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Physiological and evolutionary individuals: a metaphysical perspective

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Johannes Martens*

CNRS : SND, Sorbonne Université, Paris France

Alexandre Guay

ISP, Université Catholique de Louvain, Louvain-la-Neuve Belgique

Abstract

Evolutionary approaches have long dominated the theoretical debates on the nature of biological individuality. Most of the time, these approaches rely on the conjunction of two philosophical claims: (i) the category of biological individuals is *more inclusive* than the category of traditional organisms; (ii) biological individuals are *evolutionary* individuals. Recently, however, some philosophers have defended an alternative, pluralist conception of biological individuality which envisages the categories of physiological and of evolutionary units as two distinct—though *partially overlapping*—categories of biological individuals (Godfrey-Smith 2013; Pradeu 2016). In this paper, we propose a critical analysis of this account, and provide a detailed survey of the metaphysical interpretations that can be given to it.

^{*} Corresponding author: martens.johannes@free.fr

1 Introduction

The concepts of a *biological individual* and of an *organism* have long been considered as interchangeable in the history of the life sciences. Yet, in the 1960-70s, this tradition has been challenged by some prominent philosophers and biologists, who argued that the former was equivalent to the broader notion of an *evolutionary individual* (Williams 1966; Lewontin 1970; Hull 1978, 1980; Dawkins 1976). According to this "evolutionary view", what legitimates the inclusion of a given individual in our biological ontology is (roughly) the demonstration of its participation to some sort of selective or evolutionary process. Hence, if multicellular organisms (or even distinct physiological units) can be regarded as biological individuals—which they certainly are (though some, like Dawkins (1976), have contested this view)—this is only because of their evolutionary dispositions, that is, because of their status as *evolutionary* units.

Two ontological claims, then, lie at the core of this evolutionary account: first, biological individuals are nothing but evolutionary individuals; second, organisms are nothing but a particular class of evolutionary individuals. Because of its commitment to the first of these two claims, the evolutionary account can be envisaged as a kind of ontological *monism*—even though it remains compatible with the recognition of various sorts of evolutionary individuals (e.g. replicators and interactors).

Up to now, the evolutionary account has proven quite popular among the philosophers of biology (e.g. Clarke 2016). But recently, a few authors have defended an alternative, pluralist conception to this approach (Godfrey Smith 2013; Pradeu 2016) based on a rejection of the two claims on which it is built. To begin, these authors argue that the set of biological individuals does not resume to the set of evolutionary individuals, but constitutes a broader set of entities, whose principles of individuation do not necessarily involve an evolutionary component. Secondly, these authors claim that, within this broader set, the category of individual organis ms

constitutes a *distinct* set of biological individuals, which overlaps the set of evolutionary units, but relies on a distinct principle of individuation for its members—derived (most often) on some version of physiological theory. This particular set is best referred as the set of *physiological individuals*, as it comprises not only the traditional, multicellular organisms, but also several biological entities that exhibit a high degree of physiological unity—such as the so-called "superorganisms" (which count most eusocial insect colonies) and some tightly integrated symbiotic associations.

The conceptual scheme associated with the pluralist account can be represented by a simple diagram (Figure 1) where the category of the physiological individuals and the category of the evolutionary individuals are represented by two overlapping sets, PI and EI, included within the broader set of the biological individuals, BI.



Figure 1. The pluralist diagram.

According to Godfrey Smith (2013) and Pradeu (2016), what motivates this conceptual partition is primarily the existence—attested by the biological practices—of different criteria of individuation, physiological and evolutionary, that can be considered as equally legitimate.

Physiological criteria, on the one hand, put the emphasis on the possession of a metabolism and/or a functional integration of parts. Evolutionary criteria, on the other hand, require the participation to some important kind of evolutionary process (often but not always natural selection). Sometimes the domains of these criteria overlap—as is the case with some, though not all, multicellular organisms—sometimes not. Hence, some biological individuals are typically regarded as evolutionary individuals but not as physiological individuals, such as selfish genetic elements and viruses (which exist as units of selection but do not possess a proper metabolism), while others are typically regarded as *bona fide* physiological individuals but not as regular evolutionary individuals, such as most endosymbiotic organizations (which are physiologically integrated, but made up of different evolutionary lineages).

Pradeu (2016) also mentions two benefits of the distinction between the categories PI and EI. First, this distinction "clarifies the fact that biologists interested in identifying biological individuals and/or organisms can have very different practical aims, and raise quite different scientific questions" (p.811). The content of these "aims" and "questions" is not really made explicit in his paper, but some hints on their nature are provided by his second methodological point: later on, Pradeu indeed argues that the distinction between PI and EI is especially useful in that it allows the *combination* of different perspectives (physiological and evolutionary) on key problems that were previously envisaged under the exclusive regard of evolutionary theory. This combination, he argues, can lead to new—and various—forms of biological insights: thus, "[o]ne can ask, for instance, which kinds of selective pressures lead to an increase in physiological integration, and which don't (Pepper and Herron 2008). [...] Another important task at the physiological-evolutionary interface is to determine the role of physiological unifying processes, for example the immune system, in major transitions in evolution, particularly in so-called 'policing' mechanisms (Michod 1999; Pradeu 2013)." (p.812).

In their studies, Pradeu (2016) and Godfrey-Smith (2013) address in various detail the *biological* criteria associated with the PI and EI categories. Pradeu, as mentioned above, also envisages some of the *methodological* advantages that can result from articulating the physiological and evolutionary perspectives. But there is a point on which these two authors remain particularly evasive—not to say silent—namely: the *metaphysical* interpretations that can be given to their conceptual scheme. In effect, none of them clearly indicate how we should or could interpret the *nature* of the predicates "BI", "EI" and "PI" in the pluralist diagram (Figure 1), or how we should or could interpret the *domain* over which these predicates are defined. This relative neutrality might well be regarded as a virtue of their particular approaches. But it can also be quite confusing; for the pluralist account, as we have seen, stands as a direct *challenger* to the monist, evolutionary account of biological individuality—which, contrary to the pluralist view, *has* relatively well defined ontological commitments.

The "evolutionary account", of course, is not a monolithic view, and different conceptions of what counts as an evolutionary individual have been proposed in the literature (cf. Clarke 2016). But its main ontological commitments are relatively clear: if we identify the biological individuals with the evolutionary individuals, then all of our properties ascriptions in biology will concern evolutionary individuals or parts of evolutionary individuals—and nothing else above that. That is, any further distinction that one might draw between these individuals—e.g. by partitioning them into different classes ("organismal EIs", "genetical EIs", "colonial EIs")— will only consist in a refinement of our conceptual scheme, and not in any "addition of being" to our world.

The monist (evolutionary) account is certainly not immune to metaphysical issues/objections.¹ But, in this paper, we shall focus exclusively on the pluralistic approach

¹ For an interesting criticism of evolutionary-based definitions of biological individuality, see DiFrisco (2019), section 3.

(Figure 1). Our goal in this study will be to examine the different metaphysical interpretations that can be given to it, so as to highlight the main conceptual difficulties that their respective presuppositions entail.

At the most general level, three sorts of interpretation can be envisaged for the pluralist diagram—each corresponding to a particular "grade" of metaphysical involvement:

(1) First, one could adopt a *pragmatic* stance over this conceptual scheme, and interpret the predicates BI, PI and EI as referring to nothing more than to the scientific aims and/or methods related to (or constitutive of) the varieties of individuation practices in biology. For each of these predicates, one could thus suggest a pragmatic interpretation along the following lines:

"PI(x) = x is relevant to/part of an individuation practice in physiology".

"EI(x) = x is relevant to/part of an individuation practice in evolutionary biology".

"BI(x) = x is relevant to/part of an individuation practice in biology".

In itself, this interpretation tells us nothing about the *nature* of biological individuals and/or their properties (the variable x in the previous sentences ranges over the practical methods/interests of the biologists); so its degree of metaphysical involvement is zero. But a proponent of the pragmatic stance may well insist on its *epistemic value*, and argue that the pluralist scheme—so understood—contributes to a better understanding of the organization and diversity of biological practices/agendas relative to the topic of biological individuality.²

(2) A second interpretation might consist in envisaging the predicates BI, EI and PI as referring to different classes of *properties*:

² Waters (2018) defends a position of this sort.

"PI(x) = x is a physiological property".

"EI(x) = x is an evolutionary property".

"BI(x) = x is a biological property".

According to this particular scheme, some properties like "having an immune system" or "having an early segregated germ-line" would pertain to the intersection of the EI and the PI sets, while others, such as "being the locus of metabolic exchanges", "having a heritable expected fitness" or "being composed in part of carbon compounds", would probably belong to only one of these three classes (PI, EI and BI, respectively).

Unlike the pragmatic approach, this particular interpretation carries a certain degree of ontological implication, as it is (at the very least) committed to the existence of *objective* properties. But its metaphysical commitments remain quite shallow, since it does not make any particular assumption concerning the very nature of the "things" that instantiate these properties in the living world (the x variable ranges over properties, not over objects).

(3) A last interpretation—but surely the first that comes to mind when faced with the pluralist diagram—could be to envisage the predicates PI, EI and BI as referring to distinct but overlapping categories of *discrete particulars* or *individuals*:

"PI(x) = x is a physiological individual".

"EI(x) = x is an evolutionary individual".

"BI(x) = x is a biological individual".

Contrary to the previous one (2), this interpretation makes a further commitment toward a pluralist ontology, for it explicitly acknowledges, in the biological domain, the existence of concrete entities belonging to different kinds or classes of individuals.

All of these interpretations, in a sense, represent equally legitimate ways of "fleshing out" the pluralist diagram (Figure 1). But not all, however, can be regarded as genuine alternatives to evolutionary monism. Thus, the pragmatic view (1)—which focuses exclusively on the biological practices—makes no metaphysical commitments *at all* about the nature of biological individuality (in fact, an evolutionary monist might perfectly agree with interpretation (1), without any sort of contradiction).³ Likewise, the second interpretation is entirely compatible with the main ontological assumption of evolutionary monism, since it says nothing about the *bearers* of the physiological, evolutionary and biological properties—for all we know, they may all be evolutionary individuals.

Among these three interpretations, the only real "challenger" to evolutionary monism is interpretation (3)—which unlike (1) and (2), *is* committed to some sort of pluralistic ontology. Because (3), if true, would entail the falsity of evolutionary monism, its metaphysical groundings should be carefully considered. By restricting our attention to this approach, we shall try, in this paper, to shed light on the possible metaphysical inconsistencies that may result from any attempt to substantiate the pluralist scheme (figure 1) with a pluralistic ontology.

Despite its commitment to the existence of different classes of biological individuals, the pluralist scheme posited by (3) is very general, and leaves a number of key metaphysical questions unanswered. Two of them, more specifically, should be distinguished here.

One concerns the nature of the *particulars* falling under the predicates PI, EI and BI. In this paper, we will assume that these particulars are three-dimensional objects persisting through time. But we must stress that this specific representation—though intuitive—is in no way required by the pluralist scheme. Thus, some philosophers have recently argued that our

³ The only way to oppose interpretation (1) to the monist, evolutionary account would be to associate it with an anti-realist thesis. But in this case, the opposition between these two approaches would no longer concern *specifically* the contrast between evolutionary monism and biological pluralism with respect to the question of biological individuality.

commitment to biological individuals should be replaced by a commitment to biological processes, conceived as "four-dimensional worms" (Dupré 2012, 2018; Guay and Pradeu 2016; Pradeu 2018). This approach, if correct, would lead to a very different perception of our biological ontology, and may even provide the only proper basis to the pluralist view. In section 2.2.2, we will have a few criticisms to address to this interpretation. But overall, a full discussion of the process ontology would deserve a thorough study of its own, and we won't engage in a detailed rebuttal of this philosophical view.

The other question concerns the nature of the relation between the *properties* referred to by these predicates, on the one hand, and the individuals who instantiate them, on the other hand. This is the core issue that we will address in this paper. With respect to this problem, our argumentative line will be (roughly) as follows.

