

A Part-Dependent Account of Biological Individuality for Multispecies Consortia

*Una ontología parte-dependiente de la individualidad biológica
para los consorcios de múltiples especies*


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Abstract

This article introduces and defends a part-dependent ontology to conceive of biological individuality in conglomerates formed by organisms of multiple species. According to the part-dependent ontology, the characterization of a set or conglomerate of independent taxa as a biological individual must be based on the relationship that a specific part of that set maintains with the rest, the relationship that the rest of the parts of the set maintain with that specific part being irrelevant. Moreover, it is argued that the biological dependency relationships between the parts of a set can be asymmetric, without this affecting the attribution of individuality to said set. It is also pointed out that such a part-dependent characterization is valid not only for ideas of individuality based on evolution, but also for those based on physiology, or immunology, among others. This makes part-dependent ontology compatible with pluralism over biological individuality.

Keywords: organism; biological individual; symbiosis; inductive metaphysics.

Resumen

Este artículo introduce y defiende una ontología parte-dependiente para concebir la individualidad biológica en los conglomerados formados por individuos de múltiples especies. Según la ontología parte-dependiente, la caracterización de un conjunto o conglomerado de taxones independientes como individuo biológico debe basarse en la relación que una parte específica de ese conjunto mantiene con el resto, siendo irrelevante la relación que el resto de partes del conjunto mantienen con la primera. De otro modo, se argumenta que las relaciones de dependencia biológica entre las partes de un conjunto pueden ser asimétricas, sin que esto afecte a la atribución de individualidad a dicho conjunto. Se señala, asimismo, que tal caracterización parte-dependiente es válida no solo para las ideas de individualidad basadas en la evolución, sino también para aquellas basadas en la fisiología, o la inmunología, entre otras. Esto hace a la ontología parte-dependiente compatible con el pluralismo sobre la individualidad biológica.

Palabras clave: organismo; individuo biológico; simbiosis; metafísica inductiva.

1. Introduction

The world around us is full of objects whose borders can be easily delimited by means of intuitive criteria. Indeed, we know that we are surrounded by chairs, tables, computers, bins, etc., and we can easily distinguish where each of these objects begins and ends. This is basically because we know that each of these objects occupies a certain space that we cannot cross without displacing it, or because we know that each of these objects can be moved “as a whole” without separating each of its parts, or because we know that it has a certain functionality. These are three intuitive criteria that allow us to say that each of these objects is *one object* instead of many; or, alternatively, that something is *part of another object* instead of an object itself.

The situation in the biological world does not seem very different from these cases, at least if we think of everyday examples of biological individuals as they are perceived by humans (e.g., dogs, chickens, trees). But the situation in the biological world is not always so simple. For example, take the case of the lichen. From a spatial point of view, or even considering its development, it seems intuitive that the lichen is a single individual. However, the answer changes if we pay attention to its reproduction, since each of the two individuals that compose the

lichen (an alga and a fungus) have independent reproductive regimes.¹ Therefore, from a reproductive perspective, it could be said that there are two individuals instead of one.² The opposite, however, occurs in the case of a bee colony. Intuitively, it seems that each bee has its own biological development, while the colony does not. But only the queen can reproduce. The rest of the bees in the colony lack this capacity. Therefore, what would be an individual from a developmental perspective, would only be a part of a larger individual from the perspective of reproduction.

This paper deals with the topic of biological individuality, and the criteria to determine where the borders of biological individuals begin and end. Concretely, I will adopt an ontological perspective, trying to establish general criteria that could be applied to *any characterization of biological individual*, regardless of the research field where the scientists or philosophers are conducting their research. The reasons for adopting this approach to the research question will become clearer in sections “*Determining the borders of the individual: A plurality of criteria*” and “*The whole-dependent ontology*”.

The paper focuses specifically on the example of symbiosis. The purpose is hence to establish a basic criterion to determine where the individuality of a symbiotic or multispecies consortium begins and ends. By *symbiotic consortium* (or conglomerate, or group),³ I will mean a set of individuals of different species that interact intimately and for a long term with one another. *Intimacy* is defined in relation to the degree of intensity of the interactions, where the type and degree of intensity will be determined by the theory or biological field (physiology, evolution, immunology, development, etc.). *Long term* is defined in terms of the life cycles of the participants in the consortium. Drawing on this characterization,

¹ I am making an idealization in this example, as lichens usually have a microbiome and are hence composed of more than two individuals (Morillas et al. 2022).

² Across the paper, I will use “(biological) individual” instead of “organism” to avoid confusion. Specifically, my choice of “individual” must not be conflated with the uses of those who prefer to reserve it to the unit of evolution (Godfrey-Smith 2013; Smith 2017) or the unit of selection (Clarke 2013). From my perspective, “individual” is biologically neutral, *unless one clarifies which perspective she is taking* (by perspective, I mean scientific discipline, e.g., physiology, development, evolution, immunology, etc.). This necessarily creates a plurality of the type of individuals that exist. My reason to avoid “organism”, in contrast, lies to its association with a plurality of criteria (generally, an organism encompasses physiological, developmental and/or ecological aspects), generally excluding its evolutionary dimension. Since I am interested in thinking about biological individuality in general, regardless of the perspective one adopts, I think the term “individual” is more adequate. See “*Determining the borders of the individual: A plurality of criteria*” for my own view of individuality.

³ The three terms will be used as synonymous along the paper.

the section “*Limits of the whole-dependent ontology*” will show the necessity of introducing a new ontology of biological individuality, which I will call part-dependent ontology (“*The part-dependent ontology*”).

The structure will be as follows. First, I will show why the borders of biological individuality must be determined in relation to criteria established by different biological fields or theories. Drawing on this, I will show why pluralism about biological individuality is unavoidable. Second, I will show how the application of these criteria to multispecies consortia is based on an ontological assumption, which I call *whole-dependency*. According to this assumption, the application of any biological criteria to multispecies consortia must ontologically depend on the establishment of symmetric dependency relationships among the parts of the consortia. By *dependency relationship* I will mean any association between individuals allowing the maintenance of a specific emergent for of individuality (see below). Third, I show that the symmetry assumption is generally inadequate, but specifically inadequate when it is applied to symbiotic consortia. Fourth, I present and defend the *part-dependent ontology* of biological individuality as a solution to these problems, and as a better way of thinking of the individuality of multispecies consortia. Finally, I conclude by reflecting on the implications of part-dependent ontology for thinking about biological hierarchy.

