functional coordination for adaptation as the main criterion for organismality,[20] all MC systems—at least from a phenotypic point of view—seem to be integrated as *individual organisms*.

Elsewhere I have argued that this is not a secure position, as it does not enable us to distinguish different characters of multicellularity and their respective organizational basis (Arnellos and Moreno 2016). Below I elaborate on this claim by considering **(p.210)** examples of bacterial, early eukaryotic, and early eumetazoan multicellularity. Specifically, I will apply the organizational ontology sketched in section 3 to distinguish different schemes of collaboration in multicellular systems and to assess which types of MC organization can be said to exhibit the form of organismal integration found in unicellular organizations. As I will argue, the form of unicellular integration does not manifest itself in all types of MC collaboration and, when it does, there are still important differences with respect to the unicellular case.

4.1. A case of collaboration among single-species bacteria

Collaboration among *Myxococcus xanthus* bacteria is intense and results in a collective form of motility, which provides the MC system with the ability to engage in ‘wolf-pack’-like hunting and feeding (Berleman and Kirby 2009).[21] Independently of the intensity of collaboration between the myxobacteria, the integration between the motility of the swarm and its constitutive organization is loose. Swarming is a mere result of self-organizing chemotactic movements, and the collective interaction is the emergent net effect of numerous local interactions (Zhang et al. 2012). As argued in Arnellos and Moreno 2015, swarming exhibits no coordination attributable to the whole MC system. On the contrary, each individual cell participates in the swarm by coordinating its local chemotactic interactions with its immediate environment through its own regulatory organization (see Arnellos and Moreno 2015 for details).[22] Actually it is the richness of the environment that maintains the swarm. The cells will stop moving in a swarm when nutrients are exhausted. This is because, at the swarm level, there is no functional differentiation; each bacterium executes the same chemotactic interactions. There is therefore no collaboration on the basis of functional interdependence. Interestingly, also during ‘fruiting body’ formation, where some cells differentiate into spores and some others retain their rod shape, the whole system is frozen and immotile, waiting to be carried to a nutrient-rich environment by a passing animal. In general, associations of cells (e.g. of myxobacteria or of slime moulds) cannot at the same time be motile and participate in the construction and maintenance of their fruiting bodies.

So we see that, despite the apparent collaboration in single-species biofilms, not only is there no functional coordination at the MC level, but the whole integration is so loose that the MC organization's constitutive identity does not require interactivity,[23] while the organization itself can even be reversed to the stage where the constituents may disperse and exist autonomously as unicellular individuals. This implies that this **(p.211)** type of collaboration between unicellular prokaryotic organizations does not reflect the form of unicellular integration at the MC level.

4.2. A case of early eukaryotic collaboration

A well-studied case of relatively simple eukaryotic collaboration is *Volvox carteri*. In its adult stage, this MC alga normally consists (a) of almost 2,000 biflagellate, terminally differentiated somatic cells engaging in phototaxis and (b) of sixteen germ cells, which are non-motile but can grow through photosynthesis and reproduce (Kirk 2005). The way interaction is organized in *V. carteri* is qualitatively different from the one found in biofilms (see Arnellos and Moreno 2015 for details). There is no known direct communication among the somatic cells (Ueki et al. 2010). So, without considering the anatomical characteristics of the spheroid, the whole organization of interaction is of the type of swarms; each somatic cell swims according to its own detection of the local environment. However, because of the morphological and anatomical constraints introduced during development (the spheroid's polarity and asymmetry, combined with the immersion of all cells in the extracellular matrix; a proper orientation of the cells with respect to one another; and the reorientation of the flagella, beating in each cell towards the always heavier posterior), the collaboration in *V. carteri* is tighter and much stricter than in the myxobacteria. This structural arrangement is necessary for the proper execution of phototactic swimming and will stay unaltered during the MC alga's lifetime. It could be considered collaboration on the basis of functional interdependence. The movement of the flagella of each somatic cell requires the movements of the other cells, in the sense that proper phototaxis is the net effect of all cells' movements. One could argue that the existence of structural components spanning the whole MC system that ensure its adaptive interaction is a form of global coordination. Still, although the alga's swimming is adaptive (it manages to stay or move to euphotic conditions), *there is no central functional coordination in the sense of a regulatory system (like the TCST) that would switch the MC system between two different organizational regimes*.[24]

