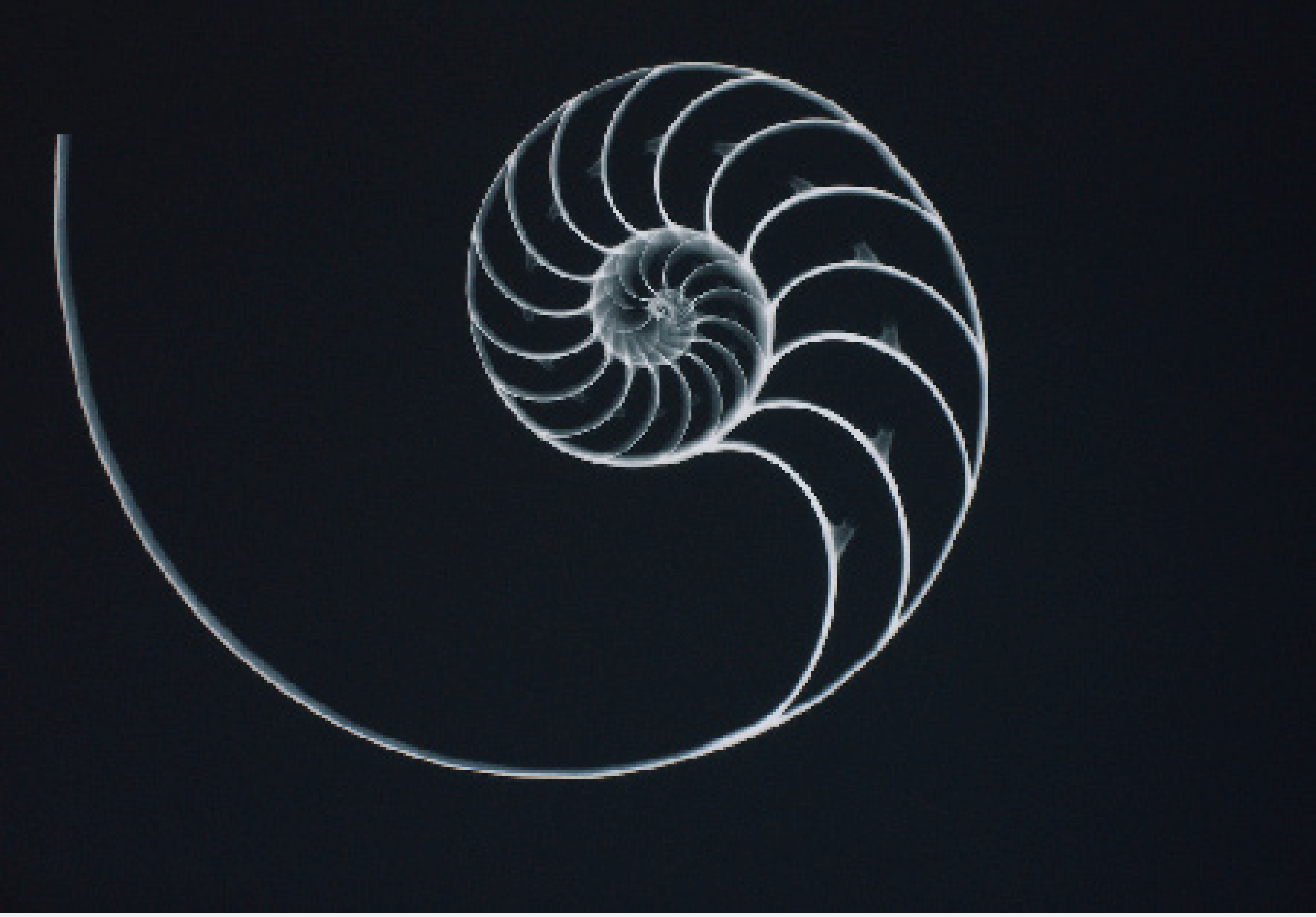

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MONOGRAPHIC SECTION: *"Philosophy of Organismal Biology: From Ontogeny to Ecology and Evolution"*

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Introducción a la sección monográfica / Introduction to the Monographic Section

What is the Philosophy of Organismal Biology?

¿Qué es la filosofía de la biología organismal?