2. Determining the borders of the individual: A plurality of criteria

The issue about the borders of biological individuals admits a plurality or responses, each of them grounded on the criteria being used. For example, Ellen Clarke (2010) distinguishes 13 criteria, some of which would occasionally be used together. These criteria are based on an array of properties, including: the reproductive capacity of the unit; its genetic individuality (one individual = one genome); the germ/soma separation (Weismann barrier); the existence of a life cycle; the histocompatibility among the parts; the presence of policing mechanisms; the manifestation of trans-temporally accumulated or engineering adaptations; or the degree of cooperation/conflict among the parts. On the other hand, historians Scott Lidgard and Lynn K. Nyhart (2017) enlarge the list to include 24 criteria, based on some properties not included in Clarke’s list like the cognitive capacity or the strength of the interactions among the parts.

These data suggest that all these criteria are ultimately grounded on the existence of intensional properties of biological individuals which are both relevant for scientific practice, and generate extensional conflicts about what counts as

an individual. For instance, it seems clear that the histocompatibility criterion is necessary for those interested in studying solid organ transplantation. However, this criterion conflicts with the genetic one, for the very existence of solid organ transplantation relies on the possibility that two individuals who do not share the same genome can ‘easily’ exchange organs with one another. In contrast, self-immune diseases reveal the opposite conflict between these two criteria, since it is sometimes the case that two organs composed of cells sharing the same genome are not histocompatible with one another.

The situation is paradoxical because of all these criteria *are interesting for us based on some of our (scientific) purposes*. But, how can these different criteria be grounded? Or, to put it differently, is this plurality internally valid? If so, can one then suggest any *ad hoc* criterion and make it a valid way of delineating biological individuals? In this paper, I will follow Matt Haber’s (2016) proposal according to which the criteria to determine what counts as a biological individual must derive from the different models and/or theories currently accepted in the study of the biological world.⁴ According to this, as contemporary biology is structured around the fields of evolutionary biology, physiology/metabolism, and immunology, one must necessarily distinguish *at least* three sources of criteria to delimit biological individuals: evolutionary, physiological and immunological (cf. Dupré & O’Malley 2009; Pradeu 2016; DiFrisco 2017; Baedke 2019).⁵

The physiological individuality of a conglomerate is characterized by means of the metabolic relationships between the parts that guarantee the persistence of the whole. This perspective is adopted by different authors. For example, Subrena E. Smith (2017) uses this perspective to define biological individuals as “essentially *persisters*.” In her approach, the persistence capacity of a whole would manifest as a continuous and integrated response to those environmental stimuli compromising its very ontogenetic existence. The capacity would be ultimately grounded on the physiological, developmental and ecological (*but not evolutionary*) relations of functional dependency among the parts. Smith’s work is based on the works of John Dupré & Maureen O’Malley (2009), Scott Gilbert, Jan

⁴ Take into account that ontology is not exclusively grounded on theories, but also on biological models. This frequently occurs in genetics, where the existence of different genetic models obliges to distinguish between interactors, replicators, reproducers, reconstitutors, and manifestors of adaptation (Lloyd 2017; Suárez & Lloyd, forthcoming).

⁵ Someone could argue that further criteria could be added (e.g., based on developmental biology, or ecology, see Huneman 2014), Nonetheless, given that my main argument is not affected by the introduction of new criteria, I will restrict my explanation to the three previous ones for reasons of simplicity.

Sapp & Fred Tauber (2012), and Peter Godfrey-Smith (2013). The latter characterizes the physiological view of individuality in terms of the environmental and energetic division of labor which is required to maintain the structure of the whole.

Evolutionary individuality, in contrast, is most times defined in virtue of the capacity of a system to behave as a unit of selection (i.e., to respond to natural selection as a whole). For this perspective, one could distinguish at least three different conceptions: interactor, replicator/reproducer/reconstitutor, and manifestor of adaptation (Lloyd 2017, Suárez & Lloyd, forthcoming). I will here restrict the analysis to the case of the manifestor of adaptation as restricted to reproduction. According to this criterion, something is a biological individual if and only if it can generate a new biological individual in the next generation through reproduction, being the latter a process which is simultaneously mediated by adaptations for such reproduction. Godfrey-Smith (2009), following this line, argues that an evolutionary individual must be a Darwinian individual, and this will be feasible both if reproduction is simple and direct (e.g., asexual reproduction in microorganisms) and if reproduction is more complex and requires reproductive division of labor (e.g., in sexually reproducing organisms). Nonetheless, reproduction in the last case only occurs—according to Godfrey-Smith—if every part of the individual cooperates with one another, thus guaranteeing that sexual reproduction happens. Godfrey-Smith argues that this cooperation will be evolutionarily gradual, and it could be detected through specific mechanisms such as germ/soma separation, the existence of a bottle-neck or the integration among the parts, all of which serve as proxies for detecting the collaboration (see Molter 2019 for further mechanisms). In the lack of any proxy, then the collective will not be an evolutionary individual, according to Godfrey-Smith.⁶

Finally, if individuality is conceived immunologically, it is common to define it in terms of the type of immunological reactions within a system, which will determine what is “in” and/or “out.” The traditional view would conceive the

⁶ Martín-Villuendas (2021) argues correctly that proposing any criterion for evolutionary individuality is more complex, as it requires a previous agreement about what other properties like variation or inheritance are. I think this is correct. However, this does not necessarily affect my approach, as it is entirely pragmatic in this regard and recognizes that different research groups may use different definitions and thus we would end up with different concepts of “evolutionary individual.” Deciding whether the existence of these many concepts is the case is an *a posteriori* task, usually identified if there is a division within the field of evolutionary studies. I will not evaluate this issue here.

immunological system as a barrier or tolerance system, i.e., one which includes or excludes, working as an “army” which protects the *self*—the individual—from the *non-self*. Recent view, in contrast, align immunology with developmental biology to define the immune system as a system that cohesively reinforces the different elements composing an individual, insofar as the immunological system integrated these different and potentially independent components into a coherent whole—the individual (see Tauber 1994, 2016). The immunological system would then be a trans-temporal ‘builder’ of individuality. Thomas Pradeu (2010, 2012, 2020) has recently defended an immunological view of individuality through his discontinuity theory. According to this, the borders of the individual are provided by the effector immune responses, which are produced due to extreme changes in the molecular motifs interacting with the immunological receptors. The immunological system will tolerate *and integrate* all those motifs within a specific range, excluding those that fall outside the range (or are too extreme to be potentially included). This makes the biological individual a constantly building unit. In this sense, whatever is included and/or excluded within an individual could change over time or during the development of the individual, due to changes in the immunological system or slow changes in the molecular motifs. Under Pradeu’s approach, the nature of the relationship between the immune system and the molecular motif of an antigen at a specific moment in time determines inclusion/exclusion, rather than the very nature of the antigen itself.