In accordance with the account we have discussed, *V. carteri* exhibits a more integrated organization than biofilms. Contrary to *M. xanthus* biofilms, the alga's constitutive identity is compatible with its interactive dimension, and its MC organization cannot be reversed to the unicellular stage of its constituents because of the absolute germ/soma division of labour. However, compared to the organismal integration of a cell, the integration achieved by this MC alga is weak. Isolated germ cells of *V. carteri* would still grow and divide under euphotic conditions (Koufopanou and Bell 1993). This means that the constitutive identity of the MC alga could be reproduced and maintained even without its interactivity; in other words, unlike unicellular organizations, the alga's relatively weak interdependence between constitution and interaction is not indispensable for the development and **(p.212)** maintenance of its organization. This type of early eukaryotic collaboration results in a recursively self-maintaining organization but it still does not achieve the form of integration its constituents entertain when in their unicellular form.

4.3. A case of eumetazoan collaboration

As I have argued, *different types of cellular collaboration result in different forms of integration for MC organizations*. This has implications for the constitutive and interactive characteristics of the cellular collaboration as well as for their interrelations. I have recently suggested that the level of minimal organizational complexity necessary and sufficient for the appearance of a MC form of integration analogous to the one exhibited by unicellular systems is met in eumetazoan organizations (Arnellos and Moreno 2015, 2016). Such organizations can deploy several different interactions with their environment in order to contribute to their self-maintenance.[25] This is possible due to the existence of the nervous system (NS)—a specialized subsystem that exerts a fine-tuned control on the numerous different processes responsible for adaptive behaviour in a given environment. However, such a subsystem is functional only in the context of specific body plans adapted to various interactions. The NS is integrated in a body plan with a set of primitive and differentiated organs, which provide the MC animal with the metabolic and biomechanical requirements for its behaviour. Besides its role as a controller of behaviour via the neuroendocrine system, the NS also regulates the development and maintenance of the metabolic processes of the body by which it is also being developed and maintained.[26]

What is of importance for our discussion is that adaptive behaviour requires unified body movement (Keijzer and Arnellos 2017). And this in turn requires functional coordination with metabolic and even developmental processes. In eumetazoan organizations, each one of the various subsystems of processes operates according to its local norms. Consequently, the control of eumetazoan behaviour cannot be achieved without functional coordination of all its different local regulatory subsystems. What is required is higher-order integration. This is what a regulatory centre provides: it functionally integrates all local norms according to a higher-level normativity (Arnellos and Moreno 2015). This is precisely the role of the NS in eumetazoa. It does not only regulate contractile epitheliomuscular tissues that generate sensorimotor interactions; it also regulates processes of development, growth, and global homeostasis (Jekely et al. 2015).

It is in this respect that such MC organizations exhibit a form of functional integration analogous to that of a unicellular organization. The MC organization's constitutive identity (encompassing both the capacity for self-reproduction and the capacity for self-maintenance) is so strongly entangled with its interactive dimension (the actions in the environment) that one cannot exist or be explained without the other. Nevertheless, in such a MC organization, the organismal form of integration is not realized in a way that is totally symmetrical to the one found in unicellular **(p.213)** entities, since, in accordance with the organizational framework I have proposed, unicellular entities are organized on the basis of a different form of functional integration from the one exhibited by a eumetazoan collaboration. Overall, a MC organization exhibiting such a form of integration can be considered *organismal* (Arnellos and Moreno 2016).[27]

5. Revisiting the Implications of Promiscuous Individualism and an Excessively Collaborative View of Life

In section 2 I discussed some implications of the thesis of promiscuous individualism and the collaborative view of life that accompanies it. I will now try to critically assess those implications and to suggest specific alternatives based on the analysis in section 3 and the results of its application in section 4.

