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**Holobionts: Ecological communities, hybrids, or biological individuals? A metaphysical perspective on multispecies systems**

***Highlights***

* The eco-immunity account of the holobiont asserts that holobionts are hybrids and not biological individuals on the basis that the microbiota is not a proper part of the holobiont.
* We use the tools of contemporary analytical metaphysics to show that the notion of parthood assumed under the eco-immunity account does not exclude the resident microbiota as being a proper part of the holobiont.
* We argue that the eco-immunity account entails that the holobiont is a biological individual.
* Overall, we show that contemporary debates about biological individuality should be assisted with the tools of analytical metaphysics to properly investigate the assumptions and implications that follow from different biological theories.

***Abstract***

Holobionts are symbiotic assemblages composed by a macrobe host (animal or plant) plus its symbiotic microbiota. In recent years, the ontological status of holobionts has created a great amount of controversy among philosophers and biologists: are holobionts biological individuals or are they rather ecological communities of independent individuals that interact together? Chiu and Eberl have recently developed an eco-immunity account of the holobiont wherein holobionts are neither biological individuals nor ecological communities, but *hybrids* between a host and its microbiota. According to their account, the microbiota is not a proper part of the holobiont. Yet, it should be regarded as a set of scaffolds that support the individuality of the host. In this paper, we approach Chiu and Eberl’s account from a metaphysical perspective and argue that, contrary to what the authors claim, the eco-immunity account entails that the microorganisms that compose the host’s microbiota are proper parts of the holobiont. Second, we argue that by claiming that holobionts are hybrids, and therefore, not biological individuals, the authors seem to be assuming a controversial position about the ontology of hybrids, which are conventionally characterized as a type of biological individual. In doing so, our paper aligns with the contemporary tendency to incorporate metaphysical resources to shed light on current biological debates and builds on that to provide additional support to the consideration of holobionts as biological individuals from an eco-immunity perspective.[[1]](#footnote-1)

**Keywords**: Hologenome; biological individuality; microbiome; metaphysics of biology; mereology; immunology

**1. Modes of biological individuation and the mereological question of parthood**

The current observation that multicellular forms of life require an abundant number of symbiotic microorganisms to survive and carry through their basic biological functions has led some biologists to suggest the existence of a new type of biological entity[[2]](#footnote-2): the holobiont (Margulis 1990, 1991; Zilber-Rosenberg and Rosenberg 2008; Dupré and O’Malley 2009; McFall-Ngai et al. 2013). Holobionts, in their simplest form, are biological entities that result from the symbiotic association between a host and the microbes that compose its microbiota. The role of the host[[3]](#footnote-3) is played by what Mindell (1992) and, more recently, Dupré and O’Malley, have characterized as a *macrobe* (animal, plant) -i.e., a visible entity consisting in the set of cells derived from a zygote that shows a considerable degree of cellular and morphological sophistication (O’Malley and Dupré 2007)-, and the microbiota includes a diverse array of microorganisms - *Archaea*, eubacteria, fungi, or viruses.

The realization of the importance of these complex host-microbiota associations has given rise to an agitated philosophical debate about whether holobionts are biological individuals (Rosenberg et al. 2007; Zilber-Rosenberg and Rosenberg 2008; Gilbert et al. 2012; Rosenberg and Zilber-Rosenberg 2013, 2016, 2018; Bordenstein and Theis 2015; Shropshire and Bordenstein 2016; Theis et al. 2016; Lloyd 2017; Roughgarden et al. 2017; Suárez 2018; Suárez and Triviño 2019, 2020) or mere ecological communities of interacting independent individuals (Moran and Sloan 2015; Douglas and Werren 2016; Hester et al. 2016; Skillings 2016; Hurst 2017; Suárez and Stencel 2020). In the context of this debate, Chiu and Eberl have developed a new framework for understanding holobionts: the eco-immunity account. According to their proposal, holobionts are *hybrids* between a host and its microbiota, which plays a role as a scaffold of the individuality of the host (Chiu and Eberl 2016). Chiu and Eberl’s account represents a new way to approach the holobiont debate. On the one hand, they address the problem from a perspective that combines the importance of the immunological system of the host for defining its individuality with the relevance of the ecological environment the host interacts with, rather than approaching it in evolutionary terms, as the debate had been mostly approached before (Morris 2018; Suárez 2018, for a review). Specifically, they pay attention to the importance of the microbiota for the maturation and maintenance of the immunological system of the host. On the other hand, they use the *hybrid framework* to characterize the holobiont, thus partially escaping from the sharp division between biological individuals versus ecological communities, which is mainly rooted in the debate about the units of selection and the concept of Darwinian individuality (Godfrey-Smith 2009).

We believe that the eco-immunity approach relies on a series of unexplored metaphysical assumptions which have substantial implications for the way of thinking about *individuality*. By arguing that the microbiota *is not a proper part*[[4]](#footnote-4) of the holobiont, as well as by characterizing the holobiont as a *hybrid,* the authors are highlighting ontological features of holobionts that, we suspect, are not so clearly present in those proposals that conceive the debate as a dichotomy between units of selection (Darwinian individuals) versus ecological communities. Concretely, Chiu and Eberl’s account highlights that the holobiont is *more cohesive* than an ecological community, without being committed to the view that it is *stricto sensu* a biological individual. Furthermore, their approach gives credit to the metaphysical dimension of the relation of parthood between holobionts and their microbiota. This aspect illustrates the general tendency to incorporate considerations regarding mereology and whole-part relations into the philosophical analysis of biological individuality (Haber 2016; Kaiser 2015, 2018; Lidgard and Nihart 2017; Molter 2017, 2019; Suárez and Triviño 2020; Suárez and Stencel 2020).

Currently, the characterization of parthood is gaining more relevance in the philosophy of biology due to its relation to the question about biological individuality. This is so because, as Kaiser has made explicit, the “parthood question” is related to the “individuation of the whole question” (2018). In other words, the question about how to individuate a whole relates to the question about which its parts are, as the whole can be individuated by means of its parts.[[5]](#footnote-5) In this regard, it is important to establish a distinction between “metaphysical mereology” and “biological mereology” (Kaiser 2018). Metaphysical mereology refers to those metaphysical theories that try to explain the general relations that exist between a part and a whole, as well as among the parts of a whole (Simons 1987, 2020), while biological mereology focuses on studying the biological conditions under which a biological object is a proper part of another biological object. Biological mereology relies on the use of biological theories and models to establish parthood relations and to delimit the boundaries of biological individuals (Godfrey-Smith 2013; Guay and Pradeu 2016; Pradeu 2016a, 2016b; Molter 2017). This is the case in Chiu and Eberl’s account, as they recur to immunological theories to provide a criterion of parthood to individuate holobionts and distinguish them from other types of biological assemblages.