First, in committing to the view that PI and EI refer to distinct, non-arbitrary sets of individuals (that is, in committing to interpretation (3)), the pluralist should logically accept that all of the PIs share (instantiate) a common property that is *not* identical to the property shared by all EIs, and conversely.⁴ But this simple commitment raises, immediately, the following questions: (i) what are the properties associated with these two sets (i.e. the properties that are common, respectively, to the members of each set)? and (ii) how should we understand their nature?

Concerning the first of these questions, most would probably agree that these properties are of the form "having some sort of physiological configuration" and "having some sort of evolutionary dispositions", though there is some room for disagreement concerning the precise meanings of these expressions. Concerning the second question, metaphysicians commonly distinguish in the literature between two types of properties (conceived as universals), namely *substantial properties* (i.e. properties that "cannot be lost" by their members without them

⁴ As written above, the alternative to this (minimal) ontological commitment would be process ontology.

ceasing to be the *same* individuals) and *mere properties* (such as "being round" or "being red", i.e. properties that are not constitutive of the identity of the objects which instantiate them). These properties, as we will show, are directly relevant to our understanding of the very notion of an individual.

If any of the two properties associated with PI and EI is of the former sort (substantial), then it is also an *individuating* property, in the sense that its instantiation contributes to make a given entity a biological individual. If, by contrast, it is of the latter sort, then the domain of objects to which it applies must be a domain of entities that are *already* individuated, i.e. of entities whose principle of individuation derives from another source—theory-based or whatever.

Based on this ontological distinction, four interpretations of Figure 1 will then be envisaged: (I) "being a physiological unit" and "being an evolutionary unit" are both non-substantial properties; (II) "being a physiological unit" and "being an evolutionary unit" are both substantial properties; (III) only "being a physiological unit" is a substantial property; (IV) only "being an evolutionary unit" is a substantial property.

The structure of the paper is as follows. In section 2, we will expose the distinction between substantial/non-substantial properties as it is most often understood in the philosophical literature (section 2.1), and examine the nature of its connection with the notion of biological individuality (section 2.2). The purpose of this section will be to show—in response to the first of our above-mentioned questions—that a substantialist ontology provides us with the best account so far for thinking about the identity of biological individuals. In section 3, we will address the second of our two abovementioned questions (i.e. the one concerning the nature of the relation between PI, EI and the members of BI) by assuming a broad substantialist reading of the pluralist diagram. In this section, we will discuss each of the four interpretations (I to IV) that can be given to this diagram, and detail the main conceptual difficulties/objections that one can make against them.

2 Substantial vs. non-substantial properties

The distinction between *substantial* and *non-substantial* or *mere* properties is central to the questions related to the individuation of particular objects. In our ordinary language, this distinction is (roughly) mirrored in the use of substantival terms and non-substantival terms, also referred to as sortal and adjectival terms. A substantival or sortal term (such as "horse") typically refers to a given *sort* of object, and sometimes, to a substantial kind—that is, to a set of objects that (i) share more than a superficial or accidental resemblance and (ii) are individuated on the basis of this shared property. A non-substantival or adjectival term (such as "white"), by contrast, usually applies to a heterogeneous set of objects which, though they happen to share a given property (e.g. whiteness, like white horses, white cups, white clouds, etc.), have presumably different ontological "substances" (Mill 1843), i.e. different persistence conditions.

In this section, we will introduce the specific aspects of this distinction that will be relevant to our discussion of the pluralist ontology (developed in section 3). To this end, we will begin by exposing, in broad outline (section 2.1), the nature of the general relation between a substantial property and a criterion of identity/individuation. Then (section 2.2), we will advance some arguments in defence of the conception of biological individuals as individual substances.

2.1 Sortal concepts and criteria of identity

There are many difficult issues surrounding the "nature" of substantial properties associated to sortal terms, including the one concerning the status of kind essences (Kripke 1980; Salmon

1982). However, rather than addressing these issues directly, we will focus on the notion of *identity* that is involved in the persistence of individual substances; for it is this aspect of substantial properties which will turn out to be the most relevant for the individuation of biological entities (as we will argue in section 2.2). To this end, we will rely on the substantialist framework developed by the philosopher E.J. Lowe, starting with a brief account of his own appreciation of the distinction between substantial and non-substantial properties (for related views about the idea of a "substance sortal", see Wiggins (2001), esp. chapters 2 and 3.).

In his many works on the ontology of natural kinds and "sortals", Lowe (2006, 2007, 2009) defends the view that what distinguishes a "substantial" sortal term from a mere "adjectival" term is the fact that only the former carries a *criterion of identity* for the objects to which it applies. According to Lowe,

"[a] criterion of identity for a sortal term tells us what determines whether or not one thing that the term applies to is the same as, or numerically identical with, another thing that the term applies to [...]. Where 'K' is a sortal term, the general form of a criterion of identity will be this: if x and y are Ks, then x is identical with y if and only if x is R_K -related to y. Here, ' R_K ' denotes a certain equivalence relation on Ks". (Lowe 2007, p.515)

To illustrate the notion of a criterion of identity, Lowe suggests the following example:

"imagine seeing the head of a tiger protrude from one side of a tree and the tail of a tiger protrude from the other side of the same tree. One might point first towards the head and then towards the tail and ask 'Is that tiger (numerically) the same as this tiger?' A satisfactory identity criterion for tigers should specify, informatively and non-circularly, the conditions which must obtain for a positive answer to this question. It will imply, for instance, that the answer is yes only if the head and the tail in question are appropriately connected so as to form parts of a single living organism." (Lowe 2003, p.90)

According to Lowe, then, a criterion of identity should always mention a *relation* R which authorises (or denies) the unification of two distinct parts as parts of the same object.⁵ This relation can be represented, diachronically, as some sort of temporal essence, which supports the persistence of the corresponding individual throughout space and time: when R begins to exist, the corresponding individual begins to exist; when R ceases to exist, the individual ceases to exist as well.⁶

A criterion of identity associated with a sortal term usually embodies a principle for *counting* the individual instances that fall under its scope (Grandy 2016). But this is not always the case; indeed, many entities that can be re-identified over space and time *cannot* be counted or individuated in a non-arbitrary way. Thus, masses or aggregates (such as mereological sums) are entities that one might perfectly re-identify at different times, but which do not have the right sort of formal unity characteristic of genuine individuals—their conditions of existence

⁵ In order to better capture this idea, one could propose an alternative definition for the notion of a criterion of identity in terms of part-whole relations. A possible formulation would be:

[&]quot;if x is a part of a K-object and y is a part of a K-object, then x and y belong to the same K-object if and only if x is R_{K} -related to y (e.g. "appropriately connected to y so as to form parts of a single living creature")".

In the tiger's identification example, for instance, R_K might correspond, presumably, to some sort of physiological connection between the parts of the whole. This is surely the most intuitive answer, and it is, unsurprisingly, the one that Lowe suggests. But as we will see in section 3.3, the view that physiological connection *per se* corresponds to the very "substance" of biological individuals is not exempt from conceptual issues.

⁶ Whether or not this relation might also support the tracking of the same individuals across possible worlds is an issue that we won't address here. To argue in favour of such a transworld re-identification, one would have to say more about the notion of an individual essence (Plantiga 1974), and assess the validity of additional hypotheses related to this notion, such as the thesis of the *necessity of origins* (Mackie 1994). But all of these queries are somewhat orthogonal to the problem of biological individuality (see however Wilson 1999, chapter 4).

and identity are entirely determined by the identities of their constituent parts (Chauvier 2016). This distinction between individuals (entities that can be counted) and masses/aggregates (entities that cannot be counted—in a non-arbitrary way—but that can be re-identified) shows that there is a clear delineation to be drawn between criteria of *identity* and criteria of *individuation* (by definition, a criterion of identity is more general than, and always included in, the definition of a criterion of individuation). However, because our main focus in this paper is on countable entities only (i.e. on individuals), we will often use the two notions interchangeably.

When speaking of criteria of identity for individual substances, it is important to distinguish between two uses of the term "individual": *cognitive* and *ontological*. According to the cognitive use, the expression "an individual" refers to *any particular* (concrete or abstract) that can be sorted out by an act of thought as a distinct object of reference or perception. Hence, a corner of a door, a mouse, a heap or a hole would all qualify as individuals from the cognitive viewpoint (Lowe 2007). In the ontological sense, in contrast, the expression "an individual" refers to an object whose boundaries are not arbitrarily delineated in the world—and which is not itself a mere part of a broader individual, nor the mereological sum of lower level individuals (Chauvier 2016; Kaiser 2018). According to this second, ontological definition, individuals correspond to those very objects which "carve nature at its joints", and which typically figure as the most basic units of predication in the natural sciences. When speaking of criteria of identity for individual substances, it is the second use that we must assume.

As mentioned above, the main purpose of a criterion of identity is to specify the different transformations that an individual substance can undergo while remaining the same individual. For Lowe, and for most substantialists (like Wiggins), this specification is inherent to the *natural kind* to which belongs this individual. This means that, associated with a natural kind

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is a substantial property which imposes peculiar constraints on the identity of those individuals who instantiate it.

The main advantage of grounding substantial properties in natural kinds is that it makes the former amenable to *empirical* and *scientific* investigations. If substantial properties are attached (or identical) to natural kinds, then questions of the form "is the property P a substantial property?" can no longer be decided on purely speculative grounds, but must be answered on the basis of more specific considerations relative to a given scientific domain⁷—such as whether P's instances participate to the same kind of causal processes, whether they appear in the same type of inductive generalizations/projections, or whether P serves as an invariant for the multiple inferences that can be made about its instances (Hawley and Bird 2011).

Traditionally, natural kinds have been associated with microstructural properties—like "having the molecular structure H₂O". But nothing, in the very notion of a natural kind, requires that a natural kind property should be assimilated to an intrinsic property, or even anchored into some sort of microstructure (Bird and Tobin 2018). Thus, in biology, the best candidates to the status of "natural kind properties" are all *functional relations*, which allow for the reidentification of their bearers, and confer upon them the right sort of dispositions to engage into a whole range of causal processes.⁸ Such candidates typically include (putative) individuating properties, like "having parts inter-connected by interbreeding relations", "being a unit of selection" or "having an immune system", which all, to various extent, contribute to explain or even predict—the different properties and behaviours that are exhibited by their bearers. (For example, knowing that a given X is a unit of selection will typically inform us—along with

⁷ This means that the constraints governing the identity and re-identification of the individuals in this domain are not fixed a priori but a posteriori (by means of scientific investigation) and remain fully revisable in light of further scientific advances.

⁸ Properties such as "having the genome G" or "having the morphological type M" are often mentioned, in the philosophical literature, as paradigmatic instances of substantial properties (e.g. Kripke 1980); but this sort of view is now clearly outdated (Okasha 2002).

complementary information about its selective environment/history, the range/distribution of the phenotypic traits in its actual population, etc.—about the possible adaptations that one can expect X to possess, or about the way X's properties may influence the evolution of its population).

Contrary to substantial terms, which are meant to refer to sorts of objects or natural kinds, adjectival terms do not have a criterion of identity associated with them. Following Geach (1962), Lowe illustrates this fact by noting that a colour term such as "red" can perfectly be applied to any red instance, though there is only arbitrary ways of counting the number of red things to which one is confronted.

"And this is not because there *is* such a number, but one beyond our power of determining—as in the case of the number of atoms in the room—but rather because it apparently doesn't even make sense to speak of such a number until the sort or sorts of red thing that one is to count is to be specified." (Lowe 2009, p.13; also Geach 1962, p.63).

Contrary to substantial properties, then, mere (or accidental) properties are not sufficiently *specific* to serve as individuating criteria: by themselves, they can be used to distinguish between different individuals of the same kind (for example, two horses of different colour), but not to determine which entity shall count as a member of a kind in the first place.