5.1. Organisms and other biological individuals

The first implication we noted was that it leads to a rather blurred definition of organisms and of the relation between organisms and other biological individuals. Let's start with the concept of the organism as a MDCL. This is an idealization of organisms on the basis of a false presupposition that all constituent (and differentiated) cells have the same genome (see Buss 1987). Dupré questions but does not dismiss the MDCL view. For the sake of promiscuous individualism, he states: 'I have not wanted to say that the MDCL is an erroneous conception…The mistake is to think that it involves a discovery of what the organism really is, and must therefore be the right conception for all purposes' (Dupré 2012: 241). From the organizational point of view, Dupré is right. The requirement for a biological organization to qualify as an organism is an indispensable closure between its constitutive and its interactive dimensions. In this respect, a biological organism need not be a MDCL.

For instance, let us take the case of the symbiosis between pea aphids and the bacterium *Buchnera aphidicola* (Moran 2006).[28] First of all, this is an obligate endosymbiosis, where the bacterium resides in a specialized compartment inside the cytoplasm of aphid cells and is transmitted vertically, through maternal eggs, roughly in the same way mitochondria are transmitted from our mothers. Second, this is more or less a case of genetic mosaicism, except that not all cases of mosaicism have lethal consequences when they are not satisfied. Third, it seems there are no aphids that do not have the *B. aphidicola* bacterium. For the aphid, the bacterium is just another cellular part, another component process of the whole aphid organization. It is more in the context of the putative application of the MDCL concept that **(p.214)** this particular biological organization is considered symbiotic than on the basis of fact that the collaboration is between a eukaryotic and a prokaryotic individual. In any case, as I have argued, organismality is a property of specific biological organizations, and the organization of the aphid (including the bacterial symbiont) satisfies the pertinent requirements. So Dupré is right to suggest that, in light of the dependence of MC organisms on diverse sets of symbiotic microbes for their successful differentiation as well as for their survival, the MDCL assumption should be questioned.

Keeping in line with promiscuous individualism, Dupré (2012: 88) suggests that there are various ways in which cells (homogeneous or not) collaborate to form integrated wholes. This is not very informative. As we have discussed, all MC collaborations seem to exhibit a degree of integration. Moreover, it is important to note that there are MDCLs that form integrated wholes but nevertheless do not qualify as *bona fide* organisms. For example, *V. Carteri* is a case of a MDCL (it achieves alignment and export of fitness, see Folse and Roughgarden 2010) yet, as I argued in section 4, it does not qualify as an organism (see also Arnellos et al. 2014 for the same argument from a complementary perspective).

Dupré (2012) avoids providing a single definition for an organism. On several occasions he seems to suggest a ‘functional’ organism concept: ‘we might also want to approach the question of what constitutes an organism from a functional perspective: what are the systems of cells that interact with the surrounding environment as organized and generally cooperative wholes?’ (ibid., 152; see also 172, 203). And, quite contrary to what promiscuous individualism would prescribe, he seems to be taking organisms ‘that interact functionally with their biological and non-biological surroundings’ to be more fundamental than ‘organisms that are parts of evolutionary lineages’ (ibid., 124–5). Dupré also uses a functional individual concept according to which organisms collaborate in symbiotic wholes, forming functioning biological individuals (ibid., 9). In principle this is not wrong. However, it seems too generic to capture the diverse characteristics of the biological world. Although Dupré is clear that we should not equate organisms to biological individuals (ibid., 207), promiscuous individualism does not inform us how and in what particular contexts the notions should be distinguished.[29]

In the organizational view we have discussed, several schemes of collaboration of biological processes result in the constitution of a system’s identity, but each constitutive organization is not necessarily integrated in an organismal way. In this respect, all organisms are also biological individuals, but not all biological individuals achieve organismal status. Wilson (1999: 89) suggested that a biological entity is a *functional individual* when it is composed of causally integrated heterogeneous parts in such a way that the entity would (typically) suffer impaired function if some of its parts were removed or damaged. Very few authors would disagree with this definition. And, even if Wilson emphasizes the current causal relation between the parts of a whole, **(p.215)** this definition could be modified to include the evolutionary dimension of individuality, resulting in what has been described as the *reproducible–functional (evolutionary) individual*. This conception includes the capacity of an organization to reproduce itself and to be maintained in its environment (see also Arnellos and Moreno 2016).