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1. Introduction. What is the philosophy of organismal biology? What are its contours and what justifies this designation?

According to a growing number of historians and philosophers of biology, in recent years we have witnessed a "return of the organism" as a fundamental analytical, epistemic, and ontological category through which to approach and rethink some of the major theoretical discussions and empirical investigations that have articulated the field (see, for example, Huneman, 2010; Nicholson, 2014; Walsh, 2015; Fábregas-Tejeda and Vergara-Silva, 2018a; Baedke, 2019; McLoone, 2020; Gambarotto and Nahas, 2022). Within the multiple disciplines and areas of research that structure biological practice, organisms have begun to be considered as causally efficacious, active ontogenetic units whose conceptualization cannot be approached solely through the isolated study of the activities and properties of their parts (e.g., their genes or cells). Gone seems to be the idea that organisms are mere "bags of genes" or simple passive vehicles whose only evolutionary function is to ensure the replication and propagation of certain alleles over generations (for illustrative examples of this trend, see Fisher, 1936; Trivers, 1971; Wilson, 1975, p. 3; Dawkins, 1976, p. 82; for a historical reappraisal of the heuristic power and epistemic limits of this view of evolution, see Ågren, 2021). Biologists and philosophers alike have argued, in marked opposition to the genetic program metaphor (see recent critiques in Martín-Villuendas, 2021a; McKenna et al., 2022; see also Moss, 2003), that organisms are in close interdependent relationship with their environments throughout development. This has led to the conclusion that organisms must play a crucial and active role in determining their ontogenetic and evolutionary trajectories by responding to, integrating, and modifying signals from their surroundings and by marshalling a diversity of developmental resources and scaffolds (Griffiths and Stotz, 2013, pp. 134-140; Stotz, 2017; Chiu and Gilbert, 2015).

In line with these considerations, multiple authors have proposed understanding developing organisms as agents constitutively open to environmental influences, recognizing the important role that plasticity and flexibility play in their material configurations, responses, and actions (see, for example, Sultan, 2015; Newman, 2022; Gilroy and Trewavas, 2022). This has paved the way for a substantial reconceptualization of the processes that structure organismal development, as well as the potential role that the latter could play in determining the *tempo* and *direction* of evolutionary processes. Instead of conceptualizing development through an internalist view, where selected genetic variation does all the work in explaining the unfolding of phenotypes, it has been proposed to recognize development as a constructive process (Laland et al., 2015): organisms have the capacity to shape their own developmental trajectories by responding to, modifying, and altering their internal and external states (for discussion, see Fábregas-Tejeda and Vergara-Silva, 2018b). This constructive view, which rejects a linear, bijective relationship between genotype and phenotype, has called into question two of the fundamental principles on which evolutionary biology has been founded over the last decades: (i) the idea that genetic change always causes and precedes phenotypic change; and (ii) the conception that variation subtending the evolutionary process is isotropic. Studies in epigenetics and evolutionary developmental biology (particularly in its 'devo-evo' branch) have shown how the organism is able to impose biases on the generation of phenotypic variation, either by modifying the connections and regulation established between the components that structure ontogenetic processes (see Gehart and Kirschner 2007, 2010) or by integrating environmental signals through epigenetic regulatory mechanisms (for examples, see Young and Badyaev, 2010; Herrera and Bazaga, 2012; for discussion, see Brun-Usan et al., 2022). In accordance with these musings, studies framed by niche construction theory have shown that organisms are capable of exerting substantive changes in their environments, being able to bias, accordingly, their own selective pressures, as well as those of their conspecifics and those of other organisms from different species with which they are linked by sustained ecological interactions (Odling-Smee et al., 2003; Schwab et al., 2019; for discussion, see Baedke et al., 2021; Fábregas-Tejeda and Baedke, 2023). Some authors have even argued that studying organisms in their environmental and ontogenetic contexts, foregrounding their agential activities, could help bridge some of the explanatory gaps left by traditional evolutionary perspectives (Sultan et al., 2021).