Overall, the key message of this section is the following. On the one hand, the three fields I have analyzed offer specific characterizations of individuality which are linked to three specific research questions: How do organisms evolve? How does their metabolism work? How does their immune system operate? On the other hand, the observation that these three fields require of different criteria linked to the different research questions of each field, and the theories and models guiding these research questions, *does not exclude that each of the criteria used in these fields is ultimately based on metaphysical principles*—even when these are implicit. In this sense, it is basic to distinguish between what Marie Kaiser (2018) calls “biological mereology” and “metaphysical mereology.” The first establishes the main biological criteria to determine whether a specific conglomerate satisfies certain biological criteria to be considered a biological individual. The second, in contrast, deals with the fundamental and often implicit metaphysical principles that are required to establish *any* characterization of individuality. In the concrete example of this paper, I follow Vanessa Triviño and Javier Suárez (2020) in their conception that metaphysics, understood as the logical framework of possibilities that are opened

due to the research on the constitutive principles of reality (French & McKenzie 2015), is necessary to determine which are the ultimate assumptions underlying biological criteria, as well as the limitations that those assumptions generate in the study of scientific objects (in this case, biological individuals; see also Guay & Pradeu 2016). In the next section, I will reveal what those principles are for later analyzing how the pervasiveness of symbiosis questions their validity.

3. The whole-dependent ontology

The different conceptions of biological individuality introduced above lie on what Javier Suárez & Adrian Stencil (2020) call “whole-dependent” ontology. By whole-dependent ontology they refer to the ultimate criterion that all theories and/or models of biological individuality are grounded on, regardless of the proximate criteria used to define individuality.⁷ Suárez and Stencil characterize the basic principle of whole-dependent ontology appealing to necessary and sufficient conditions:

a whole is a biological individual if and only if *all the elements that constitute the whole* satisfy a specific criterion of individuality (physiological, immunological, evolutionary, etc.). If some of the parts of the whole do not satisfy the criterion, then the whole is not a biological individual. (Suárez & Stencil 2020, 1309)

And a bit later, to explain precisely what whole dependency consists in, they claim:

[R]egardless of the conception of biological individuality [physiological, immunological, evolutionary] that one uses, the process of delineating biological individuals relies on an ontological assumption according to which the dependency relations among the total amount of elements that compose the whole whose individuality is evaluated are interpreted symmetrically. In other words, the whole qualifies as an individual if and only if all the parts that compose it *mutually* depend on each other. (Suárez & Stencil 2020, 1317)

⁷ I use “ultimate” as opposed to “proximate” in the following sense: a proximate criterion would refer to the field, theory or model used to define individuality, while the ultimate criterion would refer to the metaphysical principle underlying those proximate criteria.

I suggest calling this assumption the “symmetry principle” or co-dependency, which analytically formulated it will be as follows. Let G be a group composed by several individuals a , b , in biological interaction, then:

Symmetry Principle: G will be a biological individual if and only if the dependency relations between a and b are symmetric. That is, a depends on b and b depends on a exactly on the same manner.

In this context, by *dependency relation* I mean the association between (necessarily more than one) individuals making naturally—i.e., not only under laboratory or experimental conditions—feasible the maintenance of a specific form of individuality. That is, to consider a relationship between two (or more) parts a dependency relationship, the relationship must be a condition of possibility for the existence of *at least* one of the parts. I will distinguish four types of dependency relationships: mutual and non-mutual; exclusive and non-exclusive. In general, the relationships of dependency between two parts are mutual when the notion is based on the symmetry principle. This is so even though the mutuality can be established on the basis of different functional—but complementary—roles by each of the parts. For example, if a does M , which b needs for surviving, while b does N , which a needs for surviving, then their dependency relationship is mutual. If only one of the parts depends on the other, but the second one does not depend on the former, then the dependency relationship is non-mutual. Furthermore, mutual dependency relationships are frequently exclusive dependency relationship too, as it occurs when two species or taxa depend co-depend on one another. In contrast, non-mutual relationships are usually non-exclusive, as different species can obtain what they need from more than another species.

Clarifying this further, let’s examine the way how whole-dependent ontology underlies the different conceptions of individuality presented above. Let’s start with physiological individuality. Their proponents state that the parts must work *together, coherently* and, even claim that “if the parts of a system have a significant amount of metabolic autonomy, and can keep themselves going somewhat independently, this reduces the degree to which the larger system counts as an organism [biological individual]” (Godfrey-Smith 2013, 26), and “[t]he integration of differentiated parts, which allows for phenotypic accommodation, provides the basis for the idea that organisms are in some sense whole systems.” (Smith 2017, 2). These are typical demands of those holding a symmetry principle: G will be a physiological individual if and only if the parts a and b that compose G mutually

depend on one another. But, as soon as *one of the parts* is relatively independent, the *whole* is no more a biological individual, as the requirement of co-dependency is not fulfilled anymore.

Evolutionarily speaking, the co-dependency requirement is also clearly assumed. On the one hand, any criterion based on the plurality of concepts meant by the expression “units of selection” will require that the whole will be equally affected by natural selection, in a way such that the reproduction of its parts will be differential to the one expected if selection were not acting. For the specific case of the Darwinian individual, the whole must divide as a single unit. This is particularly salient in the words of Godfrey-Smith who, in his analysis of ant-tree symbiotic associations, claims:

But these ant-tree combinations are not Darwinian individuals [...] Trees have offspring trees, and ants (and ant colonies) have offspring ants (and colonies), but an ant-tree combination does not reproduce as a unit. It might sometimes be that the ants in a particular tree are the descendants of ants who lived in a parent of that tree, but that would be accidental. The most we can apparently say is that one ant-tree combination, X, is the offspring of another ant-tree combination, Y, if either the ant part or tree part of X (or both) is the offspring of the ant part or tree part of Y. Even this makes the association sound tighter than it often is, as one colony may be supplanted by another and in some cases colonies of more than one species may occupy a tree at the same time. (Godfrey-Smith 2011, 507).