According to the analysis offered here, MC organizations such as the one exhibited by *V. carteri* do not achieve organismal status, but are nevertheless evolutionary individuals. Each cell type needs the other for the whole colony to be maintained and to reproduce its organization. Somatic cells are necessary for the spheroid to be moved into euphotic conditions and germ cells are needed for the reproduction of the colony. An inverse case is the squid–*Vibrio* non-obligate symbiosis (McFall-Ngai 1994). From the organizational point of view, the squid–*Vibrio* organization qualifies as a functional individual on the basis of functional interdependence with respect to the bearer of the trait of bioluminescence. However, since self-reproduction is a capacity only of the squid and of the bacteria and not of the symbiotic organization, the latter should not be considered an evolutionary individual.[30]

5.2. The individual and the organismal status of microbial communities

The second implication I outlined pertains to the organismal status of microbial communities. Dupré (2012: 88, 152) begins by suggesting that the general conception of microbes as single-celled organisms should be revised, since most of the time microbes do not function simply as isolated individuals but rather in complex associations, often composed of highly diverse kinds of cells (e.g. the biofilms on the surfaces of our teeth). For O'Malley and Dupré (2007), these microbial communities are self-organizing entities operating as functional units. Therefore, once the MDCL concept is out of the way, the only reason for not regarding microbial communities as MC organisms is that 'the definition of multicellularity is closely based on knowledge of multicellular eukaryotes' (ibid., 176). Let us examine this in more detail.

Dupré and O'Malley suggest that biofilms possess many (but not all) of the characteristics of multicellular organisms (Dupré 2012: 88, 177). However, this does not automatically mean that microbial communities should be regarded as organisms. This is not just because of the adoption of a definition of multicellularity based on MC eukaryotes. From the organizational perspective I have discussed, apart from claiming that early eukaryotic multicellularity is not organismal, I have also argued that the requirements for MC organisms are not satisfied in systems with a lower organizational complexity than that of eumetazoa. So, irrespectively of eukaryotic multicellularity, the possession of some of the characteristics of so-called 'paradigmatic organisms' does not say much about the requirements for organismality. The objection is stronger because, if we take biofilms as self-organizing functional units, then these should qualify as organisms. But in this case, as Werndl (2013) points out, the question is: on what basis is the assumption that biofilms are self-organizing entities that operate as functional units sufficient (or even necessary) for organismality? Self-organization is a very broad term, which can be used to describe the processes in a gas container being externally heated up as well as what happens in **(p. 216)** our whole body. At any rate, as discussed in section 3, self-organization per se is barely adequate for simple self-maintenance. More seems to be needed to postulate that a self-organizing entity operates as a functional unit.

At this point, O’Malley and Dupré (2007) could say that microbial communities are much more than just individuals that happen to have mingled with one another; although they do not possess the level of physiological integrity that individual organisms do, they nevertheless exhibit a degree of integration that allows them to form organism-like communities (ibid., 177). In this case, I think we should try to examine the forms of such integrations. As far as single-species biofilms formed by *M. xanthus* are concerned, I have argued that not only is constitution completely independent of interaction at the MC level, but that there is not even functional interdependence between the individual bacteria that make up the swarm. Therefore, from an organizational perspective, such microbial communities do not even qualify as functional individuals, let alone as organisms.[31]

5.3. The distinction between life and non-life

Does a collaborative view of life blur the distinction between life and non-life? According to our discussion, it can be said that life and non-life are roughly distinguished by the realization of organizational closure on the basis of functional differentiation—that is, on the basis of the mutual dependence (for continuous regeneration) of constraints with *distinguishable contributions* to the global far-from-equilibrium self-maintenance of an organization. Viruses and prions do not exhibit such closure. Therefore, according to the organizational account I have adopted, the individual microbe remains the fundamental ontological unit in microbiology. Let us discuss this in some more detail.