This reconsideration of the potential role that organisms might play in improving our understanding of evolutionary processes has been driven by conceptual and empirical contributions from a diversity of disciplines and areas of study: evolutionary developmental biology (Evo-Devo; Arthur, 2004, chapter 7; Casanueva, 2014; Petino Zappala and Barberis, 2018; Müller, 2021; Nuño de la Rosa and Villegas, 2022), niche construction theory (Odling-Smee et al., 2003; Barahona et al., 2021; Aaby and Desmond, 2021), epigenetics (Baedke, 2018; Veigl, 2022), phenotypic plasticity research (West-Eberhard, 2003), microbiome and holobiont research (Skillings, 2016; Baedke et al., 2020a; Triviño and Suárez, 2020; Suárez and Stencel, 2020), immunology (Pradeu, 2010; Zach and Greslehner, 2023), the study of extra-genetic inheritance (Jablonka and Lamb, 2018; Bonduriansky and Day, 2020; Martín-Villuendas, 2021b), the contextual and social examination of organismal behavior (Gomez-Marin and Ghazanfar, 2019; Kohn, 2019), the debate surrounding the so-called 'Extended Evolutionary Synthesis' (Laland et al. , 2015; Baedke et al., 2020b), cancer research in systemic contexts (Soto and Sonnenschein, 2021), and developmental systems theory (Oyama, 2000; Andrade, 2017), among other converging strands of theorization.

The advances made in these fields have brought the 'organism' concept back into the focus of analysis as an explanatory category in its own right. That is, as a legitimate explanandum that cannot be subsumed entirely under a molecular-genetic perspective, and as part of the explanantia of many other biological phenomena. This epistemic undertaking demands that philosophers, historians and biologists alike face the challenging task of redefining the semantic contours that structure this concept on the basis of the results revealed by the different disciplines and areas of research alluded to above. In general, reflections traversed by this concept promise to offer new tools through which to rethink various debates that articulate biology and the philosophy of biology in the 21st century (see, among others, Ruiz-Mirazo et al., 2000; Bateson, 2005; Pepper and Herron, 2008; Nicholson, 2014; as an antecedent, see, for example, Wake, 1984).

The theoretical centrality of the 'organism' concept has even transcended the frontiers of scientific debates, permeating and involving disciplines such as philosophy. Philosophers of biology have begun to pay attention to organisms and to the study of organisms as productive *loci* of analysis in relation to other epistemic and ontological problems of the life sciences. For example, in recent years there have been many philosophical discussions on the concept of organism and the importance of organismal organization and regulative control (see, e.g., Nuño de la Rosa, 2010; Soto et al., 2016; Shields, 2017; Bich and Bechtel, 2022; for discussion on the complex historical itineraries of the concept of organism, see

Wolfe, 2010; Cheung, 2014). In the same vein, the question of what, if anything, differentiates an organism from a machine has resurfaced (e.g., Nicholson, 2013; Esposito, 2019; Bongard and Levin, 2021). On the other hand, philosophers have scrutinized the processes through which organisms sculpt, select, and adapt to various aspects of their environments, and how natural scientists approach studying these phenomena (see, for example, Trappes et al., 2021; Aaby and Ramsey, 2022). Similarly, the relationship between organism and environment, arguably one of the most important bonds investigated within biology, has become important for philosophical disquisitions. Various scholars have attempted to address the conceptual problems underlying the idea of reciprocal causation between organisms and environments (see, for example, Baedke et al., 2021; Baedke and Buklijas, 2022; Pontarotti et al., 2022; Prieto and Fábregas-Tejeda, 2022; Saborido and Heras-Escribano, 2023) and its possible theoretical extensions in domains such as human health (e.g., through the notion of 'adaptivity'; see Menatti et al, 2022) or the study of cognition as a biological phenomenon that is widely distributed and needs to be understood beyond computational-representational frameworks (see, e.g., Corris, 2020; Feiten, 2020; Sims, 2021). In fields such as behavioral ecology, intra-populational variation at the organismic (and not just genetic) level has been given increased attention, especially the ecological and phenotypic singularities of *token* organisms that have important consequences for evolutionary paths (for a philosophical analysis of these developments, see Trappes, 2022). In general, the uniqueness of *token* organisms and the temporal dimensions of ontogenetic processes are becoming fertile topics of inquiry that open unexplored questions for philosophers of biology interested in the controversy over what constitutes 'biological individuality' (see Kaiser and Trappes, 2021). Additionally, important philosophical papers have been put into circulation that contribute to organism-centered evolutionary perspectives, from explorations of the evolution of pregnancy in eutherians (Nuño de la Rosa et al., 2021) to the scholarly discussion of possible intersections between Humberto Maturana and Francisco Varela's theory of autopoiesis and the idea of 'natural drift' to account for some evolutionary dynamics (see Raimondi, 2021; Mpodozis, 2022; Etxeberria and Cortés-García, 2022). This renewed interest in whole organisms, in how they develop and interact with their environments in ecologically and evolutionarily meaningful ways, in how they are studied and conceptualized by scientists, and in how they fit into the broader theoretical edifice of biology and other neighboring sciences such as medicine and biomedicine, calls for novel and penetrating philosophical analyses that address these problems from a variety of angles.