In the substantialist account, what determines *what a given thing is* is nothing but the substantial sortal to which it belongs (Wiggins 2001): mere properties, on the other hand, can only be ascribed to an object if the object has *already* been individuated/identified with the help of a criterion of identity—that is, assigned to a substance sortal. The entities in a given domain which corresponds to a substance sortal are referred to as *individual substances*. Our claim,

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defended in the next subsection, is that every member of the category of biological individuals must be an individual substance with respect to (at least) one substance sortal.

2.2 The concept of an individual substance in biology

In the metaphysical literature, the notion of an individual (or "primary") substance has played—and continue to play—a central role in the current debates about identity, composition, modality and change. Yet, with a few notable exceptions (Wilson 1999; Dupré 2012), this concept has not received a large amount of attention in the literature on biological individuality.⁹ This might seem a bit ironic, since living creatures are most commonly cited, in both ancient and current metaphysics, as *paradigmatic* examples of primary substances. But this is not really surprising; for, up to now, philosophers of biology have been mainly interested in the study of the concepts/structures of biology.¹⁰ As a result, most of the discussions on the notion of a biological individual have focused on the *theoretical* definitions of this concept (evolutionary, physiological), rather than on the more abstract difficulties posed by the existence of multiple (and usually conflicting) criteria of individuation in biology.

In the past decades, however, two authors—with radically opposed views—have explicitly tackled the problem of biological individuality from a metaphysical perspective. The first is

⁹ Among the relevant exceptions, one should mention the works of David Hull (1978, 1986, 1992), who has developed a subtle and powerful criticism of the "substance-based" conceptions of the identity of organisms and species (however, Hull's criticism was mostly directed—at least in his landmark 1978 paper—on the interpretation of biological species as *secondary* substances, i.e. as classes of properties, and not as primary substances). Aside from Hull, Wilson and Dupré, other authors have occasionally discussed the conception of organisms as primary or individual substances, including Pradeu and Carosella (2006), Sousa (2005), and more recently Ferner (2016), Guay and Pradeu (2016) and Austin (2020).

¹⁰ Here again, Hull stands out as an exception, having been one of the first philosophers of biology from the Anglophone tradition to explore the connections between metaphysics and biology (Hull 1978; 1989).

Jack Wilson, who, in his book *Biological Individuality* (1999), has defended a strong version of ontological pluralism, based on a substantialist conception of biological individuals. The second is John Dupré, who, in his different works (Dupré 2012; 2018; Nicholson and Dupré 2018), has developed a quite radical version of process ontology—in which biological individuals are no longer conceived as substances, but as processes. In this section, we will examine the main presuppositions of these approaches, and highlight some of their implications for the interpretation of the pluralist diagram.

2.2.1. Biological individuals as individual substances

In his book, Wilson defends two metaphysical theses about the nature of biological individuals:¹¹

(i) every biological individual must belong to one substantial kind.

(ii) there are several substantial kinds in biology, and every biological individual must belong to exactly one of them.

As we will show in section 3.2, the second (and metaphysically stronger) of these two claims faces important difficulties. But the first of these theses, actually, constitutes a much reasonable assumption. It is the one that we will consider here.

¹¹ Wilson also argues for the necessity of biological origins thesis, which entails that a biological individual has *essentially* the identity conditions associated with the substantial kind to which it belongs. But, as mentioned in footnote 5, we won't discuss this metaphysical assumption in our paper.

Wilson's argument in favour of (i) is based on two premises. The first is that any biological individual is a three-dimensional particular.¹² The second is that no living thing is a particular *simpliciter*:

"[i]f we examine any living thing, we discover that it is not just a 'thing' or a 'that'; it is a thing of some particular kind or other. It may be an oak tree or a sea urchin but it must be a thing of some kind." (p.18).

As Wilson stresses, this particular claim is a biological instance of a broader philosophical conception known as *sortalism* in the metaphysical literature (Wiggins 2001; Lowe 2009; Grandy 2016; Ferner 2016). The basic tenet of the sortalist conception is simple: in order to identify a thing as *the very thing that it is*, that is, as distinct from every other entities (at any time), one has to individuate it—necessarily and in the first place—as a member of some kind or "sort", thereby answering (even if only in a tentative way) the question: "what is it?". So stated, the sortalist view is quite intuitive, though it is not uncontroversial (we leave to the skeptical reader, however, the task of demonstrating how an entity could be individuated independently of a description that we attach to it).¹³ Therefore, it is important to consider what it entails and what it does not entail—at least as far as the identification of living things is concerned.

According to Wilson, a *kind* can be characterized as any pattern of properties that is used to single out, pick out or refer to a living entity. Thus, when we identify a thing as a sea urchin, for instance, we identify it *as such* because it instantiates a pattern of properties that is more

¹² An advocate of the process ontology, then, would *not* be committed to Wilson's conclusion.

¹³ For a critical discussion of the claim that any act of individuation (i.e. any act of "singling out" or "picking out" something) is necessarily sortal-dependent, see Snowdon (2009). For an insightful rebuttal of Snowdon's arguments, see Ferner (2016), pp. 56-62.

salient than another, and which we use as a proxy for its re-identification in different circumstances. Understood in this sense, then, a "kind" can be pretty much anything (as long as it may serve as a cognitive/practical criterion of individuation). But, as Wilson notes, the simple fact that a living thing must belong to a kind or other at any time of its existence is no justification for the stronger claim that every living thing must belong to a *substantial* kind for the whole duration of its existence. To infer this stronger claim from the weaker one, we need a couple of intermediary premises. More specifically, we need to assume that:

(a) there are some changes that a living thing cannot survive.

(b) these changes are governed by the criterion of identity associated with the kind to which this thing belongs.

Claim (a) is plainly vindicated by both common sense and biological sciences. It may seem rather trivial, but it is actually pivotal to Wilson's argument; for if we agree upon the fact that a living entity is at least potentially mortal, then we have no choice but to accept that there are (at least) some changes that would completely destroy it—and so, that would prevent it from remaining the *same* individual. Claim (a) is therefore crucial in that it provides us with a direct support for the view that (b), prima facie, is true. But (a) does not, in itself, provides us with a full justification of this second assumption: what completes the justification for (b) is our evidence, derived from the biological sciences, that the persistence conditions of living things are neither completely *arbitrary* nor utterly *mysterious*, but accessible to empirical research.¹⁴

¹⁴ At this point, a nominalist may well object to the inference from (a) to (b) on the grounds that it neglects the possibility that each living thing possesses some unique set of persistence conditions. If the nominalist were right, there would be as many substantial kinds as there are biological individuals. But this nominalist stance, in our opinion, rests on a fundamental confusion, which consists in taking the most detailed level of description of the biological reality for the biological reality itself. Assuredly, no one would deny that, for any two oak trees facing the same fire intensity in the same environment, there must exist a critical temperature T such that one could

Wilson is very careful to distinguish between the epistemological and the metaphysical aspects of his argument. Thus, there is nothing, as he claims, in the conception of biological individuals as individual substances, which presupposes that the determination of the substantial kind of a biological individual should be an "easy task". Wilson is clear on this point, and insists on the fact that our hypotheses and investigations about the substantial kinds of biological individuals are both *fallible* and *revisable*:

"Our initial guess about the persistence conditions of a kind of entity are often wrong. So we revise them in response to empirical evidence or theoretical developments. This process continually takes place with many of our concepts and is not always orderly. Sessile animals may initially be identified as plants, or morphologically distinct life stages may be mistaken for distinct biological species. [...] Eventually, we find some patterns and associated identity and persistence criteria that are robust enough to survive scrutiny." (p.44)

Wilson further notes that we can—in principle—have good reasons to believe that a given x belongs to a substantial kind even if we do not *know* the substantial kind to which it actually belongs. Thus, "[t]here may be monstrous living things of which we have never thought" (p.19); and yet, if we can tell that they are *living* in the first place, we should already have some evidence that there are changes that they cannot endure. Of course, a misidentification is always possible, and it might be that what we initially thought to be a biological individual is nothing of the sort. But in this case, our initial hypothesis (i.e. that there is a substantial kind to which it belongs) should simply be abandoned.

survive to the fire but not the other. But this sort of observation, clearly, is no evidence that the persistence conditions of oak trees are incommensurable, or that they are not explainable in terms of their common functional/material characteristics.

Some category mistakes may well happen at the ontological level: occasionally, we categorize a particular thing as a biological individual, and later realize that it should have been categorized in different terms—maybe as an *aggregate* (whose identity conditions derive from that of its components) or as a *part* of a broader individual (whose identity conditions are not totally independent of the identity conditions of the kind of whole to which it belongs). Most of our initial guesses, when confronted with a new or unusual living entity, are indeed subject to this kind of ontological revision.

Wilson's basic claim, i.e. that every biological individual must be an individual substance, has in our view one main advantage: its flexibility. Concretely, this particular claim does not decide between the different conceptions that one may (or should) adopt with respect to the kinds of individuals that must be regarded as substantial in biology: what it implies is simply that the things which "come and go" in our biological ontology should have criteria of identity associated with them, and that our knowledge of these criteria determines whether they should be included in/excluded from our domain of quantification-i.e. the domain of biological individuals. Hence, when it comes to the question: "what is/are the substantial kind(s) in biology?", this substantialist claim is compatible with many sort of interpretations (one can adopt a monistic or a pluralistic ontology; one can decide that what counts as a biological individual depends on a particular theory—e.g. evolutionary theory or some interpretation of it—or that it depends, in contrast, on some general property shared by all of the living beings independently of any theoretical view, etc.). In section 3, we will restrict our attention to the pluralist scheme (Figure 1), which imposes an upper limit on the number of substantial kinds; but there is nothing, in the very conception of biological individuals as individual substances, that should commit us to this limitation (Wilson, for instance, recognizes no less than six different substantial kinds of biological individuals¹⁵).

¹⁵ Wilson (1999), p.60.

Before turning to the different interpretations of the pluralist scheme, we shall mention three alternatives to the substantialist thesis. The first two can be dismissed rather quickly. The last one corresponds to process ontology.

A first possibility could be to accept the view that every entity must belong to a kind (or other) at some point of its existence, while *denying* that every entity must belong to a substantial kind for the whole duration of its existence. In this case, one would then have to accept the existence of *bare particulars*, that is, of concrete entities that can undergo any sort of change during their existence, and whose identities do not supervene on any qualitative fact (Wilson describes them as "protean entities"). But the commitment to bare particulars, ultimately, is a price that few philosophers would be ready to pay, as it makes the notion of individual beyond empirical reach.

As an example, consider Wiggins' famous example of Lot's wife "turning into" a pillar of salt after looking back at Sodom (Wiggins 2001, p.64-65). Lot's wife falls under the sortal concept "person", and her body under the (pre-theoretical) sortal concept "organism". Thus, when she looks back at the burning city, neither her nor her body is literally "turned into" a pillar of salt: instead, as Wiggins argues, both just cease to exist, and a new entity, falling under the sortal concept "pillar of salt", came to exist. Now, someone who would *deny* that Lot's wife or her body can't lose the properties of being a person and being an organism (respectively) could well retort that one of them is actually *the same thing* as the pillar of salt. But, by accepting this possibility, one would automatically renounce to ground our identity judgements about particular entities (Lot's wife/her body) in any kind of empirical basis; and this is a consequence that, we think, suffices to reject the hypothesis of bare particulars in the context of biology (as for other scientific fields, we do not pronounce ourselves).