This is simply a criterion of co-dependency for reproductive individuality. As the ants living on a tree can be replaced by different ants, the tree does not have any symmetric reproductive dependencies with the ants. Therefore, ant-tree combinations are not biological individuals from a reproductive perspective. To be so, the tree must depend on a specific ant colony for its reproduction, and vice versa.

Finally, let's examine the immunological criterion. Pradeu claims that the key to delimit the borders of individuals lies on the immunological tolerance/intolerance triggered in response to certain molecular motifs. Those responses would occur in specific immunological receptors, which Pradeu (2012) contends must be in every organism. In his view, given that all cells are individuals—even when they belong to a multicellular organism—then all of them must have a certain type of immunological receptor responsible of the immunological tolerance. Take two random cells from a multicellular organism, and let's evaluate whether the conglomerate formed by both constitutes a biological individual, or

it is rather a set of independent biological individuals. To do so, and following Pradeu's criterion, we must evaluate whether the cells tolerate one another. If they do so, they will be. However, if one of the cells does not tolerate the other, even when the later tolerates the former, then the set formed by the two cells will not be a biological individual, as there is not a mutual relationship of tolerance. This lack will manifest because the first cell will generate certain immunological reaction to destroy the second cell, which will in turn compromise the stability of the whole. I think this analysis is perfectly correct. But what concerns me in this paper is analyzing the ontology underlying Pradeu's conception. If the fact that one cell—of a set of two cells—does not tolerate another entails that the set formed by the two cells is *not* a biological individual, then it would seem as if the symmetry principle were necessary to define immunological dependency and, in turn, to define individuality. In other words, Pradeu's criterion would be whole-dependent.

The analysis shows that the main ideas about individuality in today's literature are all based on whole-dependency. Note, though, that even while the whole-dependent ontology underlies all these conceptions, this does not make whole-dependency automatically valid. The metaphysical principles underlying scientific theories and models substantially depend on the set of phenomena that a scientific community decides to study. A change or ampliation in this set of phenomena may lead to a substitution of some metaphysical principles for different ones. Samir Okasha has recently expressed something similar. In his research on the role of agency in evolution (by agency, let's understand something similar to manifestors of adaptation as defined above) and how this relates to multilevel selection modelling, Okasha has realized that presupposing certain principles for the characterization of biological individuality is a *verbal, terminological or definitional* issue, but not a *metaphysical or substantive* one. To quote:

This is not to say that group or multi-level selection is rare, but only that it does not usually lead groups to exhibit the degree of internal harmony that a typical [reproductive/biological] individual has. Indeed, in a sense this is a definitional rather than a substantive truth, since where groups do evolve a high degree of cooperation and functional integration, we tend to elevate them to the status of 'individuals' and regard their members as parts of a single whole. (Okasha 2018, 53)

The argument underlying Okasha's claim works as follows. We *decide* that a specific set of properties taken to be necessary by some evolutionary models are necessary requirements for defining individuality. But, in fact, there are more

models—like multilevel selection models—which consider different properties to be necessary, and which also play a key role in biological research. The *decision* is, therefore, a *convention*—according to Okasha—but not a substantive truth about the ontology of biological individuality. Okasha seems not to have any problem with us making such convention, and I would contend that, at least in Okasha (2018), his attitude is related to the fact that he is not primarily interested in doing ontology—or, if he were, he is not primarily interested in understanding the ontology that underlies biological individuality. However, my position at this point differs from his, as my paper precisely examines whether the ontological assumptions that one makes about biological individuality—particularly, whole-dependency—are useful to cover most biological phenomena and models. In the next section, I show that this is not the case, and thus requires the formulation of a new ontology.

4. Limits of the whole-dependent ontology

Symbiosis poses a fundamental problem for whole-dependency since the dependency relationships between symbionts do not always satisfy the symmetry principle. This violation is not the case for every symbiotic relationship, though. For instance, there are some relationships occasionally referred to as “symbiotic” which are solely ecological relationships.⁸ That is, they are relationships in which the parts do not develop any dependency relationship with one another. A well-known example is the relationship between bees and flowers. Bees feed on flowers’ nectar and in doing so they carry the flowers’ pollen and disperse it. Given that each bee visits several flowers, it acts as a vector of the plants’ gametes, and in doing so both bees and flowers obtain a mutual benefit. However, even though the relationship between the parts benefits both members, it is not exactly a dependency relationship. On the one hand, there are thousands of flowers that bees can visit, as well as other sources of food; on the other, flowers do not exclusively depend on bees to transmit their pollen: bees are simply another means of increasing their reproductive range. Those defending a whole-dependent ontology will argue that, in this case, the parts involved in the relationship do not form a single individual, and I agree with their consideration.

⁸ Note that I use “occasionally referred to as symbiotic”, rather than directly asserting that they are symbiotic, because in fact the relationship seems to violate the requirements to be considered symbiotic that I have established in the *Introduction*.

In sharp contrast, there are some symbiotic relationships that do generate a mutual—and exclusive—dependency relationship between the parts. A well-known example is the eukaryotic cell, evolved as a result of the symbiosis between a bacterium and an Archaea (Deulofeu & Suárez 2018). In this case, the dependency relationship is such that once the bacterium and the Archaea have evolved to transform into the mitochondria and the main body of the cell, none of them can survive independently of the other, nor can they naturally change partners. The mitochondrion is the cell ‘factory,’ in charge of producing the metabolic mediation, ATP. Every eukaryotic cell has mitochondria. On the other hand, the mitochondrion depends on the Archaea, since it cannot survive if it is not an organelle of the eukaryotic cell.⁹ The symbiosis literature includes many examples of analogous relationships, in which the dependency relationships between the parts are mutual or symmetric (Moran 2006). This specific type of relationships is usually established between a specific bacterial species and a host—e.g., an insect—which makes them exclusive dependency relationships. A common example is the symbiotic union between aphids and *Buchnera aphidicola*.