We propose to adopt the label 'philosophy of organismal biology' to refer to this heterogeneous, though partially overlapping, set of debates currently taking place within the broad disciplinary orientation of the philosophy of biology (see, for example, recent treatments of the scope of the latter in Pradeu, 2017; Prieto, 2021; contrast this with the overview of the discipline outlined in Ruse, 1989).

Despite their close link with advances made in the various branches that make up biological research, these discussions have often been addressed in parallel and independently in the philosophical literature (for instance, discussions concerning ‘biological individuality’ in contrast to ‘organismality,’ the distinction between organisms and machines, the metaphysics of symbiosis and holobionts, arguments highlighting the role of organisms as agents in ecology and evolution, controversies about the boundaries between ‘development’ and ‘reproduction,’ the organism-environment relationship or discussions concerning levels of organization, cancer research in organismic and not exclusively molecular contexts, extended immunology, ecological epigenetics, evolutionary and variational dispositions of organisms, developmental scaffolding, phenotypic plasticity, etc.). The common denominator of all these philosophical debates (plural in their approaches and methods, from classical conceptual analysis and the philosophy of explanation, passing through the metaphysics of biology and including the inspection of concrete scientific practices) has been, we believe, in one way or another, their anchoring in the concept of ‘organism,’ as well as the existing relationship between all the phenomena of study previously referred to with salient organismal contexts that are scientifically investigated through experimental interventions, the construction of models with different degrees of idealization and abstraction, and the renewed recognition of the importance of having theories able to frame these phenomena and that seek to explain them. Thus, the philosophy of organismal biology intersects in various ways with the philosophy of Evo-Devo, the philosophy of ecology, the philosophy of immunology and multispecies studies, the philosophy of medicine and biomedicine, the philosophy of the cognitive sciences, the philosophy of developmental biology, the philosophy of cancer research, and the philosophy of evolutionary biology. This overlap notwithstanding, the philosophy of organismal biology is not interchangeably synonymous with these, nor is it completely subsumable to any of them, since under these diverse headings many other topics are investigated that are not directly related to organisms as integrated units of analysis. Moreover, none of these orientations in a unitary manner can grasp the breadth and scope of the questions raised by placing organisms at the forefront of the present-day biological arena. We consider that the appellation ‘philosophy of organismal biology’ allows us to account for the patent family resemblance that underlies the various debates already reviewed.