The relationship between biological mereology and metaphysical mereology is, however, problematic. Some authors have recently argued that both debates should neither be mixed up nor identified. There are two reasons that support this position. First, some properties metaphysicians are interested in are highly irrelevant to discuss in biological mereology. For instance, Haber (2016) has convincingly shown that the debate about the transitivity of some relations, which is of key importance in metaphysical mereology, plays no role when one is discussing biological mereology. Second, the biological individuals that are recognized from particular biological theories and models do not always match well with what metaphysicians would recognize as an individual. This consideration has been clearly introduced by Molter (2017, 2019), who explains that individuation in biology is performed within the framework of different theories and models which give rise to cross-classifications of the biological world (see also Dupré and O’Malley 2009; Pradeu 2012; DiFrisco 2017). Importantly, none of these different classifications would have ontological priority over the others, as they simply reflect different scientific interests.

We agree with Haber (2016) and Molter (2017, 2019) that biological theories and models should be directly taken into account when addressing questions about biological individuality or the mereology of biological objects. In this sense, *a priori* metaphysics (Lowe 2002; Tahko 2008, 2013; Chakravartty 2010, 2013), which works independently of contemporary scientific disciplines, is not able, *by itself*, to offer accurate criteria that would allow biologists to individuate the objects of their field. Thus, we discard this option here. However, we do not think that the work of metaphysicians should be ignored in contemporary debates about biological mereology. Biological theories and models rely on several metaphysical assumptions, and they often have ontological implications that are not properly appreciated in the scientific practice and require proper metaphysical scrutiny (Kaiser 2019; Triviño 2019). In terms of Guay and Pradeu: “[T]he sciences do not *by themselves* offer a pertinent and well-articulated metaphysics, which is to say that metaphysics cannot directly be read of the sciences” (2016: 3; emphasis added). In this vein, metaphysics (i.e., metaphysical theories and concepts) is understood as a *toolbox* (French and McKenzie 2012, 2015) that becomes useful to explore the metaphysical assumptions that underlie contemporary scientific research and the ontological implications that follow from it, and to address some of the perceived problems in characterizing scientific objects (see also Guay and Pradeu 2016).

Given this framework, the aim of our paper is to appeal to the metaphysical toolbox (in this case, to mereological theories and accounts of persistence) in order to: 1) clarify the metaphysical assumptions that underlie the eco-immunity account; 2) explore its ontological implications; and 3) show how some of the problems that Chiu and Eberl perceive and that move them to reject that the microbiota is a proper part of the holobiont from the eco-immunity perspective can be dissolved. In that vein, our paper shows that, from an eco-immunity perspective, the holobiont can be characterized as a biological individual.

The structure of the paper is as follows: First, we introduce the debate about the individuality of the holobiont (§2) and present Chiu and Eberl’s eco-immunity account (§2.1). Second, we argue that some of the metaphysical assumptions that underlie Chiu and Eberl’s characterization of parthood generate counterintuitive conclusions within the eco-immunity framework that they advocate. Building on that, we offer three arguments to show that the conception of parthood that follows from the eco-immunity account entails that the microbiota is a proper part of the holobiont (§3-§5). In §6, we suggest that by claiming that holobionts are hybrids and not biological individuals, the authors seem to be assuming a controversial position about the ontological status of hybrids. We argue that, contrary to what Chiu and Eberl assume, the hybrid character of the holobiont entails that it has some of the metaphysical properties that are conventionally attributed to individuals. Finally, we present the conclusions of our paper (§7).

**2. The debate about the individuality of the holobiont**

Regarding the relation between microorganisms and macroorganisms, there are three lessons that 21st century microbiology has taught us: 1) symbiosis is a universal phenomenon in the living world: all animals and plants engage in constant symbiotic relationships with microbes of different species; 2) macrobes are dependent on their symbiotic microbes to carry out their more basic biological functions, including their development and metabolism; and 3) the intervention on the normal microbiota that interacts with a given macrobe leads to an altered system, sometimes generating diseases. These observations are used by the advocates of the holobiont concept, who defend that it is not possible to understand biological individuals independently of the microbiota they interact with (McFall-Ngai et al. 2013). This leads to the formulation of the holobiont hypothesis: all animals and plants have to be considered as holobionts (host + its symbiotic microbiota), which are a genuine new level of biological individuality, as well as a unit of selection in evolution (Margulis 1990, 1991; Rosenberg et al. 2007; Zilber-Rosenberg and Rosenberg 2008).

As the upholders of the holobiont argue, the observations about symbiotic associations jeopardize some of our most traditional intuitions about the biological individuality of the macrobes (Gilbert et al. 2012; Stencel and Proszewska 2017). The biological individual is not anymore the genetically homogeneous macrobe that develops from a zygote, but the multispecies and polygenomic entity –the holobiont itself (Dupré and O’Malley 2009; Dupré 2010; Rosenberg and Zilber-Rosenberg 2013, 2016, 2018). In this regard, these authors implicitly appeal to different modes of theoretical individuation to argue that holobionts are biological individuals in an anatomic, physiological, developmental, and even in an evolutionary sense (Gilbert et al. 2012, 2017; Roughgarden et al. 2017).

Despite all the possible theoretical forms of individuation that may be used to characterize holobionts, the contemporary debate about their individuality has mainly been held in evolutionary terms, where the holobiont appears characterized as a unit of selection under the framework of the hologenome concept of evolution (Rosenberg et al. 2007; Zilber-Rosenberg and Rosenberg 2008; Rosenberg and Zilber-Rosenberg 2014, 2016; Bordenstein and Theis 2015; Shropshire and Bordenstein 2016; Theis et al. 2016; Lloyd 2017a; Lloyd and Wade 2019; Suárez 2020). Contrary to this hypothesis, though, several authors have argued that the notion that holobionts are units of selection is empirically ungrounded, as holobionts do not reproduce in the required way (Godfrey-Smith 2013, 2015; Booth 2014; Moran and Sloan 2015; Douglas and Werren 2016; Skillings 2016; Hurst 2017; Stencel and Wloch-Salamon 2018; Bourrat and Griffiths 2018). Importantly, this debate has shown a serious polarization in contemporary biology and philosophy of biology, which for the moment seems hard to resolve satisfactorily (Smith 2017; Suárez 2018; Morris 2018). Irrespective of this, by placing the emphasis mostly on the evolutionary mode of individuation, the debate about the individuality of the holobiont has been addressed in terms of the following question: are holobionts evolutionary biological individuals, or mere aggregates of independent individuals that interact in an ecological community?

**2.1 The eco-immunity account of the holobiont: microorganisms as scaffolds of host individuality**

In contrast with the predominant approaches in the contemporary literature, which discuss holobiont individuality exclusively in evolutionary terms, Chiu and Eberl have recently developed a new theoretical framework for conceiving holobionts that rests on immunological research: the eco-immunity account.According to this framework, holobionts are not biological individuals but hybrids between a host and its microbiota, which plays a role as a scaffold of the individuality of the host (Chiu and Eberl 2016). The argument the authors offer to justify their claim runs as follows:

1. Hybrids are not biological individuals
2. Holobionts are hybrids between a host and its microbiota
3. Therefore, holobionts are not biological individuals

Premise (1) is based on the authors’ conception of hybrids. Premise (2) is grounded on Chiu and Eberl’s belief that the microbiota lacks the (*sic*) “special glue” with the host that would make it a proper part of the holobiont.[[6]](#footnote-6) In Chiu and Eberl’s account, this “special glue” is provided by what might be called an *immunological criterion of parthood* (Pradeu 2010), which states that “what makes a microorganism part of an organism is not its taxonomic or functional properties, but whether it is interconnected with host components through the biochemical interactions of the immune system” (Chiu and Eber 2016: 822). In other words, microorganisms can only be proper parts of the holobiont in virtue of the *continuity* of host-microorganisms immune interactions, which are required to argue that holobionts are biological individuals. According to Chiu and Eberl, the interactions between the microbiota and the host are not continuous, which implies that the microbiota is not a proper part of the holobiont, and thus, that holobionts are not biological individuals but hybrids.