A second alternative would consist in conceiving of biological individuals not as bare particulars, but as mere *bundles of tropes*—where a trope, according to this view, refers to a

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particular property (such as "this redness" or "this squareness") that is located in space and time, but that is *not* actually supported by any particular "bearer" or object. In the metaphysical literature, this particular form of nominalism, known as trope theory¹⁶, is usually motivated by considerations of ontological parsimony.¹⁷ However, there are two reasons for which we doubt that it could illuminate the current discussions over biological individuality. First, the difficulties that one would face by adopting trope theory are notoriously more puzzling than the ones attached to the property/object relation (why, for instance, do heterogeneous tropes just "coalesce together" in relatively well-delineated bundles? And how should we understand the nature of the relation between a trope and a given bundle (Lowe 2007))? Besides, trope theory cannot explain why some properties (e.g. "being physiologically integrated" or "being a unit of selection") have—or seem to have, at the very least—the power of unifying a large number of properties into specific patterns or bundles, whereas others (e.g. "being mottled", "having a streamlined shape") don't. For those reasons, we won't develop further this metaphysical—and overly radical—view.

Finally, a third alternative would consist in envisaging biological individuals as processes rather than as individual substances (Dupré 2012, 2018). Because this last approach have become increasingly popular in the recent philosophy of biology literature, it deserves to be discussed in more detail.

¹⁶ For a general defence of trope theory, see Campbell (1990).

¹⁷ Put roughly, the motivation of trope theorists is that, by getting rid of objects or individuals, one could avoid purportedly—some difficult metaphysical issues relative to their ontological status as the ultimate "substrata" of properties.

2.2.2 Biological individuals as processes, not substances

At a metaphysical level, a *process* can be characterized as a four-dimensional entity whose temporal parts or stages are connected by a continuous series of causal steps. What determines whether different temporal parts can be considered as stages of the *same* process is primarily the nature of their causal relation (as described by our biological theories). Hence, if two stages are connected by a continuous developmental path, it will be legitimate to identify them as parts of the same developmental process; likewise, if two stages are connected by a continuous series of evolutionary steps, it will be legitimate to identify them as stages of the same evolutionary process. In the philosophical literature, this particular sort of stage-process relation is usually referred to as "genidentity" (Pradeu and Guay 2016), a relation which, contrary to classical (absolute) identity, lacks the property of transitivity. The consequence of this fact is that two distinct processes can perfectly *overlap* at a time t if they have identical temporal parts at this time.¹⁸ When it happens, the two processes can be said to be identical-at-t, though not identical *simpliciter.*¹⁹ By contrast, let's recall that two individual substances cannot exist at the same place at the same time, except if they belong to different substantial kinds (individual substances cannot be "identical-at-a-time" without being identical simpliciter).

As mentioned earlier, the process view of biological individuals has been introduced and defended in philosophy of biology by John Dupré—although an increasing number of authors have since contributed to the development of this particular view (Guay and Pradeu 2016; Nicholson and Dupré 2018). Yet, most of the arguments that have been raised either against the equation of biological individuals with substances or in support of their equation with four-dimensional processes are, we think, inconclusive. In what follows, we will therefore express

¹⁸ To illustrate: two temporal parts can well belong to the same developmental process P1, and yet belong to distinct evolutionary processes P2 and P3, in which case P1 will be said to overlap both P2 and P3.

¹⁹ For more details on the idea of *identity-at-a-time* and its relation to the notion of identity, see Lewis (1976).

our main criticisms against the process view, by addressing first the core objections that Dupré and Nicholson (2018)—in their manifesto for a process ontology—formulate against the substantialist representation of biological individuals, and by outlining a couple of metaphysical objections about the identity of biological processes.

According to Dupré and Nicholson, two different claims about biological individuals are directly supported/implied by a process ontology:

Weak claim: "different theoretical interests (e.g. ecological role, phylogenetic history) dictate different and multiply overlapping ways of dividing biological entities into kinds." (p.23)

Strong claim: "there are multiple ways of carving biological entities into distinct individuals" (p.24)

The weak claim, in our view, is unproblematic for a substantialist conception of biological individuals—as we argued in the introduction, the question of the theoretical/practical interests is, to a large extent, orthogonal to the issues relative to biological ontology. But the strong claim, in contrast, is clearly incompatible with any substantialist account of biological individuality (monistic or pluralistic). In fact, if it were correct, our interpretation of the pluralist diagram as a pluralist ontology—composed of individual substances distributed in different kinds—would be plainly misguided. It is therefore important to look at the main reasons given by these authors in favour of this second claim.

The core griefs formulated by Dupré and Nicholson against the substantialist view are condensed in the following, brief passage. None of their points, however, appears to us as really decisive or convincing: "The problem for substance ontology has always been that it is extraordinarily difficult to specify any such change-exempt descriptive properties that permanently characterize the essence of things. [...]. First, as a consequence of constant metabolic turnover, a biological individual is never materially identical from one moment to the next. Second, because of its life cycle, it undergoes massive morphological changes as it progresses through its various ontogenic phases. And, third, as a result of its ecological interrelations, the symbiotic associations that compose and maintain it change considerably over its lifetime." (p.24)

Concerning first the alleged "extraordinary difficulty" mentioned by these authors, we are not sure, exactly, about what to say. If the difficulty pointed by Dupré and Nicholson concerns the idealized goal of reaching the true nature of biological reality, then of course, the task is certainly extraordinary difficult, if even possible; but the point is rather trivial, and can barely count as an argument against biological substantialism. If, by contrast, these authors refer to the possibility of pointing to individuating relations that would be sufficiently informative and general to count as the proper substances of biological individuals, then the literature in philosophy of biology is replete with serious candidates, and we do not view this plurality as a reason for doubting of the fact that some of them might be *better* candidates than others.

To mention only one example, consider Queller and Strassmann's (monistic) description of the organism as an entity with a near unanimous cooperation and a very low amount of conflicts among its parts (Queller and Strassmann 2009). This definition refers to a clear, relational property that may serve as a "change-exempt" criterion (à la Lowe) for deciding (a) when a given biological entity should count as an organism, rather than, say, as a society or a mere group, or (b) when a thing becomes a part of an organism or ceases to be a part of it, or (c) when an organism starts and ceases to exist. Naturally, one may disagree with it, but this is beyond our point: what this sort of description illustrates is just that one can perfectly specify a property that is sufficiently general to serve as criteria of identity for a whole category of biological individuals, and which has good credentials to count as a natural—and not as an arbitrary delineated—category. (A similar description of an individuating, relational property might certainly be provided for other putative candidates, such as Pradeu's immunological criterion, but this is not the place to engage in this sort of demonstration).

The three other points mentioned by Dupré and Nicholson are, in our view, no more convincing. First, the fact that no biological individual has the same material parts at the different times of its existence is just irrelevant to the problem of its status as an individual substance: if they are any "change-exempt properties" that ground the criteria of identity for biological individuals, these properties must be *functional* properties, not material properties. Second, the existence of massive morphological transformations can only be an objection against some rather old-fashioned kind of essentialism, which takes phenotypical and/or genetical characters as "essential" to an individual (Okasha 2002). But it is surely not an argument against a criterion of identity that relies on the nature of a functional relation among a set of parts to decide whether the latter compose or not a biological individual. Finally, although the relative ubiquity of symbiotic associations might be legitimately invoked in support of a revision of our current definitions of an evolutionary individual-or even, the pluralist would argue, as an empirical case in favour of the existence of non-evolutionary individuals—we do not see any justification for regarding this case as a rationale for giving up the metaphysical idea of an individual substance in biology. In particular, we do not see why the substantialists couldn't make use of this very same observation (the quasi-ubiquity of symbioses) to simply refine their criterion/criteria of identity for biological individualsinstead of abandoning their metaphysical stance.

In addition to their criticisms of the substantialist account, Dupré and Nicholson propose a positive argument in favour of the reduction of biological individuals to processes. This

argument is based on an analogy between what they view as a paradigmatic example of a pure persisting process—the Great Red Spot on Jupiter—and the functioning of an organism:

"The mode of persistence of an organism is in many respects quite similar to that of the Great Red Spot. Just as the latter persists by drawing in matter and energy from the violent winds that surround and shape it, so the former persists by securing from its environment the matter and energy it requires to maintain its organization far from thermodynamic equilibrium. The persistence of the Great Red Spot is not based on the mere persistence of any of its individual properties or constituents; it is rather something it does—a continuous activity." (p.25)

At first, this analogy might seem persuasive. But, if one takes a closer look to it, it is easily reversed. For sure, if the Great Red Spot couldn't be conceived otherwise than as a *pure* process (not supervening on any sort of substances), and if the analogy was perfectly sound, then we would have a good reason for adopting a process view of biological individuals. But the truth is that there is nothing, at the phenomenal level, which compels us to describe the Great Red Spot as a pure process.

Pace Dupré and Nicholson, for instance, we do view the two following descriptions of the Great Red Spot as equally legitimate alternatives to the pure process view:

(i) the Great Red Spot is not a true substance, but a meteorological regularity resulting from the arrangement of substantial particles due to a combination of external and physical factors.(ii) the Great Red Spot is an individual substance, composed of physical particles arranged according to a (meteorological) principle of activity.

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In both of these statements, the Great Red Spot is described in terms of particular substantial *activities*—either of its lower level constituents, or at its own level. In both of these statements, one could refine our descriptions of the particular substances involved, as well as that of their principles of activity, in the light of our best physical theories.²⁰ Yet, nothing, in the simple comparison of these alternatives to the pure process description, vindicates the latter as somehow *superior* to the former.

There are, finally, two major objections that one could address to a process view of ontology, quite independently of its application to the problem of biological individuality. Both concern the problem of specifying a criterion of identity for processes.

The first derives from a general criticism addressed by Lowe to four-dimensionalism (Lowe 2002, p. 54). As we know, a process is made of *temporal parts* or stages. This implies that, in order to identify a given process at any time t, one should be able to identify its unique temporal part at that time. But how is this identification possible in the first place? The short answer is that it is possible only if we already know the process or object of which it is a temporal part.²¹ This is, obviously, a circular answer. But the circularity is, in our view, hardly avoidable—at least if we envisage a temporal part as an arbitrary interval of time during which a given process is occurring. Surely, one could well try to remove this character of arbitrariness by requiring that a temporal part should, in the first place, be delineated/identified by a sub-process occurring over this very interval. But this would only postpone the circle up to the point where one reaches

²⁰ Depending on whether one endorses a "generous" or a more "parsimonious" substantialist approach, one might prefer the first or the second of these two descriptions. The first, for instance, could be endorsed by an author such as van Inwagen (1990), whereas the second could be compatible with the kind of composition principles suggested by Fine (1999)—especially the ones related to "variable embodiments".

²¹ This objection, importantly, applies as well to the variants of the process view which do not deny the existence of continuants, but which still argue for the priority of processes in the individuation of the continuants (Simons 2018; Pradeu 2018).

the problem of identifying instantaneous parts; and we don't know of any instantaneous processes.

The second objection concerns the very idea of partial identity associated with the cooccurrence of pure processes. Previously, we noted that two distinct processes might share, in principle, any number of temporal parts, in which case they should be said to be *partially identical* at those times (if they share all of their parts, there is no way do distinguish them, and they must be identical simpliciter). But consider now a particular interval of time at which two processes share exactly the same stages. How, at those times, should we distinguish between these two processes? A tentative answer might consist in pointing to the existence of different causal relations holding between these different stages; but it is actually unclear how this could lead to the identification of different stages co-located at a same time. Rather, it seems to us that two processes co-occurring at the same time at the same place can only be distinguished by fiat.²²

3 Four metaphysical interpretations

In section 1, we formulated two questions relative to the interpretation of the pluralist diagram (Figure 1). The first concerned the nature of the particulars within the set of biological individuals (BI). The second concerned the nature of the relation between these particulars and the properties referred to by PI and EI. At this point, we can now respond to the first of these questions: of the four alternatives envisaged above (namely substance ontology, the bare particular hypothesis, trope theory, and process ontology), substance ontology embodies the clearest and, in our view, the most satisfactory account for the identity conditions of biological

²² Note that we do not see these objections as fatal but as serious challenges to the development of any process ontology.

individuals. However, the substantialist account still leaves the second of our questions largely unanswered; for to claim that every biological individual must belong to (at least) a substantial kind does not tell us what the relevant substantial kind(s) is/are in the pluralist diagram. In order to solve this underdetermination—and so, to make progress on our second problem—we need to engage into a more exhaustive survey of the different (substantialist) alternatives that might—prima facie—be compatible with this diagram. This is the purpose of the present section.