Although it is not quite clear what O’Malley and Dupré (2007: 184) mean when they say that ‘the individual microbe is not the fundamental ontological unit in microbiology’, promiscuous individualism implies that there is no such uniquely identified unit. In line with their emphasis on collaboration, Dupré and O’Malley (2012b: 220) push even further against the view of cells as the fundamental ontological units in biology when they say that, ‘even when single cells are considered in isolation, each cell is a complex of collaborating parts’. However, this is not inconsistent with the fact that it is exactly such complex collaborations that bring about (genuine) recursively self-maintaining organizations. At this point, one could ask why such organizations should be considered alive. Dupré and O'Malley stress the capacity for reproduction and for metabolic sustenance as two fundamental features the intersection of which becomes sufficient for considering an entity as living. But from an organizational perspective, metabolic self-sustainability, reproduction, and their intersection should be interpreted as properties *of* an organization. Extant cells are recursively self-maintaining organizations with exactly such capacities. And it is **(p.217)** from this perspective that viruses should not be considered alive, as viruses are neither self-reproductive nor metabolically self-sustaining organizations.

Dupré and O'Malley say that such commitment to an exclusively cellular view of life implies a single leap from fully non-living to fully living (ibid., 228). I do not think this is the case. In section 3 I argued that organizations exhibiting limited recursive self-maintenance should be considered biological individuals. However, in a prebiotic scenario, such a type of self-maintenance could be instantiated (a) by non-compartmentalized protocells whose self-maintaining networks are very partially coupled to the vesicles that encapsulate them and that could trigger some proto-selective process for stability and persistence (Keller 2007; Budin and Szostak 2011); as well as (b) by protocells with reproductive capacities and with such a coupling between their proto-metabolic network and the components of their membranes that their population could undergo evolution by some kind of (proto-)natural selection (Budin and Szostak 2011). And it is also very likely that the evolutionary selective paths of such individuals would not make it to the organization of existing, fully fledged living beings (see Moreno and Mossio 2015: ch. 5 for a detailed discussion). So, according to the organizational view, collaboration does not blur the distinction between life and non-life. Rather, types of collaboration result in different forms of biological organization that, in the process of originating life, could have been associated with several types of systems, from (hypothetical) protocellular living individuals to fully fledged living unicellular organisms.

6. Conclusions

The importance of collaboration as a central characteristic of life has sometimes been neglected due to the dominant neo-Darwinist view that evolution favours competent selfish competitors. There should be no doubt that collaboration is one of the main characteristics of life and its evolution. Dupré and O'Malley (2012b) are absolutely right to suggest that it is very hard to imagine life (both at the intra- and at the intercellular level) that is not collaborative. A processual view of the living realm suggests that evolution proceeds by weaving a collective network of increasingly complex and entangled processes among biological entities (which are themselves constituted by sets of processes) at different phenomenological levels and with different cohesive strengths. This leads to a conceptualization of living systems as being embedded in evolutionary and ecological webs of metabolic and reproductive interactions. However, an excessively collaborative view of life implies that the essence of biological organization lies in complex webs of processes that span across different living systems. As a result, biological entities appear to become blurred in a series of dynamic and diverse collaborations with flexible and unfixed boundaries (Dupré and O’Malley 2012b). Accordingly, promiscuous individualism declares that there are multiple ways to define individuals, and that we can divide the biological world in as many different ways as we see fit. As I have attempted to argue, this leads to an unnecessary pluralism that in many cases also becomes unmanageable. Considering that we should keep our descriptions as concrete and specific as possible, another, monistic approach to the problem is to accept that biological entities and their boundaries should not be taken for granted and that their emergence and importance should be explicated.

(p.218) This is exactly what I have tried to do in this chapter, from an organizational point of view. Specifically, adopting a process-based organizational ontology, I have suggested that the essential features of unicellular organismality are captured by a self-maintaining organization of processes that is integrated on the basis of a special type of collaboration, realized by regulatory processes that functionally coordinate its constitutive and interactive aspects. I have used this ontology to describe different types of cellular collaborations at the multicellular level, but also to examine which types of MC organization exhibit the form of organismal integration found in unicellular organizations. I have claimed that, although several types of cellular collaborations result in MC biological individuals, the exportation of the core organizational characteristics of unicellular organismality at the MC level require a genuine functional integration (a special type of collaboration realized through a regulatory centre—not just regulatory processes) between the constitutive and the interactive processes of the system. I concluded by arguing that, despite its processual basis, an organizational ontology for biology can provide specific suggestions for several implications raised from the consideration of a hypercollaborative view of life—especially relating to the distinction between life and non-life, between symbionts and host, and between organisms and other biological individuals—without undermining the importance of collaboration in understanding life and its evolution.