The arguments Chiu and Eberl offer to justify the lack of continuity between the host and its microbiota are based on the recent theories on immunity that the eco-immunity framework relies on: the discontinuity theory, according to which the immune system of an organism determines both its constituent parts (*criterion of inclusion*) and the conditions in which the organism is actively maintained in the face of constant external perturbations (*criterion of persistence*) (Pradeu and Vivier 2016); and the equilibrium model, which states that immunity should be conceived in terms of the types of reactions (signals) that are triggered as a response to the different targets that the immune system faces: intracellular signals, small extracellular signals, large extracellular signals (Eberl 2016). Building on these two theories, Chiu and Eberl (2016: 820) argue that the microbiota, together with the immune system of the host, allows the persistence and individuality of the latter: First, the immune system of the host, by determining its constituents, establishes its boundaries and thus defines its individuality (Pradeu 2010, 2012). Second, the immune system guarantees the persistence of the host throughout the immune interactions between it and its microbiota.

Despite claiming that immunity allows to establish the individuality of the host by determining its constituents, and although the host immunity is partially activated by microorganisms, the authors do not consider microorganisms as constituents of the holobiont, because their interactions with the host are not continuous. Insofar as most microorganisms are *changeable*, *transient,* and, sometimes, *shared* by other systems and processes, they are not continuously interacting with the holobiont, and therefore, they are not integrated into a single functioning and reproducing whole. This last claim entails that microorganisms cannot be considered proper parts of the holobiont, being the host the genuine biological individual. For the eco-immunity framework, microorganisms are merely scaffolds of the individuality of the host (scaffoldee), insofar as they allow its appropriate development by increasing the quality, efficiency, and stability of its developmental process. Furthermore, they also favour and sometimes control the maintenance of the immunological system of the host, as well as its proper functioning, including how it is activated and when. In this sense, the microorganisms are resources that instantiate and regulate the immunological capacities and processes necessary to determine the constituency of the host, and they do so in a way that allows its persistence (Chiu and Eberl 2016).

According to the authors, since microorganisms are not proper parts of the holobiont, holobionts are not anatomically, metabolically, and immunologically integrated organisms, which implies that they are not biological individuals (Chiu and Eberl 2016). Holobionts are hybrids resulting from the sum of the scaffoldee and its scaffolds. In this sense, the holobiont is the “heterogeneous, collective entit[y]” (Griesemer 2017: 38) “that realizes a developmental capacity” (Chiu and Eberl 2016: 831). Three main aspects characterize the realization of this developmental capacity: (1) the scaffolds play a different developmental role than the scaffoldee. For instance, gut development in mice is possible thanks to the interaction of the host cells (scaffoldee) with *Bacteroides thetaiotaomicron* (scaffold). *B. thetaiotaomicron* triggers a proinflammatory response of the host’s immune system, that makes the host to develop the protective mucus layer of its gut, which prevents from infections by other microorganisms (Stappenbeck et al. 2002; Round et al. 2011). In this process, *B. thetaiotaomicron* only triggers a response, being the host the key active player that develops the mucus layer. (2) The scaffolds might be changed by other scaffolds while the developmental capacity still gets realized. In the last example, under lab conditions, *B. thetaiotaoimicron* might be substituted by a different species and still trigger the same response in its host. (3) Changes in scaffolds sometimes correspond to different stages of development, e.g., birthing and weaning phases are characterized for the relationship with certain bacterial species that disappear in adult stages (Funkhouser and Bordenstein 2013; Gilbert and Chiu 2015; Chiu and Eberl 2016).

We now turn to examine the eco-immunity account in more detail by analyzing the arguments that Chiu and Eberl offer to reject that microorganisms are proper parts of the holobiont (§3-§5), and that hybrids are biological individuals (§6). Notice that all the discussion will be carried out by considering the metaphysical assumptions that underlie the immunological criterion of parthood and the implications that follow from it.

**3. Causal-functional integration is a kind of glue**

According to the immunological criterion of parthood, the fact that microorganisms might play some functional roles for the hosts they interact with cannot be considered as a criterion of parthood.[[7]](#footnote-7) Chiu and Eberl claim that, although there are cases in which microorganisms have been considered indispensable and highly integrated in the development, metabolism, adaptation, and reproduction of the host, these cases do not show that microorganisms are proper parts of the holobiont: “these fascinating cases at most dispel the notion that macroorganisms are self-sufficient without microorganisms. They fall short from showing that holobionts are causally integrated metabolic or reproductive wholes” (Chiu and Eberl 2016: 821). The reason, they argue, is that in the majority of cases of host-microorganisms interactions, microorganisms have *negative* or *no effects* on host phenotype and host reproduction: “Not only do holobionts contain microorganisms that have negative or no effects on host phenotypes and reproduction, the selective cases of reciprocally beneficial relations are not necessarily mutualistic or cooperative” (Chiu and Eberl 2016: 821). And this would even include those situations where microorganisms completely substitute the organ of a host (e.g. the digestive tract of a host), irrespective of the fact that they would be playing a vital function for it, because those structures would always contain microorganisms with negative or no effect.

We do not however agree with Chiu and Eberl’s interpretation of these cases. Firstly, we think that these cases show more than the mere fact that macroorganisms are not self-sufficient by themselves. We consider that, at least in principle, it seems that one would not have problems in claiming that organs are proper parts of macroorganisms. Our lungs, our heart, our liver and our digestive tract are proper parts of us. Furthermore, those organs are individualized on the basis that they perform a particular function for the organisms that bear them: the heart pumps blood, the lungs perform gas exchange between the blood and the air, the liver produces bile, etc. Thus, if there are cases where microorganisms can substitute a complete organ of a host, on which grounds should the microorganisms that perform the function of an organ not be considered proper parts of the holobiont, whereas an organ is considered to be a proper part of the host due precisely to the function it performs? Furthermore, if microorganisms are able to perform the function that is attributed to the organ then, why is it not possible to claim that microorganisms are causal-functionally integrated in the holobiont in the same way as organs of the host are? Why is functional integration not a parthood criterion for microorganisms?

In emphasizing this last point, the functional integration that seems to take place between the host and its microbiota, at least in these cases in which the microbiota is able to substitute a complete organ and perform its function, meets the necessary and sufficient criteria for parthood relations in biology proposed by Kaiser (2018: 75), namely (1) *compositional relevance*, according to which “biological parts must be involved in processes (which I will refer to as ‘part-processes’) that are in a certain sense relevant to -i.e., contribute to, are necessary to, play a causal role in, are crucial to- one or more processes that the whole engages in (which I will refer to as ‘whole-processes’)”. And (2) *substantial spatial inclusion*, according to which biological parts need to be spatially located either inside or in the region that the natural boundary of the biological whole occupies. As we see it, the compositional relevance criterion is met since microorganisms are engaging in biological processes that correspond to the biological function performed by the organ they substitute. Furthermore, the substantial spatial inclusion is also met since, in this case, microorganisms are *inside* the biological boundaries of the host in order to perform this function.