We should emphasize that debates with organisms as their focal points have a long pedigree in the history and philosophy of biology, especially in the first decades of the twentieth century in multiple corners of the globe where holistic and organicist positions thrived (see, as a sample of recent historiographical research on this period, Haraway, 1976; Etxeberria and Umerez, 2006; Umerez, 2013; Nicholson and Gawne, 2014, 2015; Esposito, 2016, 2017; Peterson, 2016; Rieppel, 2016; Shields, 2017; Brooks, 2019; Herring and Radick, 2019; Sprenger, 2019; chapters in Michelini and Köchy, 2019; Fábregas-Tejeda et al., 2021; Fábregas-Tejeda and Vergara-Silva, 2022; chapters in Donohue and Wolfe, 2023). It is no coincidence that the organism concept has been referred to by some authors as 'biology's phoenix,' given that its importance has waxed and waned throughout various periods of its history (see Benson, 1989). In becoming aware of this rich history of scientific and philosophical appraisals of organisms, we propose the name 'philosophy of organismal biology' rather than 'philosophy of organismic biology' because we believe that the emerging configuration of the former has more similarities with discussions that took place within organicist biology at the beginning of the last century (which primarily focused on the analysis of organisms as integrated and organized units).[1] In contrast, 'organismic biology' nowadays refers to an institutional classification scheme, mainly driven and exported from US-American universities (see Milam, 2010), which encompasses various disciplines (e.g., systematics, morphology, zoology, botany, mycology, ecology, paleobiology, and evolutionary population biology) that, although deal with organisms as raw material in their everyday practices, do not necessarily emphasize them as central epistemic or ontological units, or ask how their constitution and agential activities impact the construction of models and theories in biology. In this sense, we cannot ignore the fact that the notion of 'organismic biology' was a banner adopted by authors such as Ernst Mayr and Theodosius Dobzhansky in 1960s to demarcate and legitimize their naturalistic orientations in the face of the unstoppable influx of molecular biologists that were filling the universities of the United States, and not, as its *prima facie* name might suggest, to emphasize the importance of organisms as central units of biology or agents of evolution and development (for a reconstruction of the historical details of this conflict, see Beatty, 1990, 1994; Milam, 2010).[2]

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[1] At the same time, we choose not to christen this approach under the label 'philosophy of organicist biology,' as not all philosophers who could currently be framed as participants, in one sense or another, in the collective discussion on 'philosophy of organismal biology' necessarily uphold and revive the theoretical and epistemic-ontological principles of organicism *qua* movement in biological science of the interwar period (for a discussion of these, see Nicholson and Gawne, 2015; Baedke, 2019; Baedke and Fábregas-Tejeda, 2023). In that sense, to limit the considerations and reflections made to organicist biology would be akin to narrowing their scope and theoretical focus. Organismal biology, we judge, is broader than organicist biology.

[2] There is a general sense, which will not be alien to practicing scientists, according to which it can be said that, distinctively, biology (*sensu lato*) is the science that studies organisms from different perspectives and at different levels of organization; however, that generic assertion (which has also been popular within the philosophy of science, see, for example, Strong, 1980) does not capture the nuances that we want to recover in designating the space of an 'organismal biology.' In particular, at the juncture we live at the onset of the 21st century and regardless of what may have been the *ethos* of this science in the past, not all biology today is *de facto* organismal (think, for instance, of bioinformatics or omics approaches that only work with molecular preparations and extracts, such as metagenomics), since organismal contexts can easily be obviated or taken for granted (which is in fact often the case in experimental laboratories). Even the practice of traditional organismic biology, especially those disciplines that continue the valuable legacies of natural history, has been overtaken by these new developments (for a problematization, see

In sum, there is both a meta-philosophical justification (i.e., bringing together and juxtaposing a set of related discussions that are being waged in parallel by several communities of scholars and that could be enriched by this grouping movement and invitation to collaboration) and a historiographical-sociological one (i.e., the historical background of related scientific-philosophical discussions that took place in the interwar organicist movement and the coeval coexistence of 'organismic biology' in university contexts) to recognize 'philosophy of organismal biology' as a distinct sector within the confines of the philosophy of biology.[3]

This special issue of *ArtefaCToS. Revista de Estudios sobre la Ciencia y la Tecnología* seeks to take the first steps towards this recognition and, at the same time, to advance some seminal discussions related to organisms and their place in the life sciences. In these pages, the philosophy of organismal biology is conceived from a broad perspective that takes into account its ontogenetic, ecological and evolutionary dimensions, as well as its interfaces with other disciplines of scientific relevance such as medicine and biomedicine. With this initiative, we sought (1) to establish bridges and connections between the various debates that potentially structure the current philosophy of organismal biology, and (2) to publish contributions, mainly by authors from Ibero-America, that delve into some of its sub-themes, thus helping to further our understanding of this field of inquiry. In order to fulfill these objectives, we have collected seven contributions from some of the main active contributors to the debates that articulate what we have decided to call here 'philosophy of organismal biology.'