The two cases just described represent two extreme examples in a spectrum: the lack of dependency and co-dependency. But, are there examples of one-sided dependency? And, if there were, does it make sense to consider these examples as instances of biological individuals?

To start with, I will consider the first question, and I will leave the second one for the next section.¹⁰ A unilateral dependency will exist every time that one of the members of the pair does not experience any consequences if there is a lack of interaction, while the other clearly does. Determining those effects will of course depend on the criterion one chooses: physiological, immunological, evolutionary. Let’s take a hypothetical example to better understand the unilateral dependency conditions. Let’s imagine a multicellular individual that interacts with a specific bacterium. The effects of cancelling out the interactions must be obvious and contrasting for each of the members of the pair: while of them becomes compromised physiologically, evolutionarily or immunologically (even dying or losing its capacity to reproduce), the other does not. The scientific literature is full of examples of this kind, as I will just show (the examples are taken respectively

⁹ Take into account, for clarity purposes, that this is a very idealized way of telling the story, since it would be strange saying today that a eukaryotic cell is a conglomerate of two individuals, rather than as a single one resulting from a process of endosymbiosis.

¹⁰ Of course, these questions must be resolved together, as they complement one another. But the arguments can be separated to analyze better each question and each answer. I will follow this argumentative strategy.

from Stappenbeck et al. 2002; Mendoza et al. 2018; Olszak et al. 2012; for a philosophical analysis, see Suárez 2019, 2020; Suárez & Stencel 2020; Suárez & Triviño 2020).

A. Physiology. *Bacteroides thetaiomnicron* is a well-known symbiont of several mammals, including humans or mice. If mice grow in laboratory conditions and do not interact with *B. thetaiomnicron*, they develop serious problems in their blood vessel structure. This justifies saying that mice physiology depends on their interactions with *B. thetaiomnicron*. However, the reciprocal is false: *B. thetaiomnicron* has a diversified ecology, and it may change across different hosts, and even live host-free. The dependency is not symmetric, but asymmetric, even though it is exclusive.

B. Evolution. Vampire bats (bats with an obligatory blood-sucking diet) bear a genome which is clearly maladaptive for their diet, and such maladaptiveness is complemented via its microbiome. In fact, an important amount of the traits that vampire bats need to survive in their blood-sucking diet are provided by their symbiotic microbiome. Without their microbiome, vampire bats wouldn't survive and it would even be impossible to explain how the family evolved. There is thus a dependency between vampire bats and their microbiome. However, the reciprocal is false. The microorganism species composing the microbiome of vampire bats can easily survive across different bat families—frugivorous, carnivores, etc. In fact, a 16S rRNA analysis reveals the lack of species diversity in vampire bats as opposed to other bat families. There are *striking* functional differences across the microbiome of different bat families—frugivorous, carnivorous, etc.—but the differences are not mirrored at the species level which suggests that the microorganisms that compose vampire bats' microbiome could survive in different environments. If this is so, then it would seem that these microorganism species do not evolutionarily depend on vampire bats, even though they functionally provide the latter with some of the essential factors for their survival and having made the evolution of vampire bats feasible. The dependency is thus asymmetric, and it is not exclusive in any of the directions.

C. Immunology. *Bacteroides fragilis* has been identified as one of the main microorganisms triggering the maturation of the immune system in mammals. Concretely, the interaction between the immune cells and the polysaccharides of the capsule of *B. fragilis* is essential to correct deficiencies and disequilibria in T-cells, as well as in the development of the lymphatic system. Gnotobiotic or germ-free mammals do not develop the lymphatic system, nor do they avoid

constant disequilibria in their T-cells. There is a clear immunological dependency between mammals and *B. fragilis*. However, the interaction is not reciprocal. On the one hand, *B. fragilis* survives across different hosts, having been detected in many mammals. On the other, *B. fragilis* has also been detected as a free-living bacterium. This independency occurs without any deficiency in the immunological system of *B. fragilis*. The dependency is thus asymmetric and, probably, non-exclusive.

These three cases suggest that whole-dependency clashes with empirical observations, as there are some asymmetric relationships between different individuals. Note that this does not suppose a knock-down argument against whole-dependency: no one defending whole-dependency believes that asymmetric relationships are impossible. They only implicitly assert that they are *not sufficient* to consider a group of individuals as an individual. To justify the lack of correctness of whole-dependency, I must present a different argument showing why groups of parts establishing asymmetric relationships with one another must be considered individuals. That is, I must respond to the second question of the two questions presented a few paragraphs above. I will justify why this is so at the end of the next section but I will first introduce the part-dependent ontology as a better way of conceiving biological individuality.

5. The part-dependent ontology

The part-dependent ontology arises from the observation that at least a set of the biological relationships that must be elevated to the status of individuals violates the symmetry principle. This suggests that we must get rid of that requirement and substitute it by a different one. *A priori*, the main candidate would be a criterion of asymmetry, which could be formulated as follows. Let G be a group composed by several individuals a, b , in biological interaction, then:

Asymmetry Principle: G will be a biological individual if and only if the dependency relations between a and b are asymmetric. That is, if a depends on b , then b does not depend on a and vice versa.

However, such criterion does not work. On the one hand, I already said that the relationships between the parts of many individuals are symmetric, something that defenders of whole-dependency have shown and this is a claim they are right about. It seems clear that the dependency relationships between the cells of a multicellular organism are symmetric, especially since the death of some of

them usually entails the death of all the others. Taking a principle like the asymmetry principle would lead to erroneously rejecting these cases, and we would be throwing the baby with the bath water.

A weaker criterion, one recognizing the possibility that *many* of the dependency relationships between the parts of an individual are symmetric, without renouncing to the fact that *not all* of them need to be so, is required. Suárez & Stencel (2020), whose conception of individuality I follow in this paper, suggest that the relationships between the parts must be non-symmetric. In contrast with the asymmetry, which requires:

$$1. \quad \forall xy (P_{xy} \leftrightarrow \neg P_{yx})$$

Non-symmetry is built as the set of relationships that satisfy:

$$2. \quad \exists xy (P_{xy} \ \& \ P_{yx}) \ \& \ \exists xy (P_{xy} \ \& \ \neg P_{yx})$$

That is to say, the relationships are sometimes symmetric and sometimes asymmetric. This allows for a more pluralistic conception of individuality than the one proposed so far, as it is reflected in Figure 1.