Chiu and Eberl could adduce that such functional structures constituted by microorganisms include some microorganisms with negative or no effect, and thus, they do not really have any compositional relevance, thus contradicting one of Kaiser’s conditions. Yet, even if this is so, it does not really dispel the possibility for those microorganisms to be proper parts of the holobiont due to their interactions with the host. As it is well known, there are many units in the organism that contain proper parts that do not contribute to its function, as it happens with cysts in some organs. Furthermore, there does not seem to be any problem in accepting that macroorganisms can possess proper parts, such as organs, with deleterious functions, or with no function at all. In this respect, few would argue that the appendix, for instance, is not a proper part of us. Yet, it is not clear that the appendix has any function.[[8]](#footnote-8) Furthermore, it is also possible to refer to cases of organs that do not perform their function properly, i.e. cases of malfunctions (Millikan 1989; Mossio et al. 2009; Saborido 2013). A pancreas might not produce enough insulin to properly regulate blood sugar levels in an organism, for instance. However, in cases of malfunction, the organ is still considered to be a proper part of the macrobe.

If this is so, then it seems unclear why microorganisms with negative or no effect over the host deserve a different treatment. Why should the criteria of parthood be different for microorganisms belonging to a holobiont than for the organs of a host? In fact, by rejecting the causal-functional integration of the microorganisms with the host, the authors seem to be simultaneously applying two different criteria of parthood for the different entities that compose the holobiont, namely microorganisms and the zygotically-derived components of the host. However, it is not clear why this has to be so: what is exactly the reason why the criteria of parthood that would apply to a malfunctioning pancreas or an appendix would not equally apply to the persistent elements of the microbiota? The authors might argue that the reasons are genetic: all the elements that derive from the zygote (tissues, organs, etc.) share the same genome, and thus the criterion of parthood that applies to them might be different from the criterion of parthood that applies to the members of the microbiota. Yet, we consider that this argument is not completely convincing. First, because it is not true that all the tissues and organs that derive from the zygote are genetically homogeneous (Dupré 2010, 2012), and still we consider organs and tissues as proper parts of the host. Second, because in the case of transplants, it seems that one would not have any problem in recognizing that the new organ is a proper part of the individual, even using immunological criteria, despite the fact that it is not genetically derived from the zygote (Pradeu 2012).

There is still another way Chiu and Eberl might justify their denial of the existence of a functional integration between the host and its microbiota. As we said in §2.1, according to the immunological criterion of parthood, microorganisms would be considered as proper parts of the holobiont only when they are interconnected with the host components through the *continuous* biochemical interactions of the immune system. On these grounds, the authors conclude that the immunological criterion of parthood shows that microorganisms are not proper parts of the holobiont since their interactions with the host are *discontinuous*, and the microorganisms that at time *t1* interact with the immunological system of the host might perfectly disappear (or be substituted by microorganisms of different species) at a later time *t2*.

This might be true, but there does not seem to be a direct connection between discontinuity and lack of integration. Cell turnover, for instance, is a well-known phenomenon that affects all macrobes, by means of which their cell types get constantly renewed and replaced by new cells. Despite the constant changes in cells, there seems to be no reason to claim that cells are not proper parts of the macrobe. We think that the examples the authors provide to illustrate the discontinuity of the microbiota, which are mainly cases where the microorganisms play an active role in the development of the host, do not require a different treatment than the one that cellular turnover requires: if one considers that the existence of cell turnover in all our organs does not jeopardize the notion that those organs are functionally integrated in our bodies, then it is hard to see why the case of the microbiota should require a different treatment.

**4. Proper parts of an object can change**

Chiu and Eberl might offer a counterargument to our objection that cell turnover and what can be called “microbiota turnover” do not seem to require a different treatment. They might claim that there is still a substantial difference between both processes. In the case of microbiota turnover, certain species that used to interact with the immunological system of the host stop interacting after a certain time, whereas in the case of cellular turnover the same cell types are constantly being produced. In fact, Chiu and Eberl offer different arguments that are based on this *changeable* character of the species of microbiota that interacts with a particular host of a given species to argue that there is no “special glue” between the microbiota and the host and, thus, that the microbiota is not a proper part of the holobiont. In the remainder of this section, we pay attention to these arguments, that we divide in three categories: *contingency*, *interchangeability*, and *sharing*. We argue that none of these arguments is properly grounded from a metaphysical perspective and, indeed, the rejection that the microbiota is a proper part of the host from an eco-immunity perspective does not really follow (see Suárez and Triviño 2020, for an elaboration of the specific form of identity that holobionts realize).

*Contingency*

First, Chiu and Eberl argue that although microorganisms are necessary for the host to perform processes such as development, they are also contingent: “in the regulation of immune responses microorganisms are necessary for the maintenance of host individuality, but *specific* microorganisms responsible for the regulation are highly *contingent*” (Chiu and Eberl 2016: 825, emphasis added). For the authors, this contingency (i.e. the fact that the microorganisms that bring about the processes of development for a host might differ among different hosts of the same species) should make us refrain from considering that there is a glue between the host and its microbiota, and therefore, that the microbiota is a proper part of the holobiont.

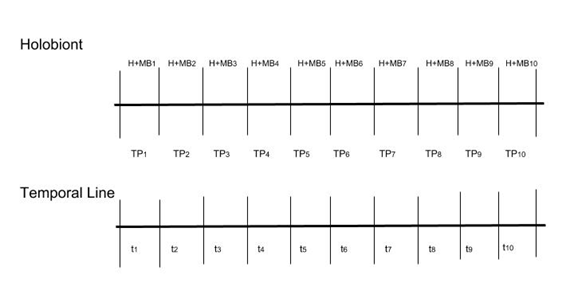
Chiu and Eberl are right to observe that the particular species of microorganisms that interact with the hosts of a given species are highly variable and depend on various external conditions, such as environmental pressures, kinds of social relationships of the host, diet, etc. However, the contingency of the microbiota does not seem to entail that there is not a special glue between the host and its microbiota. In this regard, metaphysical studies concerning persistence and change can serve us to make sense of this idea: let’s consider that the microbiota with a concrete species-profile MS1 interacts with the host H1 of species HS, while the microbiota with a different species-profile MS2 interacts with the host H2 of the same species HS. The consideration of whether MS1 is a proper part of the holobiont (H1+MS1) (due to its interaction with H1) is independent of whether MS2 is a proper part of the holobiont (H2+MS2) (due to its interaction with H2). To establish parthood relations, it is not relevant whether both hosts belong to the same species, or whether they have the same species-profile in their microbiota. Parthood relations in composite objects only concern the “glue” that is established among the parts of the composite object, irrespective of what happens in other objects. Thus, metaphysically, what is a proper part of one holobiont is independent of what is a proper part of a different holobiont. In this case, as long as the microbiota is playing a particular function within the host it interacts with, it can be considered as a proper part of the holobiont, regardless of whether there is a different species of microbiota that is playing the same function for a different host of the same species. In this respect, therefore, some additional reasons should be provided to justify the claim that the contingent character of the specific microorganisms that interact with a particular host species excludes them for being proper parts of the holobiont. As we will discuss in the next section, xenotransplants are a good illustration of this point.