Acknowledging the collective dimension of life does not mean ignoring the individual organization of living systems, which has, after all, played a key role in the history of life as the locus of mechanisms, of adaptations, and of selective–evolutionary dynamics. An understanding of the diversity of the biological world requires, I have suggested, an appeal to the organization of individual living systems. I think this is a safe and promising direction, since a theoretically well-founded notion of an individual biological organization is conceptually coextensive with a naturalized account of other fundamental concepts of living systems, such as genetic information, functionality, agency, autonomy, and cognition (Ruiz-Mirazo and Moreno 2012). Moreover, it seems to me that, without such a notion, it would be difficult to make a clear-cut distinction between organisms, parts of organisms, groups of organisms, and other forms of cooperative or ‘ecological’ networks, and thereby to understand the diversity of the biological realm (Arnellos et al. 2013; Arnellos et al. 2014; Arnellos and Moreno 2016).

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Notes:

([1]) There should be no doubt that, as Dupré and O’Malley (2011b) have stressed, collaboration is one of the main dimensions of life and its evolution. Actually, even the concept of autonomy in biology (which places emphasis primarily on individual organisms) is theoretically and philosophically elaborated as entailing interdependence (through interactive openness) between an autonomous entity and its environment (see Rosslenbroich 2014; Moreno and Mossio 2015; Arnellos 2016). Therefore, my objective here is not to undermine the importance of the concept of collaboration in the description of the biological realm, but to suggest alternatives to some of its (in my view) undesirably pluralistic implications.

([2]) The issues discussed in this section are based on the work of Dupré (2012), who has so far offered the most inclusive discussion of the conceptual implications of the adoption of a process view in biology.

([3]) The idea that systems can be individuated completely separately from the situated position of the observer is in principle dismissed. However, there are many causal properties that can serve as a basis for a principled specification of system identity and that are not entirely observer-dependent (Collier 1988; Collier and Hooker 1999; Christensen and Bickhard 2002; Campbell 2009).

([4]) Some organizations of processes persist more than others in an environment. It is in the context of a persistent (and relatively robust) organization of processes that collaboration—either in the form of cooperation between processes in the organization or in the form of competition between old and new processes for participating in the organization—could be considered inherent in a process-based metaphysics.

([5]) Cohesion is defined as the causal closure of the relations among ‘elements’ that constitute a ‘thing’ in a way that keeps it (within a limited range of conditions) from being disrupted by internal and external forces (see Collier 1988, Collier and Hooker 1999, and chapter 4 for a detailed treatment of the concept).

([6]) Chapter 7 also discusses far-from-equilibrium systems and their relevance to process views of biology.

([7]) Constraints are macroscopic structures that harness microscopic processes by reducing their degrees of freedom, that is, by ‘ordering’ them (Hooker 2013).

([8]) As pointed out by Campbell (2009), the ability of a system of processes to be self-maintaining is an emergent causal power of its organization and not of its constitutive processes, which are constantly altered through participation in the organization.

([9]) Functions are indispensable to biology. This becomes apparent as soon as one attempts a functional-free description of any biological, or even protobiological, system.

([10]) The same (degree of) organizational complexity can also be met in chemical self-maintaining systems such as autocatalytic cycles (Kauffman 2000). The cycle is not maintained only by the external boundary conditions, but also (although in a minimal sense) by catalysts, and the catalysts are maintained by their own action (minimal organizational closure). The point here is that an autocatalytic cycle internalizes many constraints of a single type (catalysts).

([11]) In a cell, the membrane and the enzymes constrain the microscopic dynamics of the molecular flows produced by chemical reactions in different ways (see Arnellos and Moreno 2012 for a relevant analysis).