2. The special issue "Philosophy of Organismal Biology: From Ontogeny to Ecology and Evolution"

In his article, Guido I. Prieto offers a systematization of different perspectives available on the distinction between 'organisms' and other 'biological individuals,' identifying eight ways in which the two terms have been juxtaposed in the philosophical literature (some advocating for the elimination of one of the two *designata*, others arguing for full equivalence between them and, finally, others that draw out a specific difference that makes organisms a

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Shanker and Guttal, 2021).

[3] As far as our knowledge goes, the only published mentions of the expression 'philosophy of organismal biology' can be found in Maienschein (2009, ix) and Fulda (2017, p. 70), although in both cases this notion is used in passing and without further substantive explication. Both omissions are fully justified within the frameworks of the specific problems addressed in their respective texts. For example, in the second case, the philosopher Fermín Fulda does not devote much commentary to the idea of 'philosophy of organismal biology' because the theoretical target that concerns him in that piece is the putative link between cognition and the agency of organisms such as bacteria (and not the meta-philosophical distinction of a research area that can be circumscribed within the philosophy of biology).

special kind of biological individuals). Prieto argues that this whole range of positions faces conceptual challenges in delimiting the organism from other biological individuals, from imprecision to conceptual narrowness and the risk of eliminativism, and suggests some promising ideas on how to move forward with the debate.

From the standpoint of inductive metaphysics, Javier Suárez approaches the problem of biological individuality by focusing his analysis on one of the most controversial case studies of recent times: the conglomerates formed by individuals of multiple symbiotic species. To this end, he points out the limitations of a shared whole-dependent ontology and advocates the adoption of a part-dependent ontology. Suárez argues that the relations of biological dependence between the parts of a set can be asymmetric without this compromising the attribution of individuality of the conglomerate.

Contributing to recent discussions of organismal perspectives on the problem of phenotypic trait origination (see, for example, McLoone, 2020), the article by Cristina Villegas and Vanessa Triviño addresses the characterization of homologous traits, as well as their variational tendencies, in the organicist approach of evolutionary developmental biology. In their contribution, Villegas and Triviño argue that a deep understanding of the causal and explanatory role of these traits requires metaphysical consideration. More specifically, they propose a metaphysical characterization of the variational tendencies of traits as dispositional properties, conceptualizing homologous traits as dispositional natural kinds. They conclude by highlighting the need to reorient the approach through which existing debates in biology have traditionally been addressed. To this end, they propose to adopt an innovative meta-scientific framework that considers new interactions and interanimation between metaphysics and biology: metaphysics *from* biology (see also Triviño, 2022).

Moving on to another subject, as the article by Alfredo Marcos shows, the philosophy of organismal biology can also dialogue with "bio-philosophy" (see, for example, Köchy, 2008) and with what has recently been called "continental philosophy of biology," under which the reflections on organisms and the phenomenon of the living by authors such as Georges Canguilhem, Maurice Merleau-Ponty, Helmuth Plessner, Kurt Goldstein and Hans Jonas, among others, are emphasized (see the chapters in Bianco et al. , 2023, e.g., Gandolfi, 2023; see also Michelini et al., 2018). Marcos focuses on the concept of "organism" in the work of Hans Jonas, exploring the existing connections with other areas that structure the influential work of this German philosopher.

In his article, James Marcum makes use of reflections coming from the organicist tradition to face a problem of extraordinary practical relevance: the articulation of a biomedical framework that allows to overcome the conceptual and experimental limitations inherent to the currently accepted model (see also Soto and Sonnenschein, 2018, 2021, 2023). To this end, Marcum performs a characterization and critical analysis of the reductionist medical model that has predominated to the present day, dissecting the conceptual assumptions on which it is founded. Through two case studies, hemostasis and the carcinogenic process, Marcum exemplifies the main shortcomings of this classical framework. As an alternative, he proposes to articulate a novel biomedical framework with organicist and holistic underpinnings: an organismal systems biology. Marcum discusses how this new framework has the potential to solve the problems bequeathed by the old mechanistic-reductionist framework. This is proof that the philosophy of organismal biology constitutes an extremely fertile field through which to structure philosophical reflections that allow us to confront pressing problems of our present juncture.