*The interchangeability of microbiota*

Another argument developed by Chiu and Eberl to deny that the microbiota is a proper part of the holobiont refers to its *interchangeable* character, namely the fact that the species of microbiota that interact *with a particular host* might vary during the lifetime of the host.

However, the interchangeability of the microbiota does not necessarily entail that it is not a proper part of the holobiont. From the metaphysical perspective, there does not seem to be any problem in recognizing that proper parts of an object can change at different times during the existence of the object, without this implying that these are not proper parts of the object itself. In fact, metaphysical theories of persistence are oriented to explain how proper parts of an object can change while the object remains to be the same. Two main contemporary metaphysical theories are oriented to explain the phenomena of change and persistence: *endurantism*, according to which entities persist by being “wholly present” i.e. by having all their parts present at each time at which they exist. In this account, change consists in entities having different spatial parts and/or properties at different times at which they exist (Lowe 1987; Simons 2000; Miller 2010). And *perdurantism*, for which entities persist by having different temporal parts each of which exists at different times at which the entity exists. In this account, change means having different temporal parts (with different properties) at different times (Quine 1950; Armstrong 1980; Heller 1990; Sider 2001; Miller 2010).

The metaphysical debate concerning the persistence of objects can also be applied to the case of holobionts. In this regard, let’s imagine the holobiont (H+MB), as being a spatially and temporally extended entity that exists from time t0 to t10.[[9]](#footnote-9) At each time, a particular temporal part of the holobiont is manifested, such that we have ten temporal parts: TP1…,TP10 (see Figure 1).



**Figure 1.** **The persistence of the holobiont**. This figure represents the holobiont as a spatially and temporally extended entity. In this case, the holobiont persists by perdurance, i.e. by having different temporal parts (TP1-TP10) that are manifested at different times (t1-t10) over the interval at which the holobiont exists. Each of the holobiont’s temporal parts is constituted by a host (H) and its microbiota (MB), which might be different in each temporal part (MB1-MB10). A change in the holobiont refers to a change in the temporal part that is manifested at a given time. Temporal parts, therefore, are manifested at different times. However, despite not being manifested at a present time, all temporal parts are, in fact, parts of the entity that they constitute.

According to perdurantism, an entity changes insofar as the different temporal parts that constitute it might differ among them, by instantiating, for instance, different qualities. However, this is not problematic. Since each temporal part is manifested at a particular and different time than the others, the object does not possess incompatible properties manifested at the same time, but different properties manifested at different times. In the case of holobionts, we can claim that a particular holobiont is the same entity that exists throughout an extended period of time, and at each time at which it exists, a particular temporal part is manifested. These temporal parts might be different among them by having, for instance, different specific microbiota. Thus, at t1, the temporal part of the holobiont TP1 refers to the host H and the microbiota MB1; at t2, the temporal part of the holobiont TP2 refers to the host H and the microbiota MB2; and so forth. In spite of the microbiota being different at the different times at which the holobiont exists, in all these cases, the microbiota of the holobiont can be considered as a proper part of it, since it is possessed by one or more of the temporal parts that constitute the holobiont.

Specifically applied to the case of holobionts, this view of change and persistence entails that, *at least during the period of time* at which the microbiota interacts with the host, it can be considered as a proper part of the holobiont, especially since, as the authors recognize, they might play essential developmental functions. In this sense, instead of claiming that the microbiota is not a proper part of the holobiont, insofar as at different times at which H persists, e.g. t1 and t2, the microbiota is different, i.e. MB1 and MB2, respectively, it might be equally argued that the holobiont is composed at different times t1 and t2 by different proper parts, that is MB1 and MB2, respectively. Thus, some additional reasons should be provided to justify their claim that the contingent character of the specific microorganisms that interact with a particular host species excludes them from being proper parts of the holobiont.

Furthermore, and despite the previous argument, Chiu and Eberl are right to observe that the particular species of microorganisms that interact with a given species of host are highly variable and depend on various external conditions (environmental pressures, kind of social relationships of the host, diet, etc.). However, they fail to appreciate that even if the *species* that interact with a given host might change during the lifetime of the host and among hosts of the same species, there are other things that are kept stable. First, it is never the case that the host completely eliminates the microorganisms it interacts with –as they recognize, the absence of microorganisms is pathological for most host species (Chiu and Eberl 2016: 828). Second, the microorganisms that can play the roles of maintenance and development of the host are mainly limited to a few phyla (Dethlefsen et al. 2007; Chiu and Eberl 2016: 831). Recent empirical evidence strongly supports the idea that “the players might change while the game still remains”, i.e. the traits or functions encoded by the microbiota remain stable despite changes in the taxa that the host interacts with (Clarke et al. 2011; Taxis et al. 2015; Lemanceau et al. 2017; Doolittle and Booth 2017; Doolittle and Inkpen 2018; Suárez 2020).

This last evidence can be interpreted, *contra* Chiu and Eberl, as supporting the thesis that the microbiota is a proper part of the holobiont. Analogously with the microbiota, some of our organs might be replaced by structures that play the same function but come from different organisms. Transplants are a good example of this. Our kidneys, for instance, are interchangeable with the kidneys of other humans, provided they are histocompatible, and it is even believed that some organs from animals of other species could be transplanted to humans. It seems counterintuitive to deny organs their status as proper parts of us on the basis that they are interchangeable by other structures, or to deny the new structures their role as proper parts of us once they have been transplanted. By analogy, therefore, it does not seem accurate to deny microorganisms that compose the microbiota their status as proper parts of the holobiont on the basis that they are highly interchangeable, insofar as our current evidence supports the claim that this interchangeability is limited to those microorganisms that can play the same function (e.g. Taxis et al. 2015; Hester et al. 2016). Interchangeability, thus, is not a reason to deny a part its status as a proper part of a bigger whole.

*Sharing*Another reason Chiu and Eberl offer to reject microorganisms as proper parts of the holobiont is the fact that, differently to organs, the microbiota is sometimes shared by two (or more) different macroorganisms instead of being possessed by one macrobe exclusively. The authors illustrate this idea by appealing to the phases of birthing and weaning, throughout which “microorganisms are often passed on from individuals around us, especially from the mother. [...] Microorganisms are horizontally transferable through frequent social interactions and also in turn influence social behavior (Archie and Tung 2015). These studies might also show that resident microorganisms are shared between collectives instead of exclusively owned by single individuals” (Chiu and Eberl, 2016: 832-833). In this sense, the microbiota, insofar as it is shared by different hosts in the community, would not be a proper part of the holobiont, according to Chiu and Eberl.