To this end, the approach that we will adopt is simple. On the pluralist diagram, PI and EI refer to distinct (but overlapping) predicates whose members share, respectively, the properties "being a physiological individual" and "being an evolutionary individual". Conceived of as universals, each of the properties associated with PI and EI admits two possible interpretations—either as a substantial property (a natural kind) or as a mere/accidental property. Combining them, four metaphysical interpretations of the diagram can then be formulated:

Interpretation I: neither PI nor EI refers to substantial (individuating) properties. Interpretation II: Both PI and EI refer to substantial properties. Interpretation III: Only PI refers to a substantial property. Interpretation IV: Only EI refers to a substantial property.

In this section, we will address each of these (mutually exclusive) interpretations in turn, so as to assess if any one of them might be used to flesh out the pluralist ontology. As we will see, however, all of these interpretations raise *in fine* more difficulties than they really solve.

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3.1 Neither PI nor EI refers to substantial properties

The first interpretation that we will consider—hereafter Interpretation I—takes the predicates PI and EI to refer (intensionally) to non-substantial properties. According to this interpretation, the properties "being a physiological unit" and "being an evolutionary unit" are just like any other accidental property—such as "red" and "round"—and must therefore be defined on a domain of objects that is *already* identified. On the pluralist's diagram, this domain of objects is represented by the set BI; but merely pointing at it doesn't help us to find out the criterion of identity (if there is one) for the sortal "biological or evolutionary conditions (otherwise we would fall back on something like Interpretations II, III or IV). Hence, for Interpretation I to prove meaningful, we need to find a plausible but independent source for the identification of the members of BI.

In our view, four possible options can be envisaged, prima facie, to derive and/or ground such a general criterion of identity for BI *independently of*—or prior to—any physiological or evolutionary considerations. But, as we will now show, none of these options turns out to be scientifically or metaphysically receivable.

First, one might simply derive our general criterion for BI directly from common sense. But common sense, admittedly, would only provide us with a *cognitive* criterion for identifying biological individuals, not with an ontological criterion. So this possibility can be confidently discarded.

Second, one might suppose that this general criterion has its roots in some fundamental property of biological individuals (e.g. "being alive")—a property which *doesn't* resume to more specific properties such as "having a physiology" or "being an evolutionary unit". But this possibility amounts to a form of vitalism which, aside from being of dubious scientific

value, is both circular and non-explanatory: given the current state of the biological sciences, we just don't have the conceptual resources to explain what it would take or mean for a given entity to "be alive" if not, either, having some form of functional (even though minimal) configuration (as presumed by PI) or having some form of evolutionary dispositions (as presumed by EI).

A third possibility would consist in equating the domain of biological individuals with the domain of *physico-chemical or material objects*. At first, this suggestion might seem to better fit with our traditional representation of scientific ontology (conceived of as a hierarchy of higher-level properties "supervening" on lower level properties/entities). But like the previous options, we do not think that it is metaphysically acceptable. For, unlike other categories of physical entities (such as fundamental particles), the category of "physico-chemical *aggregates*" do not form a homogeneous class of individual objects. This point is clearly stated by Lowe in the following passage:

"material object' is not a sortal term and doesn't express or convey a sortal concept. [...] it is simply not the case that all material objects are governed by the same criterion of identity. Thus, for example, both cats and mountains are material objects, but they do not share the same criterion of identity." (Lowe 2007, p.518).²³

In a sense, the only putative criterion that one could possibly suggest for material aggregates is physical cohesion. But physical cohesion refers to a myriad of different sorts of physico-

²³ Material objects, in effect, are nothing but mere *aggregates* of matter with arbitrary boundaries, and that is why there is no point to try making statements about their identities *as individual substances per se*—at least if we don't know, in the first place, what kind of individuals they are.

chemical interactions, and is therefore of no use *if* we are looking at a general and *non-arbitrary* way of individuating material objects.²⁴

Finally, a last option that one might consider here is *eliminativism*.²⁵ According to the most radical versions of this view, there are simply no such things as material objects, aggregates or biological individuals—only an endless plurality of physical particles arranged in an (almost infinite) variety of ways. Among these particular arrangements, some constitute the ultimate truthmakers of our claims about biological individuals (physiological and/or evolutionary). But, for the eliminativist, our representation of the living world in terms of BI, PI and EI is just a useful fiction: at bottom, what truly exists are nothing but simples arranged in particular ways that we—limited by the structure of our cognitive architecture—perceive and describe as biological individuals, physiological individuals and evolutionary individuals.²⁶

If eliminativism were true *simpliciter*, Interpretation I could surely be defended: the only departure from the substantialist account exposed in section 2 is that we would now have to drop the assumption that every biological individual corresponds to an individual substance. For the properties referred to by BI, EI and PI would represent nothing more than our own, fictional descriptions of what there really is, viz. the combinations of simple, physical substances. Yet, although eliminativism might be a defensible option as far as *material* objects are concerned, we don't think that it should be regarded as a relevant option in the case of living entities. To see why, let's return to the analogy between the Great Red Spot and an organism. The Great Red Spot, as we perceive it, is most naturally categorized as a meteorological

²⁴ Surely, one way to qualify this argument would be to point at the *constraints* which bear on the identity of material objects (for example, two distinct material objects of the same sort cannot have the exact same location; otherwise they should be identical). But these constraints cannot in themselves constitute a criterion of identity for biological individuals, as they only apply to objects *of a given sort* (Wiggins 2001, ch.2).

²⁵ Another name for this philosophical stance is (compositional) nihilism.

²⁶ For a useful exposition of the differences between eliminativism, reductionism and antireductionism about material objects, see Baker (2007), ch.2.

phenomenon—a giant storm. But it is also, more fundamentally, a physical phenomenon. And although some properties of giant storms might well (one day) be proven irreducible to lower physical interactions, it does not seem unreasonable—to the extent that the description of storms as physical events remains uncontroversial—to seek for a reductive explanation of their macrostructure in terms of a "mere" arrangement of physical particles (e.g. as an apparent, stormy pattern of particle interactions). In the case of organisms, however, our prospects for a reductive explanation are almost nil. For, unlike storms, the description of their structure necessarily involves a *functional* dimension that is completely alien to the language of physics. Of course, the eliminativist could well retort that the challenge is precisely to understand how a mere arrangement of physical particles might account for the truth of our functional descriptions in biology. But, given the irreducible character of this functional dimension, we don't see how this challenge could be overcome if not by fiat, and so, in a purely non-explanatory way.²⁷

In addition to these problems, a last worry that we should mention here concerning Interpretation I is that it doesn't account for the theoretical *rationale* behind the pluralist's diagram. As Pradeu (2016) notes, when physiologists and evolutionists investigate the nature of biological individuality, they do so—most of the time—in order to bring out the existence of causal links between *physiological* properties (associated with organisms) and *evolutionary* properties (associated with units of selection). That is, their aim is to establish general statements about different sort of properties that don't simply occur *by chance*—unlike, for instance, the sort of relation one can observe between redness and roundness—but because of specific factors that are responsible for the re-occurrence of robust and repeated patterns of functional relations (Pepper and Herron 2008). These relations often occur in both ways, from

²⁷ For a related line of argument illustrating the failure of nihilistic/eliminativist accounts to apply to living beings, see van Inwagen (1990), ch.9.

physiological properties to evolutionary dispositions and back²⁸, and explain why many units of functioning and many units of selection coincide in nature. But if these causal relations are truly systematic, as it seems to be the case, then it doesn't seem right to conceive of the relation between the properties "being an organism" and "being an evolutionary unit" as being *of the same sort* as the relation between such properties as "being a red object" and "being a round object".

3.2 Both PI and EI refer to substantial properties

As just outlined, the coincidence between PI and EI in Figure 1 cannot be explained by "chance alone", for numerous facts attest the existence of systematic, causal relationships between physiological properties and evolutionary dispositions. Interpretation I clearly fails to accommodate this point; but Interpretations II, III and IV do not have this problem, for all interpret *at least* one of the two predicates PI and EI as some sort of natural kind.

At first, Interpretation II, III and IV seem equally well equipped to account for the existence of such causal relations. But Interpretation II, in one respect, is more appealing, as it succeeds in reconciling *both* those physiologists and those evolutionary biologists who think, respectively, that physiological and evolutionary units correspond to fundamental categories of

²⁸ Thus, having functionally integrated parts is typically a cause of an increased survival and reproduction of evolutionary units (Pepper and Herron 2008). Reciprocally, many evolutionary dispositions (such as a potential for variation in reproduction) are directly relevant to the functional integration of these same units. For instance, a common fate among the parts of an evolutionary unit (like the vertical transmission of the symbionts in a multicellular organization) is an important causal factor which positively affects the functional integration of the whole unit—by increasing its degree of organismality in a systematic, predictable way. The degree of organismality of a given biological unit is, of course, affected by many evolutionary factors, such as the mechanisms of transmission, the intensities of intergroup and intragroup selection (e.g. competition between the cells of a multicellular collective and between the multicellular units), the structure of the fitness payoffs among its parts, etc.

individuals. Furthermore, it also conveys a rich, pluralist ontology about biological individuality; and this very fact, by itself, is likely to constitute a desirable feature to the eyes of many philosophers and biologists. Unfortunately, these two attractive features do not save Interpretation II from a major metaphysical inconsistency. For, as we will now see, this interpretation leads to contradictory statements about the *identity* of those biological individuals located in the middle of the diagram (in the zone of overlap).

The source of this problem has to do with a fundamental dimension of the concept of a natural kind. As explained in section 2, any natural kind (or substance sortal) is characterized by a criterion of identity, which governs the identification and re-identification of those objects who share—putatively—the same common substance. To recall, the fact of sharing a common substance (such as "having a molecular structure XXX" or "having functionally integrated parts with respect to some system S") is something that is truly constitutive of what it is to be a criterion of identity. This implies that an individual who belongs to a given kind cannot undergo a change in kind *while remaining identical to itself*. Put simply, a substantial property P_K associated with a kind K imposes a formal constrain upon the possible changes that a member of K can undergo.

This line of thought is very intuitive. But it is clearly at odds with Interpretation II. Indeed, a substantial account of identity forbids the existence of partial overlaps between natural kinds (Wilson 1999).²⁹ As Lowe writes: "it is not even metaphysically possible that objects of kinds governed by different criterion of identity should be identical" (Lowe 2007, p.520).

To illustrate the logical consequences of this metaphysical constraint on the relation between PI and EI (as envisaged by Interpretation II), we need first to recall the general form of a criterion of identity. Let's use again Lowe's formulation—namely: "if x and y are Ks, then x is

²⁹ For a detailed discussion of this point, see Wiggins (2001) ch.2, especially p.67 footnote 7. Wilson (1999) provides a slightly different argument for this impossibility, and concludes that cases of transubstantiation involve a contradiction (section 1.5).

identical with y if and only if x is R_K -related to y" (Lowe 2007, p.515). Applying this formula to our biological predicates PI and EI, we get the following criteria of identity for PI and EI:

- (i) If x and y are PIs, then x is identical with y if and only if x is R_{PI}-related to y.
- (ii) If x and y are EIs, then x is identical with y if and only if x is R_{EI} -related to y.

Now, imagine a single individual—let's call it "x"—that would be *both*, at some time t, a member of PI and a member of EI. Suppose that, at t + 1, x undergoes a transformation T, after which a new individual—let's call it "y"—occurs, which is still a member of PI, but no longer a member of EI. Should we consider that x is *the same individual* as y? Well, the answer is: yes *and* no.