The article by Jorge Luis Hernández-Ochoa, Melina Gastelum-Vargas, Agustín Fuentes and Francisco Vergara-Silva shows that organismal biology can have fruitful crossings with embodied cognitive sciences and philosophical reflections from conceptual frameworks such as enactivism. The authors propose to analyze play behavior in *Homo sapiens* from an ontogenetic-constructivist perspective, a case study so far underexplored that could simultaneously enhance our understanding of evolutionary processes and shed light on how we perceive, inquire, know, transform and interact in the world as situated organisms. They focus on exploring the importance of play in the processes of cultural, selective and ontogenetic niche construction, and in the dynamic emergence of human cognition. Play, according to their examination, could strengthen and expand a vast network of evolutionary and enactivist concepts in various disciplines that draw from them.

Finally, the work of Arantza Etxeberria Agiriano, David Cortés-García and Mikel Torres Aldave explores the evolutionary significance of collaborative relationships between organisms. To do so, they propose an innovative conceptual strategy that transgresses the traditional boundaries on which reflection on the concept of organism has pivoted: starting from the ideas outlined in the theoretical work of Pyotr Kropotkin. Combining both historical and philosophical aspects, the authors demonstrate to what extent the ideas of intraspecies relationships and altruism outlined by Kropotkin allow us to rethink crucial aspects of the evolutionary process, including the importance of inter-organismic collaborative interactions and inter-dependencies in development and in the formation of new evolutionary individuals. To exemplify these reflections, they analyze case studies that deal with symbiosis and viviparous reproduction in eutherian mammals.

Overall, the agenda of the philosophy of organismal biology points to an extremely lively field whose contours are just beginning to be delineated and re-negotiated. Therefore, the contributions to this special issue only constitute a small sample of the possible philosophical discussions and thematic connections that can be addressed within it (see the introductory section of this article). Some of the potential meta-scientific extensions that remain to be addressed could be: assessing the role given to organisms within scientific explanations and theories in the various fields that make up the contemporary research landscape in biology and biomedicine; envisioning the need for a methodological restructuring of modeling practices in order to more accurately reflect the epistemically central role of organisms and their activities in our understanding of the phenomena studied (e.g., the case of model organisms; see Ankeny and Leonelli, 2021); examining the place of organismality within current debates on individuality in the biological and biomedical sciences; discussing how organismal agency might fit into naturalist positions and debates on life-mind continuity (see Gambarotto and Nahas, 2023); rethinking some bioethical debates, for instance, on the value of life or the notion of 'death,' that arise from distinct concepts of 'organism' (see Rendón and Klier, 2017; Nowak and Stencel, 2022); and becoming aware of the possible conceptual and epistemological limitations of a scientific practice based on the organism as the central epistemic and ontological unit of biology, thus avoiding falling into a reification regime similar to that committed by population thinking. In short, multiple epistemological, ontological, heuristic, methodological, pragmatic and axiological issues related to organisms as *loci* of analysis in the life sciences remain to be thoroughly articulated and linked.

Furthermore, some of the possible debates that could structure the field in direct connection with scientific work include: the agency of organisms in development, ecology and evolution;[4] critical analyses of the variational and dispositional properties of organismal development; studies of the boundaries of organisms in the context of development, reproduction and interactions with their environments; the relationship between 'organisms' and 'holobionts' in development and evolution; the possibility of structuring an inclusive notion of inheritance that detaches from the germline condition and captures the constructive ecological activities of organisms; the conceptualization of an idea of plasticity that picks up the intuitions underlying the notion of 'constructive development,' leaving aside the traditionally adopted genocentric view based on the idea of reaction norms; and the articulation of connections with developments in 4E cognition, basal cognition studies, the free energy principle, and embodied robotics and artificial intelligence studies (for propitious contributions to build these bridges, see, among others, Castro Garcia, 2011; Colombo and Wright, 2021; Heras-Escribano *et al.*, 2022; Hernandez-Ochoa and Vergara-Silva, 2022; Harrison et al., 2022).

We would like to conclude this introduction by remarking that, although the philosophy of organismal biology constitutes a burgeoning area of academic discussion within Anglo-Saxon and Ibero-American communities (as this bilingual issue

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[4] For example, the study of organisms as active, responsive entities to their changing environments could have implications for how species conservation initiatives are framed (see Feiner et al., 2021).

of *ArtefaCToS* purports to show), it also manifests itself in additional philosophical communities that perhaps have not received the consideration they should (see, for example, Yılmaz, 2022). We hope that the contributions published here will serve as an encouragement to consolidate in the future the philosophy of organismal biology as a valid, vivid and nurturing orientation within contemporary philosophy of science on an international scale.