It is true, as the authors remark, that most of the members of the microbiota are not “born with us”, or “developed with us”, as it happens with our organs, and that this creates a difference between the two. Nonetheless, it is not clear that *being shared* and *being a proper part* should necessarily be mutually exclusive properties. In this regard, metaphysical theories of persistence also take into account cases of overlapping “where A overlaps B just if there is some C such that C is part of A and part of B” (Miller 2010: 44). A standard example used to illustrate overlapping is that of the statue and the lump of clay it is made of (Lowe 2002; Miller 2010). Both the statue and the lump of clay can be recognized as two different persistent entities insofar as they are characterized by different properties. Thus, both have different persistence conditions. For instance, a lump of clay can survive events that a statue cannot, such as being squashed flat; and a statue can survive events that a lump of clay cannot, such as having the clay from which it is sculpted replaced by bronze (Miller 2010). Despite having different properties, during the time(s) the statue and the clay coincide they share the same intrinsic properties, such as being brown, for instance. The metaphysical theory of perdurantism has explained cases of overlapping such as this one. According to perdurantism, both the statue and the lump of clay are different entities composed of different temporal parts. However, there are times at which they both share the same intrinsic properties insofar as they share the temporal parts that constitute them at those times.

Applying this metaphysical argument to the case of holobionts, it could be argued that, *if it were the case* that microorganisms were shared, *at the same time*, by two different hosts, such as in the case of conjoined twins that shared different parts or organs, there would not be a metaphysical problem in claiming that these microorganisms are proper parts of the two different holobionts at the same time. What would happen, in this case, is that both holobionts shared a common temporal part at a particular time, and that temporal part is characterized by having a particular microbiota that is the one that interacts with and characterizes both hosts at the same time.

However, when Chiu and Eberl talk about the possibility for microorganisms to be shared by two different hosts, they are not referring to the idea that microorganisms are possessed *at the same time* by two different hosts. By “being shared” the authors refer to the idea that the microorganisms that once interacted with a particular host, *pass on* *to a different host* and interact with it at a different time. In this regard, we consider that it is also possible to claim, without generating problematic metaphysical implications, that the microorganisms that pass from the mum to the offspring during birthing and weaning, for instance, are no proper parts of the mum anymore: they are proper parts of the newborn. It is not really relevant, when talking about parthood, that the microorganisms that were interacting with a host at time *t1* are, at a different time *t2*, interacting with a different host. Again, what is a proper part of a composite object is independent of what currently is, was, or will be, a proper part of a different composite object at a different time.

This kind of metaphysical reasoning concerning the possibility for an object that is a proper part of a composite object at time *t1*, to be a proper part of a different composite object at time *t2*, also illuminates, in our view, the parthood relations that appear in transplants and transfusions. If someone donates a kidney to her child, for instance, the kidney might be said, without contradiction, to have been a proper part of the parent until *t1*and a proper part of the child at *t2.* In fact, as James Griesemer has convincingly argued, all cases of reproduction require a stage of material overlapping between parents and the offspring, i.e. that parts that used to belong to the progenitors in the past do now belong to their offspring (Griesemer 2000, 2014, 2016).

As we see it, the existence of this material overlap would prove precisely the opposite of what Chiu and Eberl assume it proves, unless the authors are prone to accept that every entity that is generated through reproduction lacks proper parts. Alternatively, they might eventually argue that the criterion of parthood that is applied to the elements of the microbiota should be different from that applied to other elements of the body of the host. But again, they should give a further reason to justify why this is so. Metaphysically speaking, there does not seem to be any reason, *a priori*, to suspect that the microbiota should require a different treatment than any other proper part of an animal or a plant.

**5. Parthood is not a special case of scaffolding**

Finally, another problem we perceive in Chiu and Eberl’s account of the holobiont is that it is not clear in what cases they are referring to resident microbiota (i.e. the elements of the microbiota that reside in the host during its whole life cycle) and in which cases they are not. This is a non-trivial aspect that requires more clarification since it makes a difference regarding the kind of microbiota that can be considered a proper part of the holobiont. At some points in their paper, the authors seem to be talking about the resident microorganisms: “developmental phases are associated with drastic changes in microorganisms constitution, and that changes in *resident microorganisms* [...] can have long term consequences for feature immune capacities” (Chiu and Eberl 2016: 282, emphasis added). In fact, the gut bacteria that allow phase transitions and host development in mammals are usually examples of resident microorganisms. However, when the authors talk about external microorganisms that might affect the macroorganism, they are referring to non-resident, transient microorganisms, whose ontological status in relation to the holobiont is not even agreed upon among the holobiont advocates.[[10]](#footnote-10)

Chiu and Eberl seem to rely on this ambiguity, shifting their talk from one type of microorganisms to another, to present their case against considering microorganisms as proper parts of the holobiont. In fact, they seem to base their arguments to claim that resident microorganisms are not proper parts of the holobiont in the difficulty to establish to what extent external microorganisms can be considered or not as proper parts of it. Due to the difficulties in claiming that external microorganisms that interact for a short period of time with the host are proper parts of the holobiont, the authors conclude that no microorganism is a proper part of the holobiont: “on one extreme of the landscape, resident microorganisms can be considered proper parts of the host organism: when it is not dependent on other microorganisms, is specialized and necessary for the host and the host only. However, the conceptual map shows that “parthood” is merely a special case of scaffolding (Sterelny 2010)” (Chiu and Eberl 2016: 833). Yet this conclusion problematic: Whether (or not) non-resident microorganisms are proper parts of the holobiont is a different question from whether (or not) resident microorganisms are proper parts of it. Thus, to reject that the last are proper parts of the holobiont the authors need to present a further reason.

In this regard, the authors might reply that they justify their position on the grounds that parthood is a special case of scaffolding, along the lines of Sterelny’s work (Sterelny 2010). However, scaffolding and parthood should not be directly identified. Sterelny’s paper studies the role that environmental resources play in human cognition. He appeals to two different models that explain this role: 1) the Clark-Chalmers extended-mind model, and 2) the niche construction model. According to the Clark-Chalmers model, the environmental resources that play a role in enhancing and amplifying human capacities (e.g. a notebook enhancing memory) *are proper parts* of human cognitive systems. The niche construction model, in contrast, states that human cognitive capacities depend on, and have been transformed by, environmental resources. However, Sterelny argues, those resources *are not proper parts* of human cognitive systems, but scaffolds of them, i.e. external resources that enhance those capacities.

According to Sterelny, the Clark-Chalmers model poses some problems insofar as it seems to imply that *all* environmental factors that enhance human capacities are proper parts of human systems. Thus, if glasses enhance human vision, glasses should be considered as a proper part of human systems (2010: 472). The niche construction model, however, makes *weaker* ontological commitments: it does not require us to accept that those external resources are proper parts of human systems, but only that they are resources that *help* in the construction of the human cognitive systems.