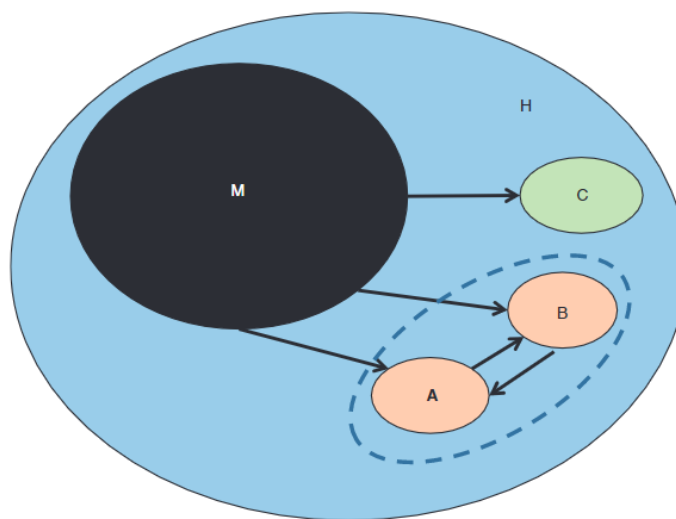


Figure 1. Graphic representation of the contrast between whole-dependent and part-dependent ontology. Let *A*, *B*, *C* and *M* be independent individuals, and let *H* be a higher-level individual. The arrows represent dependency relations (physiological, reproductive or immunological). According to the whole-dependent ontology, only the set formed by *A* and *B* would be a biological individual, while the set *H* would be a group

of individuals. According to the part-dependent ontology, however, both H , and the set formed by A and B , as well as C , are all individuals. From Suárez & Stencel (2020, 1319, Fig. 1).

At this point, it must be clear to everyone who has followed the argument that something like (2) underlies the ontological nature of biological individuality, given that the case of the microbiome shows that the dependency relationships are *not always* symmetric. I suggest calling the principle expressed in (2) non-symmetry principle, and I will specify it as follows. Let G be a group composed by several individuals a , b , in biological interaction, then:

Non-symmetry Principle: G will be a biological individual if and only if there are dependency relations between a and b in at least one direction. That is, if a depends on b , but not the other way around; or if a depends on b and b also depends on a .

The non-symmetry principle *does not establish any empirical criterion* to determine that there is a dependency among the parts, though. As I said above, the empirical requirements to study individuality must always be grounded in biological theories or models, such as physiology, immunology or evolution. Despite this, the non-symmetry principle *does* establish some conditions to determine when a conglomerate of biological individuals is a group vs when it is an individual, by requiring that *at least* one of the parts a of a conglomerate establishes a dependency relationship with another b , regardless of its reciprocity. I propose calling this ontology *part-dependent*, in contrast with the whole-dependent ontology I introduced above. The main feature of part-dependent ontology is that the criterion of individuality, and the borders of what counts as part of a biological individual, is determined by reference to a privileged part of the group, evaluating the dependency relationships (physiological, evolutionary immunological) that this part established with the rest of the parts of the group.

One may accept my argument and still contend that the point I am raising is not biologically relevant. In the end, I would have established an *a priori* criterion which is not directly connected with empirical reality, since I explicitly admit that the latter depends on specific biological criteria. In other words, and paraphrasing Okasha, the part-dependent ontology is a definitional matter, subject to pragmatic considerations about what we want our terms to mean, but they are not a substantive matter of discussion. I do not think this would be correct, though: my defense of the part-dependent ontology is grounded on a substantive perception about how the biological world functions. In what follows, I will

articulate my answer to this objection further and, in doing so, I will reply to the question I raised on whether it makes sense to consider multispecies conglomerates as individuals.

To understand why my answer is affirmative, let's consider the example of the Hawaiian bobtail squid *Euprymna scolopes* and its primary symbiont, the bacteria *Vibrio fischeri*. This case has been cautiously studied by Elisabeth A. Lloyd and Michael J. Wade (2019) so I will follow their analysis here. The Hawaiian bobtail squid (family: Sepiolidae) is a small squid (maximum length: 30 millimeters; average weight: 3 grams) which lives in the coasts of Hawaii and Midway in the Pacific Ocean. The species is well-known for its bioluminescence. The trait is produced in its bioluminescent organ, which produces an electric response when it receives sunlight, and it activates during night. The squid can partially control the intensity of the light by modifying its ink gland, which opens and closes the bioluminescent organ regulating its behavior.

The most interesting aspect of bioluminescence is how it is produced. The development of the bioluminescent organ as well as the emission of light during the life of *E. scolopes* is mediated by the bacteria *V. fischeri*. The organs, tissues and processes allowing bioluminescence are controlled by several genes in *E. scolopes*, and the trait plays a key role for its survival and reproduction. It is thus a clear example of a 'designed' trait, produced by the engineering or trans-temporal accumulation of small adaptations. Some of the traits allowing the appearance of bioluminescence include: (i) the patterns of bacterial recognition, allowing to distinguish *V. fischeri* from other bacteria; (ii) the development and further loss of cilia in the squid, which allow the acquisition of bacteria during the first stages of development and block its acquisition after the organ has been formed; (iii) the development of bottle-neck mechanisms allowing the acquisition of very few bacteria; (iv) the development of expelling mechanisms guaranteeing that 95% of the bacteria that have grown are expelled each day; (v) the development of ecological mechanisms allowing the growth of bacteria in the organ such that their average numbers are kept constant despite their daily expel.

All these traits have evolved in the squid-*V. fischeri* system, as they are squid adaptations to this specific symbiont. However, the reciprocal is not correct, as most of the engineering adaptations in *V. fischeri* allowing their interaction with the squid either phylogenetically pre-date their symbiotic association, or are a byproduct of traits that evolved to favor their free-living stages. According to Lloyd & Wade (2019), this generates a situation in which an engineering adaptation is produced unidirectionally, so the consortium would be what they call a

demibiont. However, the evolution concerned is an evolution *of the consortium*. That is, the adaptations, even though they only evolved on the squid-side, would not have evolved in the same or similar way if the squid had not evolved in interaction with *V. fischeri*. Furthermore, any genetic model trying to explain the evolution of bioluminescence in *E. scolopes* must be structured by considering the biological properties of *V. fischeri*: how it can contribute to the consortium, how it can “trick” the squid, how it can penetrate the squid, etc. Otherwise, it is impossible to understand why the Hawaiian bobtail squid has evolved in the way it has done so, as we would be neglecting a part of its evolutionary history. It is therefore necessary to consider the squid-*V. fischeri* system as a biological individual, *even though the evolutionary dependency relationships between the parts are asymmetric*.