If we agree with the view that a substantial property is part of the identity of all of the individuals who possess it, then the answer is no; for in our example, the fact of losing the property "being an evolutionary unit" would automatically falsify the claim that x and y are identical. Yet, if we accept the criterion of identity for PI as formulated in (i), then the answer may well be yes; for in the light of this specific criterion, there is no metaphysical inconsistency in the fact of imagining that x and y, while differing with respect to EI, remain related by R_{PI} (i.e. remain the *same* functionally integrated individual at different times). In effect, R_{PI} is logically independent from R_{EI} ; hence, nothing prevents x and y from being identical according to R_{PI} , even when y is no longer a member of EL.³⁰

A similar reasoning could be made by considering the case of an individual x that would lose its substantial property of being a physiological unit, while retaining its substantial property of being an evolutionary unit (y). In this case, the criterion of identity formulated in (ii) would

³⁰ This could happen, for instance, if a mutation occurring in a part of x *without disrupting its functional integration* (x and y remain identical with respect to R_{Pl}) led to a dissolution of the common fate among its constituent lineages (e.g. by providing an opportunity for some of its constituents to reproduce independently at a later time).

stipulate that both x and y are identical, though this would contradict the initial assumption that being an organism is part of the identity of x *as an individual*.³¹

In the face of these difficulties, two possible defences of Interpretation II could be envisaged. A first possible option could be to renounce to the assumption that substantial properties are part of the temporal essences of individuals. But, as we have seen (in section 2.2), this conceptual move would amount to a pyrrhic victory; for if we agree that individual substances are ontologically *prior* to their substantial properties, then we should also accept (or be ready to accept) the possibility that individual substances are completely opaque, "hidden behind" their protean identities, and so inaccessible to any kind of empirical verification.³²

A second alternative, by contrast, would be to construe the functions PI(.) and EI(.) not as relations of predication, but as relations of constitution—a solution first suggested by Wilson (1999) in support of (strong) ontological pluralism. This solution would avoid the foregoing contradictions due to the overlap of different substantial kinds. But, as we will now see, it lacks a proper conceptual justification.

In the metaphysical literature, the *constitution* relation is generally invoked to explain how two or more objects (usually a thing and its matter) can occupy exactly the same place at the same time. According to this view, a statue and the lump of bronze of which it is made of, or a person and her body, share all of their categorical properties, but are nevertheless distinct

³¹ This counterfactual scenario, we must say, is not just a conceptual fantasy, and is actually supported by *some* construals of the relation between physiological integration and evolutionary individuality. Thus, the biologist Daniel Janzen argues that any clonal entity produced by a single zygote (or spore) counts as a genuine unit of selection (Janzen 1970). However, what is best for a clone, Janzen notes, is not necessarily to be functionally integrated: indeed, there are many environments in which a clone would rather maximize its fitness by developing in a "scattered" way (in the field, for instance, many plants adopt a "Guerrilla" pattern of expansion with loosely related parts, in order to better exploit their ecological resources that are dispersed in patches). So, in Janzen's world, an evolutionary individual could perfectly cease to be functionally integrated while remaining the same individual. But clearly, such a "Janzen world" would be incompatible with Interpretation II.

³² According to this solution, individual substances would be no different from bare particulars.

objects, because they are not governed by the same persistence conditions—e.g. a lump of bronze could survive flattening, whereas a statue could not.³³ To account for the relation between such coinciding objects, the "constitution view" stipulates that, even though they are not identical, both exist in the same place at the same time in virtue of the fact that one of them (e.g. the lump of bronze) *constitutes* the other (e.g. the statue). In those cases, the relation of constitution corresponds to an asymmetrical relation between two (or more) objects, which belong to different substantial sortals.

As mentioned above, Wilson (1999) is to be credited with the idea that something akin to the constitution relation may account for the existence of multiple—and overlapping—substantial kinds of biological individuals. Wilson does not really specify the nature of the constitution relation, but he seems to interpret it (partially, at least) as one of mereological composition.³⁴ For him,

"The same parts can compose more than one object simultaneously. [...]. The discovery of one natural kind of living entity, for example, the *genetical individual*, does not preclude the existence of a member of the natural kind *functional individual* even if functional individuals sometimes overlap with genetical individuals. [...] the complete overlap of matter does not

³³ Some authors (Geach 1962) have claimed that the statue and the lump of bronze of which it is made of are identical *relative* to some sortal but not relative to others (in this particular example, one should say, for instance, that the statue and the lump of bronze are the same *lump of bronze* but not the same *statue*). Yet, the major problem with this view is that it stands in direct contradiction with Leibniz's law; and this is a price that very few philosophers would be ready to pay (Lowe 2002, pp.62-64; Noonan & Curtis 2018).

³⁴ One possible way of understanding the notion of constitution in terms of the notion of composition is the following: if x constitutes y at some time t, then there must be a level of mereological decomposition at which both x and y share the same parts. Wilson seems to adhere to this particular clause. However, not every philosopher would agree with it, and we should stress that there is no inconsistency in *denying* that constitution is a kind of relation that can be directly analysed in mereological terms (e.g. Baker 2007; ch.9).

entail identity because of the different persistence conditions associated with individuals of those kinds." (p.47)

Wilson's argument is easily transposed to the pluralist diagram. Suppose that, in place of the genetical and functional individuals,³⁵ we have the evolutionary individuals and the physiological individuals, plus a variable x ranging over aggregates of matter/particles (Wilson's "parts"). In this case, PI(.) and EI(.) could then be interpreted as follows:

PI(x, y) = x composes/constitutes a physiological individual y.

EI(x, z) = x composes/constitutes an evolutionary individual z.

According to this interpretation, no contradiction arises from the fact that x simultaneously composes/constitutes a physiological individual y and an evolutionary individual z; for this composition/constitution relation—which is neither symmetrical nor transitive—is distinct from identity.

Wilson's solution consists, basically, in admitting the existence of an n-place relation between a given set of parts (or a given aggregate of particles, if one prefers) and n - 1 different sorts of individuals (in our case, a physiological individual and an evolutionary individual). This relation might well obtain between a lump of bronze, a statue and the set of parts that composes/constitutes them. But it is certainly *not* equivalent to the relation that is posited by the metaphysicians to explain the existence of two (or more) co-located objects. In the case of

³⁵ Wilson takes the category of genetical individuals to be a distinct category from that of evolutionary individuals. It corresponds, in his view, to the class of entities whose parts are genetically identical (e.g. a clone of aphids). His category of functional individuals, by contrast, is largely alike our category of physiological individuals. We won't discuss the details of his particular categories here. But for our part, we don't think that the so-called genetical individuals deserve to be regarded as individuals at all: in our view, they are better envisaged as mere aggregates of genetically identical things.

the statue and the lump of bronze, the traditional constitution relation is not a 3-place relation, but a 2-place relation between the statue and the lump of bronze which constitutes it.

To decide whether the relation between (overlapping) physiological and evolutionary individuals might be legitimately envisaged as a proper relation of constitution, one should actually verify if the essential features of the latter are also possessed by the former. One of these essential features is supervenience: in the classical examples of constitution, the properties of the constituted object (a statue, a person) always *supervene* on the properties of the constituter (a lump of bronze, a body). This presupposes, not only, that a certain formal relation of covariation must hold between the properties of the constituter and that of the constituted object, but also that a certain asymmetrical relation of metaphysical determination must hold between these properties (Kim 2003). Thus, to mention only the most famous example: if all of the neural states of a particular body are fixed, then all of the mental states of the person coinciding with this body must be fixed too.

Is there plausibly something like a relation of supervenience holding between two co-located physiological and evolutionary individuals? We don't think so. To illustrate, suppose that Phy and Ev stand, respectively, for a physiological individual and an evolutionary individual. Suppose, moreover, that both exist at the same place at the same time. In this case, the relevant hypotheses are:

- (i) *Phy* is constituted by *Ev*.
- (ii) *Ev* is constituted by *Phy*.

To assess them, one should now ask whether the properties of Phy (Ev) supervene on the properties of Ev (Phy). But a quick examination suffices to see that neither (i) nor (ii) satisfies the supervenience condition.

Consider first the hypothesis that the properties of Phy supervene on the properties of Ev. As we know, the two sets of properties—evolutionary and physiological—are (to some extent) correlated. But a relation of supervenience does not hold in this case; for any given profile of evolutionary properties that Ev might instantiate would turn out to be compatible with a large variety of physiological profiles that Phy might instantiate (in effect, different physiological systems can perfectly have the same evolutionary consequences in a given selective environment). Hence, the first hypothesis can be confidently discarded.

Consider now the second hypothesis (the properties of Ev supervene on the properties of Phy). Here again, fixing the properties of Phy would surely affect, to some extent, many of Ev's substantial dispositions (its heritability, its fitness, for instance). But evolutionary properties, by definition, always depend on the nature of the relation between their bearer and the other members of the population; hence, a same set of physiological properties will typically lead to different evolutionary dispositions, depending on the nature of the selective environment. Consequently, a proper supervenience relation does not hold in this case either.

For these reasons, it seems to us rather doubtful that the relation between two co-located biological individuals might be sensibly envisaged as a proper relation of constitution—in the sense in which this relation is typically understood by metaphysicians. As it is, and in the absence of a better justification, the foregoing interpretation of PI(.) and EI(.) in terms of composition/constitution seems more like an ad hoc fix—designed to elude some undesired consequence of strong ontological pluralism—than an independently motivated claim.

3.3 Only PI refers to a substantial property

Interpretation III relies on two distinct assumptions. The first has long been part of the traditional conception of biological individuality: it is the claim that physiological integration

is *par excellence* an individuating property (Aristotle, *Categories*). The second has no clear counterpart in the philosophical literature: it is the assumption that the properties with evolutionary consequences are only instantiated by *already individuated* objects—that is, by objects with a definite identity and formal boundaries. Taken at face value, this metaphysical picture seems reasonable. But Interpretation III, actually, faces two important difficulties. One is epistemological, the other ontological. In this section, we will address them in turn.³⁶

The first—epistemological—problem consists, for the advocate of Interpretation III, in providing an explanation to the ontological status of those physiological units which, presumably, belong to PI but not to EI (such as many host-symbiont associations and biological societies). As mentioned above, Interpretation III supposes that the criterion of individuation for physiological units derives from some relation of physiological integration. But ultimately, physiological integration is nothing but an instance of functional integration. So, in order to provide a criterion of individuation that doesn't rely on evolutionary conditions, one should begin by proposing a non-evolutionary account of functional integration—that is, a non-evolutionary account of *function*.

In the philosophical literature, there are two main accounts of biological function. The first is the selected effect account (Wright 1973; Neander 1991), the second the causal account (Cummins 1975). According to the selected effect account, the function of a trait is—roughly the effect for which it has been selected in the past evolutionary history. According to the causal account, the function of a trait (e.g. the heart) is its causal contribution to some capacity of a system (e.g. the capacity of blood circulation). The selected effect account is hardly compatible with Interpretation III, for it resumes the functional integration of organisms to some kind of adaptation—which, itself, must derive from some sort of evolutionary dispositions. The causal account, by contrast, does not rely on evolutionary considerations; but it is not better suited for

³⁶ A common (but crucial) objection to Interpretation III and IV is discussed in section 3.5.

Interpretation III. In effect, the choice of a (causal) system is always *relative* to the interests of the researchers;³⁷ and this character of arbitrariness is plainly incompatible with a commitment to the existence of physiological individuals as individual substances.

Since none of these accounts turn out to be really appropriate for the purpose of Interpretation III, we must look for an alternative. To begin, let us recall the general formulation of a criterion of identity for physiological individuals:

"If x and y are parts of some o member of PI, then x and y are parts of the same o iff x is R_{PI} related to y."³⁸

From there, the main (epistemological) difficulty is to find a way of naturalizing this criterion *without* the help of an evolutionary basis. We know that a fundamental requirement for any criterion of identity is to rely on a non-circular definition of R (cf. Lowe's definition in section 2.1). But is it possible to define R_{PI} in a non-circular *and yet non-evolutionary* way? This is, we think, unlikely.