Within the framework that Sterelny defends, when he claims that extended minds are limiting cases of environmental scaffolding, he is not referring to Chiu and Eberl’s idea that “‘parthood’ is merely a special case of scaffolding”. In fact, Sterelny does not directly talk about proper parts. He highlights the usefulness of the niche construction model insofar as it makes sense of the idea that environmental scaffolding is a *general phenomenon*. That is, the niche construction model applies to both cognitive and non-cognitive capacities. In this respect, Sterelny offers the modification of food resources and the form we eat them as examples of non-cognitive capacities that are environmentally scaffolded. However, Sterelny continues, no one would talk about an “extended digestion”: a pot is not a proper part of my digestive system.

In the same line, the author argues that the resources used for enhancing cognitive capacities are scaffolds, in the same way as the ones used to enhance non-cognitive capacities. Thus, the extended mind is a case of a more *general phenomenon*, i.e., that of adaptive phenotypic plasticity based on environmental resources. Regarding the enhancement of cognition, there could be cases in which the environmental resources are so individualized and trusted that *they could seem to be* proper parts of an extended mind. However, Sterelny rejects this idea: these cases are really strange, and they continue to be cases of scaffolding, although, maybe, very special ones (Sterelny 2010: 480). Sterelny, therefore, is arguing for the advantages that the scaffolded mind have over the extended mind, and not about what must be considered as a proper part or not (Sterelny 2010: 473).

We consider Chiu and Eberl have interpreted Sterelny’s argument as follows: start considering all the external elements as being scaffolds and then argue that some of those scaffolds are *also* proper parts of the individual, whereas others are just mere external scaffolds (Chiu and Eberl 2016: 833). We believe that this interpretation of scaffolding is problematic, as it gives rise to conclusions that seem metaphysically difficult to accept. If parthood is a special case of scaffolding then, all proper parts of a composite object are also scaffolds of it, whereas not all of its scaffolds are proper parts of the object.

There are two problems regarding this characterization of scaffolds. Firstly, there is the question of how to determine which elements of a holobiont are scaffolds of the host and which are not. In other words, which is the criterion to consider some entities components of the host and others as scaffolds? Is it genetic, so that those cells that do not share the same genetic makeup in a multicellular organism would also be scaffolds and not components of the host (cf. red blood cells, mitochondria in eukaryotic cells)? Or is it just a mere intuition about the physical boundaries of the host? In this respect, it seems that they only provide an intuitive idea of what counts as a scaffold, but do not provide any substantive reason to justify why this has to be so. Secondly, let us assume we have a criterion to recognize scaffolds. How can we differentiate between scaffolds that are proper parts and scaffolds that are not proper parts? Is it because the scaffolds that are proper parts are more integrated? If this is so, then it seems that the authors need to recognize that there is, in fact, some kind of glue between the microbiota and the host. However, if integration is not a criterion for talking about scaffolds that are proper parts, which seems to be what Chiu and Eberl suggest, then they still need to specify the reasons why one should consider that some scaffolds are proper parts, whereas others are not.

**6. The question of the individuality of hybrids**

Finally, we will raise an issue concerning Chiu and Eberl’s first premise, namely the claim that hybrids are not biological individuals (§2.1). Contrary to the authors, who assume that hybrids are not biological individuals, we believe that such type of claim is either false or, at least, requires further clarification. First of all, there is currently an agitated debate in philosophy of biology concerning biological individuality. As Clarke has convincingly shown, there are different non-overlapping ways of classifying biological individuals attending to different criteria, including immunology, development, or metabolism, among others (Clarke 2010; see also Dupré and O’Malley 2009; Dupré 2010, 2012; Pradeu 2016a, 2016b; DiFrisco 2017; Lidgard and Nyhart 2017). The characterization of holobionts as hybrids seems to satisfy at least some of these criteria, as Chiu and Eberl explicitly admit when they claim that holobionts are the entities that realize a developmental capacity. Of course, it might occur that they do not satisfy all these criteria and, particularly, it might happen that they do not satisfy the evolutionary criteria (i.e. they are not Darwinian individuals in Godfrey-Smith’s sense, a claim that has been made by many authors; e.g. Douglas and Werren 2015; Moran and Sloan 2016), but at least they satisfy developmental and immunological criteria, in the eco-immunity account. Yet, despite this, the authors claim that since holobionts realize a developmental capacity *of the* *host*, they are not developmental individuals.

As in the analysis we have made in the previous sections, we also see this from a different point of view. We believe that, insofar as the holobiont is the entity that realizes such developmental capacity, there seems to follow that the holobiont, rather than the host, is the developmental individual. Of course, one might argue that the developmental capacity that the holobiont realizes is only perceived by perceiving the development of the host (host tissues, host organs, etc.). However, as Chiu and Eberl recognize, and as many other authors have also argued (Gilbert 2017), these processes are systematically mediated and maintained by the microbiota, which activates the realization of some of these processes and maintains them through the host’s lifetime. Since this is so, and since Chiu and Eberl explicitly recognize that the entity that realizes these developmental processes is the hybrid (i.e. the holobiont), we believe that there is no reason to deny that the hybrid is the developmental individual, and thus the holobiont is a biological individual from the point of view of development. For, how can the entity that realizes the developmental capacity not be a developmental individual?

Furthermore, the eco-immunity account is grounded on the equilibrium model of immunity, according to which the immune system would develop according to the reactions it triggers in response to different kinds of stimuli. Those stimuli are a consequence of the encounters of the immune system of the host with different elements of the microbiota. In this sense, the immune system does not develop if it does not encounter any member of the microbiota, which suggests that the holobiont could be conceived as an immunological individual, especially if the equilibrium model is combined with the discontinuity theory of immunity, as the authors do. If the immune system is what defines the biological individual by deciding which parts are accepted and which parts are excluded from its boundaries, and the microbiota is accepted as a part (i.e. it is not excluded as a “foreign” object), then there seems to be no reason to deny that the holobiont is an immunological individual. In this sense, one can argue that the holobiont is the hybrid that realizes the immunological capacity and, thus, it is the immunological individual, since the capacity is neither realized by the host, nor by the microbiota independently from each other (see Suárez & Triviño 2020). Therefore, it seems that Chiu and Eberl’s conception of the holobiont as a hybrid does not exclude, *a priori*, the possibility of considering it as a biological individual, at least in a developmental and immunological sense, which is one of the key arguments used to defend the view that holobionts are biological individuals (Gilbert et al. 2012, 2017; Roughgarden et al. 2018).

Thus, we believe that the authors need to be more explicit about their conception of hybrids and why it leads, as they think, to a rejection of the claim that holobionts are biological individuals. For, as Griesemer has recently suggested “[w]hen scaffolded is involved in facilitating developmental processes, I think it is often apt or useful to consider the collective to be an entity in its own right, even if it is not so integrated, autonomous, or persistent as the sort of thing we usually call (biological) individuals” (Griesemer 2017: 38).[[11]](#footnote-11) Maybe holobionts are not individuals in all the senses suggested by Gilbert et al. (2012, 2017) and, especially, maybe they are not Darwinian individuals (units of selection). But yet, if they are hybrids, Griesemer argues, they are biological individuals in a minimal sense (immunologically and developmentally, at least), and this would have important metaphysical consequences about their ontological status.