Note that, explained this way, the argument I have provided *seems* epistemological rather than ontological. But this is not really the case. What I am arguing here is that, if the Hawaiian bobtail squid has evolved with its symbiont such that its adaptations are primarily responses to the symbiont, then the squid-*V. fischeri* system constitute a biological individual at least in relation to the trait of bioluminescence.¹¹ Just to make it clearer: the conception of biological individual is introduced to refer to *whatever evolves, whatever has its own physiology, whatever has its own immunological system*, etc. regardless of whether we know whether it does or doesn't (as this question is open to scientific investigation). Showing that the squid-*V. fischeri* system is all that, or at least some of that (whatever evolves) with respect to one of the parts of the consortium (*E. scolopes*), demonstrates that the concept of individuality can be applied to the squid-*V. fischeri* system. This would have also applied even though biologists had not discovered this to be so yet. Thus my argument is not that if we assume that the squid-*V. fischeri* system is an individual, then we know why it evolved how it did. Rather, the point is that the squid-*V. fischeri* system is an individual *because in fact it has evolved how it did*.

6. Beyond individuality: The part-dependent ontology and the problem of the biological hierarchy

This paper shows how the data generated from scientific disciplines allows enriching some metaphysical hypothesis, as well as improving our understanding

¹¹ Regarding bioluminescence. I would accept that this is not the case for other traits. But my view of individuality precisely accommodates the notion that there are individuals across different levels without requiring that the existence of an individual at one specific higher-level rules out the individuality of all its lower-level components.

of the nature of concepts. Particularly, I have argued that our current understanding of the phenomenon of symbiosis forces us to rethink the ontological assumptions underlying most conceptions of biological individuality, as it questions the symmetry principle, or the necessity of co-dependency among the parts of an individual. In other words, whether a conglomerate constitutes an individual or not rest on the dependency relationships among the parts, but does not depend on those being necessarily symmetric (as it is erroneously assumed by most conceptions of individuality). On the contrary, *it only depends on the relationship between a part of the conglomerate and the rest of the parts*. I have called this non-symmetry principle, insofar as I do not require that all relationships must be asymmetric, but rather admit that these relationships may sometimes be asymmetric, without this asymmetry compromising the individuality of the whole. The non-symmetry principle grounds what I have called part-dependent ontology.

I want to finish the paper with a very brief reflection of the implications of part-dependent ontology to rethink the problem of biological hierarchies (already introduced in Suárez 2019). I use *hierarchies* and not hierarchy since, according to the notion of individuality I have defended, it is always necessary to specify the criterion being used (physiology, evolution, immunology, etc.) before establishing any classification. In general, it is assumed that any hierarchy of biological individuals *must be nested*. That is, the individuals in the higher-level are fully composed by all the individuals at the lower-level, which they include mereologically. For instance, we argue that a lichen is a higher-level individual because its individuality nested-ly comprises the individuality of the alga and the fungi composing it, and as such every part of the fungi and every part of the alga necessarily belongs to the lichen simultaneously. I think this assumption is a logical derivation from the fact that individuality is usually thought as whole-dependent—as I have shown above—and so the biological hierarchy must be so as well. But, is hierarchical nestedness a precondition for thinking of *any* biological hierarchy? Or, to put it differently, is it possible that the hierarchy is sometimes non-nested? By non-nested I mean that higher-level individuals do not need to include as components each of the parts of all the lower-level individuals composing them. That is, there will be at least one part which belongs to the lower-level individual and does not belong to the higher-level individual. Following Suárez (2019), I suspect that the assumption of a part-dependent ontology entails that biological hierarchies are non-nested, as the higher-level individuals generated do not always compromise the individuality of its lower-level counterparts, as at least one part of one of the lower-level components still retains its independency. Another

way of seeing this claim more clearly would be this: Let A and B be two components that establish asymmetric relationships with one another from A to B . Let x and y be two parts of B . The unilateral dependency results from A establishing dependency relationships with x , but not with y . Therefore, the individuality of A is compromised—because, from A 's perspective, the individual would be the A/B conglomerate—but B does not—for at most a part of B is compromised, but not B as a whole. Note that Suárez's (2020, 2021) stability of traits criterion, according to which not every component in a biological relationship necessarily participates in the relationship, is not but another way of underscoring the same point. The biological hierarchy would thus be non-nested when analyzed from a part-dependent perspective.¹²

7. Conclusion

In this paper, I have defended a part-dependent ontology to think about the biological individuality of multispecies conglomerates. In the first part, I have introduced the necessity of relying on the criteria of specific scientific fields and/or theories to determine the borders of biological individuals. I used this to suggest the inescapability of pluralism about biological individuality. In the second part, I have shown that most of these criteria are based on what I have called whole-dependent ontology, something that becomes crystal-clear when these criteria are used to think about symbiotic consortia. According to whole-dependent ontology, the application of each of these criteria to a group ontologically depends on the establishment of symmetric dependency relationships between the parties involved in the group. In the third part, I have shown that this assumption is inadequate in general, but more particularly inadequate in its application to symbiotic consortia. In the fourth part, I have presented and defended the part-dependent ontology of biological individuality as a solution to the aforementioned problem. According to part-dependent ontology, the dependency relationships that must be established between the parts of a multispecies consortium can be non-symmetric, without this lack of symmetry necessarily compromising the individuality of the whole. Finally, I have outlined a small reflection on the implications of the part-dependent ontology to think about the nature of biological hierarchies.

¹² I am conscious that this would require further argumentation. I only aimed to draft the main idea, so that the implications of a part-dependent ontology can be appreciated.