By excluding evolutionary characterisations, three possible definitions of R_{PI} can be envisaged. The first corresponds (more or less) to the definition that an advocate of the causal account may give: $xR_{PI}y$, in this case, would mean something like "x causally contribute to some global capacity of the same system than y". Yet, as noted above, this criterion is of no use if we look for an ontological—and not a cognitive—principle of individuation for physiological

³⁷ The beatings of the heart, by helping a trained physician to properly diagnose an heart disease, contribute to the capacity of a physician-patient system of having the life of the patient prolonged; but making noise is surely not a "proper function" of the heart—at least not one that would justify the assimilation of the physician-patient system to a genuine individual (in the *ontological* sense).

³⁸ This is the "mereological variant" of the formulation introduced in section 3.2. Cf. also footnote 4.

individuals. Besides, it is blatantly circular (it cannot avoid a reference to "the same system"); so we have to find another option.

A second possibility could be to define R_{PI} by means of some transcendental or structural condition. Some interesting works in theoretical biology have explored this possibility, and even proposed a formal characterisation of the organism that exclusively refers to the structural/causal relation among its parts (Rosen 1991; Mossio *et al.* 2016). In this line, xR_{PI}y could be interpreted, for instance, as: "x and y are both included in an open chain of organic processes that is closed to efficient causation" (the familiar reader would have recognized Rosen's definition of the organism). Unfortunately, these structural definitions—when they do not rely on some primitive or transcendental understanding of the notion of an organic whole— usually involve a reductive analysis of "closed" functional systems in terms of some abstract pattern of causal interactions, which make them fall prey to the same problem as the particular version of causal account on which they are based.

Finally, a third option might consist in conceiving of the substance of physiological individuals (i.e. physiological integration) as a function of the evolutionary interactions occurring at the level of their *constituents*—such as the cell lineages.³⁹ In this case, R_{PI} could be interpreted as follows: "x's evolutionary interests are arranged in such and such way with y's evolutionary interests". The problem is that this sort of definition—which leaves open the possibility of a reduction of the "substance" of physiological individuals to that of their evolutionary constituents—does not really support Interpretation III. After all, one could well argue (while holding this very definition) that the *real* biological individuals are not the

³⁹ This last option must not be conflated with the selected effect account (which reduces the functional integration of physiological individuals to their evolutionary dispositions). For unlike the latter, it accounts for the individuality of physiological individuals in terms of the evolutionary dispositions of their constituents, not of their whole being.

physiological units at the level N + 1, but those very evolutionary units located at the level N and whose proper functions give rise to an appearance of functional unity at the level N + 1.

Aside from these epistemological issues, the advocate of Interpretation III also faces some serious ontological problems when it comes to providing a *consistent* (and non-arbitrary) criterion of identity for physiological individuals. In his paper, Pradeu (2016) proposes the following—and rather consensual—definition of physiological individuality:⁴⁰

"Physiological individuality consists in the interactions between bodily components and the regulation of these interactions, particularly through control over variations." (p.800)

Based on this definition, one could decide that a set of "bodily components" *instantiates* a physiology if it achieves—and secures—by its various activities (including transfers of matter and energy from its environment) the stability of some vital interaction among its parts.⁴¹ However, although this principle might serve as a general criterion for identifying the presence of *life* in a given system (a rock, for instance, is not a living entity according to this view, because its internal stability is not the outcome of its own regulatory activities), it cannot serve as a proper ontological criterion of *individuation* for physiological substances.

The reason is simple. Given the above definition, many kinds of processes or relations, such as nutrition-like processes (e.g. trophic/nutrients exchanges) or various mechanisms of resilience (e.g. colony defences, immune systems, thermoregulation systems), are equally entitled to count as "physiological". As a result, any of these various processes can be used as a legitimate criterion of identity for physiological individuals (in place of R_{PI}). In itself, this diversity is not problematic; for there is no contradiction in acknowledging various forms of

⁴⁰ Pradeu, as far as we can tell, is not a proponent of Interpretation III.

⁴¹ The coordinated activity which ensures the persistence of function in a living system is usually called *homeostasis* in physiology (Turner 2000).

physiological individuals.⁴² But the inconsistency arises from the fact that most, if not all, of these physiological processes and relations tend to *massively overlap* in the biological world. Thus, some stable chain of trophic or nutrient exchange R could well, according to this definition, serve as a basis for individuating a given physiological system S; yet, in most cases, this system will also be involved—wholly or in part—into numerous additional sorts of physiological activities R', R", etc. occurring at different scales (e.g. various metabolic chains, various physiological processes of collective resilience, etc.) which each, in turn, could well be used as particular criteria of individuation for an indefinite number of overlapping physiological units S', S", etc.⁴³

Of course, a possibility could be to take "at face value" the reality of such overlaps. But this would amount to endorse the metaphysical view that two (or more) individuals *of the same substantial kind* can share a large majority of their parts; and we do not see, quite frankly, how this metaphysical claim could plausibly make sense. Hence, if we want to preserve the spirit of the physiological criterion, while avoiding the hypothesis of massively overlapping individual substances, it seems that we have no choice but either (i) to renounce to the substantial character of physiological individuals⁴⁴—and so, to Interpretation III—or (ii) to look for another definition of physiological individuality.

⁴² Note furthermore, that it is not metaphysically absurd (though it might be biologically or philosophically debatable) to suppose that some "odd cases", like a termite mound, a forest, or even the Earth (Gaia) may count as physiological individuals, as long as there is some systemic, biological process that they instantiate, and which justifies their assimilation to this concept (Turner 2000).

⁴³ Even though any *particular* physiological relation might well delineate a unique relation between some set of biological entities, the *general* relation "is physiologically connected with", by contrast, is most certainly true of any two living beings on Earth, even if they are only loosely connected by some chain of multiple and distinct physiological relations.

⁴⁴ This is an alternative that the advocates of a process ontology would willing embrace, but we have already expressed our reservation about this type of view.

If we opt for this second alternative, a natural move would be to adopt a *stricter* definition of what a physiological individual is. Pradeu, for instance, has argued in several places (Pradeu 2010, 2016) that the most accurate criterion for the individuation of physiological units is based on immunological theory. His definition goes as follows: "[a]n immunological individual is a functionally-integrated whole made up of heterogeneous constituents that are locally interconnected by strong biochemical interactions and controlled by systemic immune interactions." (Pradeu 2010, p.258). Pradeu recently defended an interpretation of this criterion in terms of the process view (Pradeu 2018); but there is no reason for which one could not adopt a substantialist interpretation of his particular definition instead.

Pradeu's criterion is appealing for two reasons. First, it puts the emphasis on the heterogeneity of physiological individuals—including ourselves—which (most of the time) are made up of a complex imbrication of symbiotic lineages. This dimension of the PIs has long been neglected by both philosophers and biologists; so a criterion which takes into account this characteristics is surely desirable. Second, this immunological criterion is much more specific than the above physiological definition, as it excludes all those units whose parts are not "locally interconnected by strong biochemical interactions and controlled by systemic immune interactions". As a result, the non-overlapping part of the set PI appears much more restricted than what it would have been if we had opted instead for a physiological criterion of individuation—it will include, for instance, multicellular individuals whose parts are R_{PI}-related by a common immune system, as well as several tightly integrated endosymbioses and some multicellular colonies, such as invertebrate colonies of *Botryllus schlosseri* or siphonophores.

Pradeu's immunological criterion is undoubtedly a good candidate for PI. But it has two shortcomings when it is envisaged as a *substantial*—and not as a cognitive—criterion of individuation (as requested by Interpretation III).⁴⁵

The first problem with Pradeu's criterion is actually a resurgence of the naturalisation issue discussed earlier in this section. If we assume that $xR_{PI}y$ means something like "x is functionally integrated and locally interconnected with y and both are controlled by systemic immune interactions", then one needs to provide a non-circular explanation of R_{PI} . Should we explain it in terms of selected effect account or in terms of another theory? And if the latter, how could functional notions such as "immune system" or "functional integration" be naturalized? This is a difficult issue, because what we are looking for (again) is not a mere cognitive criterion of individuation, but one that best describe the biological entities. By reducing the relations of "immune interactions" to some kind of evolutionary interactions, one would surely end up with a theoretical view which is no longer compatible with Interpretation III.⁴⁶ But, as we have argued, all of the alternatives to the evolutionary account are either circular or hard to vindicate from a metaphysical perspective.

The second problem is more accurately described as a set of difficulties rather than as a single, unified issue. It is intimately related to the clause of "strong biochemical interactions" that figures in the very definition of an immunological individual. To set the stage for its discussion, we will refer to C as "the class of functionally-integrated wholes made up of heterogeneous constituents that are locally interconnected by [some material relation] and controlled by systemic immune interactions". Henceforth, we will refer to this description as the "functional core" of Pradeu's definition. According to this definition, the class of

⁴⁵ The "when" is important here; for recall that there is nothing, in Pradeu's definition, which compels us to endorse this substantialist interpretation.

⁴⁶ This reductive horizon seems difficult to avoid, though; for the immune system is clearly an evolutionary *adaptation* of most living beings.

immunological individuals corresponds to the *restriction* of C—let's call it C-restr—whose members are such that their parts are "locally interconnected by strong biochemical interactions". But what is, exactly, the nature of the relation between C and C-restr? As we shall see, there are (at most) three hypotheses that can be proposed to account for this relation—in line with Interpretation III. None of them, however, turn out to be fully satisfactory.

A first possible interpretation would be to envisage C-restr as the *only* substantial kind. But this hypothesis is immediately problematic; for why should C-restr deserve this privilege, rather than any other possible restriction of C? Thus, why should we consider that C-restr has better claims to count as the "true" category of immunological individuals than, say, the broader restriction of C comprising only the members of C whose parts are locally interconnected by *weak* biochemical interactions? Or why—to take a different example—couldn't we recognize (alongside or in place of the class of immunological individuals), the class of, say, "pheromonal individuals" as a distinct, substantial kind of individuals—whose definition would be identical to that of immunological individuals, except that the term "pheromonal" would be used in place of the term "biochemical"? We see no principled answers to these questions.⁴⁷

To avoid this problem—i.e. the problem of isolating (in a *non-arbitrary* way) the subclass of C that should be regarded as "the" only substantial kind—one might be tempted to adopt a more "generous" hypothesis. Thus, instead of regarding C-restr as "the only substantial kind", one might prefer to envisage it as *one* substantial kind *among a few or many others* within the broader class C. But this particular move, obviously, would only shift the difficulties that we are trying to elude. For the threat of arbitrariness would now be displaced from the choice of the true substantial kind to the choice of the true partition of C corresponding to the set of its

⁴⁷ In response to these worries, one could respond that C-restr is the class of individuals which best matches or approximates our intuition about what a genuine biological individual is (after all, C-restr mostly includes multicellular and unicellular organisms, and a few cohesive colonies). But, obviously, one should not let this kind of pre-theoretical intuitions to interfere with our choice of the relevant scientific categories of individuals.

substantial restrictions. Besides, one would now have to account for the metaphysical role played by the functional core of C in the individuation of living things; for the latter is, by definition, consubstantial to *all* of the material subkinds of C, and so cannot, by itself, serve to individuate the members of these subkinds.⁴⁸

There is, finally, a third possibility that one might envisage here: why, after all, couldn't we simply assume that the functional core of Pradeu's definition constitutes or embodies *itself* a criterion of identity for immunological individuals—without the need for an additional material clause? By adopting this assumption, one would not only elude the previous difficulties, but also preserve the functional core (i.e. the "spirit") of Pradeu's definition. So what could be wrong with this particular view?