Following the ideas of Griesemer and those given in the holobiont debate as this has been framed by Chiu and Eberl, we believe that the hybrid conception of the holobiont would entail that holobionts bear emergent properties, a claim that we have argued extensively elsewhere (Suárez & Triviño 2019, 2020). In other words, the holobiont would be the entity that realizes immunology and development and thus how these properties have appeared, evolved, and how they have been transgenerationally maintained requires a closer analysis at the level of both the host and its microbiota. For, importantly, some of the traits that characterize immunology and the developmental processes of most animals will be localized in the microbiota, rather than on the host genome. And, thus, the maintenance of these traits (especially the traits in the microbiota) would be intimately connected to the survival of the holobiont. Our view is that the hybrid is, hence, a biological individual, for it is the entity that realizes these capacities and whose properties must be biologically studied as a single unit. Importantly, the consideration of the holobiont as a biological individual *qua hybrid* entails that it is possible to study it as an entity that exhibits *downward causation*. We do not have space to elaborate here what this hypothesis entails (although see Suárez and Triviño 2019, 2020), but it supposes a radical shift in the way of exploring host-microbiota interactions. Considering the hybrid otherwise (i.e. as Chiu and Eberl) could miss an important dimension of the nature and properties of hybrids (in general), and of the holobiont (in particular). And, in addition to that, it would require adopting a contradictory metaphysical position about the relationship between the properties of hybrids and their ontological status.

**7. Concluding remarks**

In this paper, we have examined Chiu and Eberl’s eco-immunity account of the holobiont, according to which (1) holobionts are hybrids, and (2) in virtue of being hybrids, they are not biological individuals. We have argued that thesis (1) was based on their rejection of the role of the microbiota as a proper part of the holobiont (due to its lack of a special glue with the host) that, as we have argued, is not conclusive. In this respect, we have argued that the authors rely on the use of two different notions of parthood: one applied to microorganisms and another applied to the rest of the monogenetic elements of the host. On these grounds, we have disputed their claims by defending that such distinction is illegitimate and thus, their conclusion is non-sequitur. Secondly, we have also defended that their rejection that hybrids are biological individuals contrasts with the conventional use of the concept of “hybrid”, as popularized by Griesemer, and seems to entail a minimal conception of holobionts as individuals, at least from the immunological and developmental perspective. Our arguments have been based on the use of both metaphysical and philosophical resources to clarify the type of metaphysical commitments that underlie the eco-immunity account, and the type of conclusions that follow from it. Based on our analysis, we consider that, the eco-immunity account of the holobiont does not offer a rebuttal to the thesis that holobionts are individuals, but rather suggest a new and original way of analysing their individuality. Overall, our paper shows that contemporary debates about biological individuality should be assisted by the tools of analytical metaphysics as a way of assessing the implications that follow from different biological theories.

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1. The authors declare they have contributed equally. [↑](#footnote-ref-1)
2. In this paper, “entity” and “individual” should not be equated. The term “entity” will be used with an ontologically-neutral meaning, i.e. it could refer to an individual or to a community. [↑](#footnote-ref-2)
3. By “host” we will always mean the monogenomic set of cells produced by division from a zygote, or from a process of asexual division in the macrobe, in the lineages where reproduction proceeds asexually (Dupré 2010). [↑](#footnote-ref-3)
4. Throughout the paper, the term “proper part” can be equated to the term “part”. Yet, we have preferred to use the notion of “proper part” because it is the one that Chiu and Eberl use, and they do so because this concept is used in metaphysics to exclude the possibility of a whole to be a part of itself (Lowe 2002; Varzi 2019). [↑](#footnote-ref-4)
5. In this regard, it is also important to take into account that the individuation of the whole is also useful to determine the parts that constitute it (Kaiser 2015; 2018). This is so since the whole constraints the individuation of its parts (Moreno & Mossio 2015). [↑](#footnote-ref-5)
6. Notice that the “special glue” refers to the set of biological properties that keep the host and its microbiota together. Different accounts of the holobiont may appeal to different types of “special glue”: metabolism, immunology, development, evolution, etc. [↑](#footnote-ref-6)
7. Notice that, as we will argue, “causal-functional” integration is entailed by the immunological criterion of parthood. That’s the reason why this section is articulated around the concept of causal-functional integration, because we suspect that Chiu and Eberl’s rejection of that criterion is inconsistent with the metaphysical nature of the immunological criterion of parthood. [↑](#footnote-ref-7)
8. Kaiser has explicitly highlighted that cases such as the one of the appendices are problematic since they do not seem to properly meet the criteria of biological parthood (Kaiser 2018). We agree that there might be a problem here. Our point in this regard, however, is to highlight that if we continue considering the appendix a proper part of the host, then the parts of the microbiota that do not perform a function for the host can still be considered as linked to the host by the “special glue” that would make the holobiont an individual, unless we can offer arguments that reject that any of those elements with no function are not proper part of the biological individual (regardless of whether they are microorganisms or organs). [↑](#footnote-ref-8)
9. Here, we are using perdurantism to illustrate that the microbiota of a host might vary without this implying that it is not a proper part of the holobiont. We are using this metaphysical account of persistence since it allows us to explain our argument in a simpler and better way. However, we consider that there is no problem if the characterization of holobionts and proper parts were made from the framework of endurantism, since we agree with those authors who accept that perdurantists and endurantists accounts of persistence are equivalent (McCall & Lowe 2003, 2006; Miller 2005, 2010; Triviño and Cerezo 2015). [↑](#footnote-ref-9)
10. Some defenders of the holobiont have argued that the holobiont should exclusively include the permanent microbiota (Lloyd 2017; Roughgarden et al. 2017), whereas others believe that also transient microorganisms can be included as proper parts of the holobiont (Theis et al. 2016). In any case, it is clear that there are biological techniques especially designed to study exclusively the resident microbiota, rather than the whole set of organisms that interact with a host irrespectively of whether they are resident or non-resident (Knight, personal communication). [↑](#footnote-ref-10)
11. One reviewer has pointed out that if holobionts are scaffolded entities that realize a developmental capacity, then they would be “reproducers”, in Griesemer’s sense (2000) and, hence, they would be units of selection. We do not fully agree with this interpretation of scaffolding, nor are we sure that the conceptual move from holobionts as “realizers of a developmental capacity” to holobionts as “reproducers” is legitimate. First, for Griesemer, reproducers are entities that realize a developmental capacity, where development is understood as “acquiring the capacity to reproduce” and appear in virtue of a material overlap with their progenitors. Thus, reproducers can be understood as units of selection in the sense in which Oyama (2000), or Griffiths & Gray (1994) have conceived the notion of “unit of selection” This definition is however at odds with Chiu and Eberl’s notion of development, which does not refer to acquiring the capacity to reproduce, and so our use of the term scaffolding is connected to their use, rather than to Griesemer’s use. Second, it is not clear that there is the kind of transgenerational material overlap among holobionts that would be required for them to be units of selections, and this is precisely what undermines the hologenome concept of evolution, according to some authors (Moran & Sloan 2015; Douglas & Werren 2016; Hurst 2017). Notice that we are not adopting a position in the debate about whether holobionts are units of selection (although see Suárez 2020; Suárez & Triviño 2019), we are only arguing that the points we make in this paper can be made without entering in that debate. [↑](#footnote-ref-11)