References

- Baedke, J. (2019). What Is a Biological Individual? En J. Martín-Durán y B. Vellutini (eds.), *Old Questions and Young Approaches to Animal Evolution*. Fascinating Life Sciences. Cham: Springer.
- Clarke, E. (2010). The problem of biological individuality. *Biological Theory*, 5(4), 312-325.
- Deulofeu, R., Suárez, J. (2018). When Mechanisms Are Not Enough: The Origin of Eukaryotes and Scientific Explanation. In A. Christian, D. Hommen, N. Retzlaff and G. Schurz (eds.), *Philosophy of Science*. European Studies in Philosophy of Science, vol 9. Cham: Springer.
- DiFrisco, J. (2017). Kinds of biological individuals: Sortals, projectability, and selection. *The British Journal for the Philosophy of Science*, 70(3), 845-875.
- Dupré, J., O'Malley, M.A. (2009). Varieties of living things: Life at the intersection of lineage and metabolism. *Philosophy, Theory and Practice in Biology*, 1, 1.
- Engelhard, K., Feldbacher-Escamilla, C.J., Gebharter, A., Seide, A. (2021). Inductive Metaphysics, *Grazer Philosophische Studien*, 98(1), 1-26.
- French, S., McKenzie, K. (2015). Rethinking outside the toolbox: Reflecting again on the relationship between philosophy of science and metaphysics. En T. Bigaj, y C. Wüthrich (eds.), *Metaphysics in contemporary physics, Poznan studies in the philosophy of the sciences and the humanities* (Vol. 104, pp. 25-54). Brill: Rodopi.
- Gilbert, S., Sapp, J., Tauber, A. (2012). A symbiotic view of life: We have never been individuals. *The Quarterly Review of Biology*, 87(4), 325-341.
- Godfrey-Smith, P. (2009). *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press.
- Godfrey-Smith, P. (2011). Agents and acacias: replies to Dennett, Sterelny, and Queller. *Biology & Philosophy*, 26(4), 501-515.
- Godfrey-Smith, P. (2013). Darwinian individuals. In F. Bouchard and P. Huneman (eds.), *From group to individuals: Evolution and emerging individuality*. Cambridge, Massachusetts: The MIT Press.
- Haber, M. (2016). The biological and the mereological: Metaphysical implications of the individuality thesis. In A. Guay and T. Pradeu (eds.), *Individuals across the sciences* (pp. 295-316). Oxford: Oxford University Press.

- Huneman, P. (2014). Individuality as a Theoretical Scheme. I. Formal and Material Concepts of Individuality. *Biological Theory*, 9, 361-373.
- Kaiser, M. (2018). Individuating part-whole relations in the biological world. In O. Bueno, R.-L. Chen, and M. Fagan (eds.), *Individuation, process and scientific practices* (pp. 63-90). Oxford: Oxford University Press.
- Kaiser, M. (2019). Normativity in the philosophy of science. *Metaphilosophy*, 50, 36-62.
- Lidgard, S., Nyhart, L.K. (2017). *Biological individuality: Integrating scientific, historical and philosophical perspectives*. London: The University of Chicago Press.
- Lloyd, E. A. (2017). Units and levels of selection. In E. N. Zalta (ed.): *The Stanford Encyclopaedia of Philosophy*. <https://plato.stanford.edu/entries/selection-units/>
- Lloyd, E. A., Wade, M. J. (2019). Criteria for Holobionts from Community Genetics. *Biological Theory*, 14(3), 151-70.
- Martín-Villuendas, M. (2021). Una reconsideración pluralista del concepto de herencia. *Contrastes. Revista Internacional de Filosofía*, 26(3), 25-47.
- Mendoza, M. L. Z., Xiong, Z., Escalera-Zamudio, M., et al. (2018). Hologenomic adaptations underlying the evolution of sanguivory in the common vampire bat. *Nature Ecology and Evolution*, 2, 659-668.
- Molter, D.J. (2019). On mycorrhizal individuality. *Biology and Philosophy*, 34, 34-52.
- Moran, N. (2006). Symbiosis. *Current Biology*, 16(20), R866-71.
- Morillas, L., Roales, J., Cruz, C., Munzi, S. (2022). Lichen as Multipartner Symbiotic Relationships. *Encyclopedia*, 2(3), 1421-1431. <https://doi.org/10.3390/encyclopedia2030096>
- Okasha, S. (2018). *Agents and Goals in Evolution*. Oxford: Oxford University Press.
- Olszak, T., An, D., et al. (2012). Microbial exposure during early life has persistent effects on natural killer T cell function. *Science*, 336, 489-493.
- Pradeu, T. (2010). What is an organism? An immunological answer. *History and Philosophy of the Life Sciences*, 32(3), 227-247.
- Pradeu, T. (2012). *The limits of the self: Immunology and biological identity*. Oxford: Oxford University Press.
- Pradeu, T. (2016). The many faces of biological individuality. *Biology and Philosophy*, 31, 761-773.

- Pradeu, T. (2020). Philosophy of biology: immunology and individuality. *eLife*, 8, e47384.
- Smith, S. (2017). Organisms as persisters. *Philosophy, Theory and Practice in Biology*, 9, 14.
- Stappenbeck, T.S., Hooper, L.V., *et al.* (2002). Developmental regulation of intestinal angiogenesis by indigenous microbes via Paneth cells. *PNAS*, 99, 15451-15455.
- Suárez, J. (2019). *The Hologenome Concept of Evolution: A Philosophical and Biological Study*. PhD Dissertation. University of Exeter.
- Suárez, J. (2020). The stability of traits conception of the hologenome: An evolutionary account of holobiont individuality. *History and Philosophy of the Life Sciences*, 42, 11.
- Suárez, J. (2021). El Holobionte/Hologenoma Como Nivel de Selección: Una Aproximación a La Evolución de Los Consorcios de Múltiples Especies. *Theoria*, 36(1), 81-112.
- Suárez, J., Stencel, A. (2020). A part-dependent account of biological individuality: Why holobionts are individuals and ecosystems simultaneously. *Biological Reviews*, 95(5), 1308-1324.
- Suárez, J., Triviño, V. (2020). What Is a Hologenomic Adaptation? Emergent Individuality and Inter-Identity in Multispecies Systems. *Front. Psychol.*, 11, 187.
- Triviño, V., Suárez, J. (2020). Holobionts: ecological communities, hybrids, or biological individuals? A metaphysical perspective on multispecies systems. *Studies in the History and Philosophy of Science Part C*, 84, 101323.