In our opinion, the main risk associated with this option (i.e. dropping the material clause) would be to end up with a class of "immunological individuals" that is too *heterogeneous* to form a clear substantial kind. To illustrate this worry, imagine what would happen if one were to dissociate the functional core of Pradeu's definition from the particular clause of "strong biochemical interactions"—viz. the clause restricting its application to (roughly) the unicellular/multicellular/colonial entities endowed with complex (innate or adapted) molecular defences. In this case, one would be left with a general criterion of identity for immunological individuals. But our criterion would inevitably apply to a large bunch of organizations which, obviously, would not have much in common with the abovementioned examples. Thus, by characterizing an immune interaction in broad (functional) terms as, say, "some kind of systemic control that reinforces/sharpens the identity of the whole relative to the other wholes in its surroundings", many social organizations, including human groups and/or institutions,

⁴⁸ To account for this metaphysical role, a possibility could be to conceive of the relation between the functional core and each of its material restrictions as an instance of the metaphysical relation between a *determinable* and its *determinates* (Wilson 2017). But, in order to warrant further discussion, this interpretation would have to be fleshed out and developed in detail (a task that we shall leave to those who are willing to pursue it).

would automatically qualify as "functionally-integrated wholes made up of heterogeneous constituents that are locally interconnected by [various interactions] and controlled by systemic immune interactions". But clearly, one might legitimately wonder *why* these sorts of cases should be categorized as genuine instances of immunological individuals, rather than as mere instances of some *metaphorical* application of this idea.

In response to this worry, an advocate of the functional approach could well respond that the apparent "oddness" of these cases should not impinge on our judgments regarding biological ontology. In support of this view, she could even embrace something like the following line of reasoning:

- (i) Immunology is one of the most cutting-edge branches of contemporary biology.
- (ii) When it comes to scientific ontology, our metaphysical inferences should be exclusively constrained by/informed by our best scientific theories, without regard for our pre-theoretical intuitions.
- (iii) If immunology tells us that some humans groups (or other prima facie "odd cases") are genuine immunological individuals, then given (i) and (ii), one should just accept it.

However, this line of reasoning seems to us questionable—for two reasons. First, and even by accepting the truth of premises (i) and (ii), it has a strong air of paralogism. For surely, it does not follow from (i) *alone* that immunology is the kind of theory that could or should serve as a basis for our biological ontology (as requested by (ii)). Maybe, after all, immunology is just a special branch of physiology, which is itself nothing but a special branch of evolutionary biology, in which case one might reasonably doubt of its independence (or generality) as a proper theory. In any case, the theoretical status of immunology in relation with the other "branches" of biological sciences would have to be determined in the first place for a conclusion such as (iii) to be acceptable. Secondly, the plain acceptation of (ii) does not entail that one

should not be *careful* about the scope and the conclusions of our metaphysical inferences. Hence, and as noted above, a suspicion of mere, superficial resemblance between the members of the broad kind "immunological individuals" should certainly weigh in the balance when deciding whether the functional core of Pradeu's definition conveys or not (by itself) a criterion of identity for immunological individuals—besides, we don't see why this sort of concern could be dismissed as scientifically unmotivated or "pre-theoretical" (a natural kind, in effect, is meant to reflect a causally relevant pattern of resemblances, not a superficial one).

3.4 Only EI refers to a substantial property

Interpretation IV, like Interpretation III, relies on two assumptions. The first is that *some* evolutionary properties are individuating—i.e. substantial—properties. The second is that physiological integration—envisaged separately from its evolutionary consequences—is not an individuating property. As we will see, both of these assumptions turn out to be metaphysically acceptable in the substantialist view. However, both of them are also somewhat counterintuitive, and so deserve a closer examination.

Confronted with the first of these assumptions, one could object that evolutionary properties (such as heritability or fitness) are not *the kind of* properties that can support the individuation of an object. Evolutionary properties or dispositions, as is well-known, are by essence *relational* or extrinsic properties. Yet, in the philosophical tradition, substantial properties (such as "gold") are typically associated with intrinsic properties (Locke 1689; Kripke 1980), not with extrinsic or relational properties—the latter being mostly regarded as "superficial" or "inessential" to their bearers. Thus, in transposing this reasoning to the case of biological individuals, one could similarly argue that the identification of biological individuals—which are often regarded as *paradigmatic* individual substances—should only rely on their intrinsic properties, such as a

particular internal organisation, but *not* on any sort of relational property, such as the ones involved in the definition of an evolutionary unit.

An obvious answer to this objection, obviously, would be to reject the claim that relational properties cannot serve as principles of individuation. But is it a viable option? We think it is, for two reasons. First, it is very hard—from a metaphysical point of view—to draw a sharp ontological line between intrinsic and relational properties. Granted, putative substances such as gold or water are commonly defined by their inner atomic or molecular structure. But we might as well characterise these substances by specifying the sets of *causal relations* in which they are embedded. Some would probably object that this is an impossible task, as long as there is no way of exhausting the very definitions of these substances by listing all of the nomological conditions associated with them (this is the famous problem of provisos). But the idea that substantial properties—including properties such as "being gold" of "being water"—resume to the sum of their causal powers is currently a rather popular view among metaphysicians (Bird 2007). And if this view is acceptable, then rejecting the metaphysical distinction between pure intrinsic properties and pure relational properties stands, at least, as a *plausible* option.

Furthermore, there is nothing, beyond our intuition, that truly vindicates the idea that *only* intrinsic properties can serve as a criterion of identity or individuation for particular substances. In particular, there is nothing which should prevent a given entity from being individuated by the specification of its position in a broader network of spatiotemporal or causal relations. Weak discernability in quantum physics is typically a case (though a controversial one) where no intrinsic property can individuate qualitatively identical and yet distinct particles (Saunders 2003). Besides, the current debate in philosophy of physics about the ontological status of structure is largely founded on the capacity of relations to individuate objects (French 2014). In the absence of a specific argument, then, we don't see any reason to assume that things should be fundamentally different in biology.

What about the second assumption of Interpretation IV, namely the claim that having a physiology is a *non-individuating* property? Interpretation IV, ex hypothesi, is committed to the view that physiological dispositions only supervene on already individuated entities. But this assumption, admittedly, is rather counterintuitive, for physiological integration has long been (and is still) considered by philosophers and biologists as the "cement" of biological individuality—i.e. as what "holds together" the parts of biological individuals. Thus, one may wonder if there is any metaphysical reason which can be given in support of it.

To address this point, we must distinguish first between two possible interpretations of this philosophical claim: by asserting that having a physiology is a *non-individuating* property, one could mean, either, that this property is a non-sufficient condition of biological individuality, or that it is a non-necessary condition of biological individuality. Each of these interpretations raise different issues, and must be envisaged separately.

Let us consider, briefly, the first of these two interpretations: is physiological integration a *sufficient* condition of biological individuality? We think that is unlikely. As explained in the previous section, most of the physiological criteria that can be invoked for this purpose are either too generic (leading to the identification of massively overlapping physiological units) or overly specific (such as Pradeu's criterion, which involves a rather ad hoc restriction on the nature of biochemical interactions that can be regarded as "immunological"). Hence, it is quite debatable that physiological properties might serve as a genuine, sufficient basis for biological individuation.

Now, someone could well retort that the same general problem applies to putative individuating, evolutionary properties, such as the property "being a unit of selection"; for presumably, there are many cases where biological entities can legitimately be regarded as units of selection but *not* as genuine individuals. This is the case, for instance, when units of selection are instantiated on *collectives* that are composed themselves of (lower) units of selection, such

as in the case of group selection (Okasha 2006). But is it a reason for dismissing Interpretation IV? We don't think so. For although being a unit of selection might not be a *sufficient* condition for biological individuality (after all, some groups can be units of selection), that is *not* what Interpretation IV asserts: instead, what this interpretation stipulates is that being a unit of selection (of some sort) is a necessary (*essential*) condition of being an individual—and so, is not the kind of property that a biological individual might lose while remaining the same individual. In other words, the central assumption of Interpretation IV is that being a unit of selection is *part of the very substance* of any biological individual which instantiates this property; but that doesn't imply that every unit of selection has to be a biological *individual*.

Returning now to the claim that having a physiology is a non-individuating property: could it be argued (against Interpretation IV) that, like the property "being a unit of selection", this property is a *necessary* condition of "being a biological individual"? This is doubtful; for many evolutionary units do not possess a physiology at all (like viruses and selfish genetic elements) and yet still count as biological individuals according to the criterion associated with EI. Of course, some might retort that such a view would commit us to a category BI that is too large potentially including memes and other curious entities that one would only reluctantly consider as "biological" in kind. But, although this issue should be envisaged seriously, we are more inclined to envisage it as a good reason/incentive to further *refine* our current notion of an evolutionary individual, rather than as a genuine reason to dismiss Interpretation IV.

3.5 A common objection to Interpretation III and IV

There is, finally, a common issue to Interpretation III and IV which, in our view, should be considered at face value by whoever inclines toward one or the other of these two interpretations. This problem results from the inclusion of PI \cup EI in the set BI, and is independent of any of the previous queries that we have addressed in sections 3.3 and 3.4.

In Interpretations III and IV, one set (let us call it S1) corresponds to a substantial property, while the other (let us call it S2) corresponds to a non-substantial property. In any of these two interpretations, both S1 and S2 overlap, which means that all of the members of S2 *that are also members of S1* are already individuated by the substantial criterion associated with S1. But what about the status of those members of S2 that are *not* members of S1? Surely, a pluralist should agree that they are still biological individuals (at least if we assume that part of what it means to be a pluralist *about biological individuals* is to assume the existence of a plurality of *sorts* of biological individuals).⁴⁹ But clearly, this "solution" would only postpone the aforementioned difficulty: for how, ultimately, should we individuate those members of the set S2 \ S1? If we reply by saying that their criterion of individuation is the same as the criterion of individuation for biological individuals, then we fall back on the same objections that we addressed against Interpretation I. For this reason, it is doubtful that the set BI might be conceived of as ontologically distinct from either EI or PI.

4 Conclusion

Does the pluralist diagram (Figure 1) provide us with a *consistent* partition of biological individuals, envisaged as discrete, three-dimensional particulars? As we have seen, it is difficult to end up with a positive answer to this question; for none of the metaphysical interpretations that can be given to this diagram turn out to be exempt from contradictions. The first is certainly the less ontologically involved, but it doesn't really account for the criterion of individuation for BI (section 3.1). The second corresponds to the strongest form of ontological pluralism, but

⁴⁹ This requirement is illustrated by the inclusion, in Figure 1, of the set S2 \setminus S1 in the set BI.

it conflicts with the notion of what an individual substance is—an individual substance, remember, cannot have two criteria of identity associated with it (section 3.2). The third faces some difficulty in accounting for the epistemological and ontological status of the set PI \ EI, and is silent on the source of the principle of individuation for the set EI \ PI (section 3.3). Besides, it fails to explain why the members of EI \ PI should be included in BI (section 3.5). The fourth is relatively convincing with respect to the justification of its main assumptions, but fails to explain why the members of PI \ EI should be included in BI (section 3.5).

What, then, could be the best philosophical attitude to adopt toward the proposition of a pluralist ontology? Should we give up on this representation, and embrace instead the orthodox, evolutionary conception of biological individuality? This is a possible option.⁵⁰ But that is not the message that we would like to convey. Rather than suggesting which conception of biological individuality might be "the best" or even the more promising, we would like to call for a more *reflective* equilibrium between our biological practices and our current metaphysical theories. Figure 1, as such, is problematic because its initial justification (in Godfrey-Smith (2013) and Pradeu (2016)) goes exclusively in one direction—namely, from our biological practices/theories to our biological ontology. Yet, if we want to *assess* our ontological conception of biological individuality, it is—we think—crucial to also take into account the nature of our metaphysical views about the biological categories we are contemplating. Our critical analysis of the different pluralistic interpretations was only a first step in this direction; but we hope that more attention will be paid in the future to the metaphysical underpinnings of our current conceptions of biological individuality.

⁵⁰ By reducing the set BI to the set EI (thereby avoiding the objection raised in section 3.5), Interpretation IV would be undistinguishable from a kind of evolutionary monism.

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