([12]) Self-reproductive capacities are presupposed in the prebiotic scenario we discuss. In case they were not, such protocellular organizations would be what Wilson (1999: 60) describes as a *functional* (biological) *individual*. See section 5 for further discussion.

([13]) The internal organization appears significantly more integrated with respect to its environment than a borderless autocatalytic network or a candle flame.

([14]) In this respect, all unicellular organizations are considered *evolutionary (functional) individuals*.

([15]) Cellular reproduction is not just controlled through genetic replication. There is a key role played by metabolism and, consequently, by the ongoing interactions with the environment in the cell division cycle.

([16]) The TCST mediates the temporal detection of differences in the concentration of environmental nutrients to flagella’s motor output in a global way that enables adaptation (Bijlsma and Groisman 2003).

([17]) This is characteristic of both metabolism-independent and metabolism-based chemotaxis. For details, see Alexandre 2010.

([18]) Overall, *E. coli* chemotaxis is regulated by the TCST as the selective choice of a subset of particular metabolic pathways among the available repertoire (see van Duijn et al. 2006 for a relevant discussion).

([19]) All bacterial chemosensory systems are variations on the chemotaxis TCST (Kirby 2009). Eukaryotes such as paramecia detect nutritious gradients in the same way, but they use detectors at both of their ends, and then compare the inputs.

([20]) The common conception is that an organism is an integrated biological entity, spatially separated from others and made out of interdependent parts that are integrated so that they work in coordination with each other for the proper function of the organized whole (Wilson 1999).

([21]) *M. xanthus* cells form structured single-species biofilms with motility-mediated expansion (formation of tentacle-like packs, cell groups, and synchronized rippling waves of oscillating cells) when other microbial nutrients are available in the environment, and massive spore-filled aggregates that rise upwards from the substratum to form fruiting bodies, mainly when exposed to low or no nutrients.

([22]) Within the swarm, individual cells are constantly moving, transiently interacting with one another, and independently reversing their gliding direction (Kaiser and Warrick 2011). Cells alignment and the formation of clusters could even be due to pure mechanical interactions among cells and between the cells and the substrate (Balagam and Igoshin 2015).

([23]) The interactive activity is not even compatible with the constitutive one, in the sense that the fruiting body of the biofilm cannot be motile.

([24]) There is just one self-maintaining process organization in *V. carteri*: that of swimming. Turning (changing direction) is just the net effect of somatic cells moving their flagella (swimming) differently as a result of detecting different light intensities due to their being placed at opposite sides in the spheroid (see Ueki et al. 2010 for details).

([25]) For instance, a jellyfish can swim fast when escaping predation and slow when eating or migrating.

([26]) Neuropeptides are abundant in jellyfish and play an important role in regulating a variety of developmental and physiological processes (Hartenstein 2006).

([27]) From this perspective, plants qualify as basically organismal, since their interactive dimension coincides with the constitutive one (see Arnellos and Moreno 2015 and 2016 for more detailed discussions).

([28]) The problems symbiosis imposes on aspects of individuality and organismality deserve a separate treatment. Here I aim to provide some preliminary directions and ideas to deal with this phenomenon from the organizational perspective. The implications of symbiosis for the prospects of a process ontology for biology are also considered in chapters 1, 5, 9, and 15.

([29]) An immediate predicament is that, if organisms are integrated biological wholes (i.e. functional individuals), then in what sense does this differ from the standard view of organisms (organisms are unicellular entities, microbes, and multicellular ones, as Dupré mentions), assuming that we do not reject polygenomic wholes?

([30]) See chapter 9 for a complementary discussion of this case study.

([31]) The case of multispecies biofilms is more complicated and deserves a separate treatment. From an organizational point of view, the ascription of a loose form of functional individuality to multispecies biofilms seems possible, whereas the requirements for evolutionary individuality don't seem to be satisfied. At any rate, the latter is a highly controversial topic even from adaptationist and evolutionary perspectives (see e.g. Ereshefsky and Pedroso 2015; Clarke 2016).