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‘Organism’ *Versus* ‘Biological Individual’: The Missing Demarcation

‘Organismo’ versus ‘individuo biológico’: la demarcación faltante

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Abstract

The demarcation of organisms from other biological individuals has received relatively little attention. In this paper, I extricate and systematize the different ways in which the organism–biological individual relationship has been construed: (1) coalescence of the two concepts, (2) biological individual eliminativism, (3) organism eliminativism, (4) organism as a ‘paradigmatic’ biological individual, (5) organism as a limit state towards which biological individuals tend in evolution and development, (6) organism as instantiating the whole in a part-whole hierarchy of biological individuals, (7) organism as equivalent to physiological individual, and (8) organism as a special kind of physiological individual. I show that, in most of these stances, the organism concept is too imprecise to be demarcated from other biological individuals, which fosters some form of eliminativism. I also argue that the comparisons between organisms and biological individuals are performed in two different modes: ‘horizontally’ (i.e., between individuals not related hierarchically) or ‘vertically’ (i.e., between individuals belonging to different levels within the same hierarchy). Finally, I explain the challenges that each of these comparison modes face and suggest that the ‘vertical’ mode adumbrates a potential way forward.

Keywords: biological individuality; organismality; organism; paradigmatic individual; part-whole relationship; agency; major transitions in evolution; autonomy.

Resumen

El problema de la demarcación entre el organismo y otros tipos de individuos biológicos ha recibido relativamente poca atención. En este artículo desgloso y sistematizo las diferentes formas en las que se ha interpretado la relación 'organismo'-'individuo biológico': (1) coalescencia de estos dos términos, (2) eliminativismo del individuo biológico, (3) eliminativismo del organismo, (4) organismo como individuo biológico 'paradigmático', (5) organismo como estado límite al que tienden los individuos biológicos durante la evolución y el desarrollo, (6) organismo como instanciación del todo en una jerarquía parte-todo de individuos biológicos, (7) organismo como equivalente a individuo fisiológico y (8) organismo como un tipo especial de individuo fisiológico. Muestro que, en la mayoría de estas posturas, el concepto de organismo es demasiado impreciso como para ser demarcado de otros individuos biológicos, lo cual promueve alguna forma de eliminativismo. También argumento que las comparaciones entre organismos e individuos biológicos son llevadas a cabo de dos modos: 'horizontalmente' (i.e., entre individuos no relacionados jerárquicamente) o 'verticalmente' (i.e., entre individuos pertenecientes a diferentes niveles de la misma jerarquía). Finalmente, explico los desafíos que enfrentan cada una de estas formas de comparar y sugiero que el modo de comparación 'vertical' deja entrever un posible camino a seguir.

Palabras clave: individualidad biológica; organismalidad; organismo; individuo paradigmático; relación parte-todo; agencia; grandes transiciones evolutivas.

1. Introduction

The organism concept is widely debated both in biology and its philosophy because organism-centered perspectives are currently making a comeback (Gilbert & Sarkar, 2000; Ruiz-Mirazo *et al.*, 2000; Etxeberria & Umerez, 2006; Huneman, 2010; Nicholson, 2014; Baedke, 2019). It should be kept in mind, however, that organism-centered stances have been jeopardized not only by reductionist, gene- and population-centered perspectives but also by their problems in satisfactorily articulating the very organism concept which they have sought to build (on the waxing and waning of the importance attributed to 'organisms' throughout the history of biology and the challenges that organism-centered perspectives have faced, see Benson, 1989; Baedke, 2019). So, if the organism concept is to be advanced as the centerfold conceptual and explanatory unit in the life sciences, it needs to be spelled out. And this customarily entails demarcation work.

Organisms—if nothing else—are living beings embedded in their environments. Correspondingly, attempts have been made to demarcate them from (i) non-living things and (ii) the environment. The former demarcation was central to the vitalism-mechanism debates and the rise of the organicist tradition in the early 20th century (Nicholson & Gawne, 2015). The latter has received attention especially in recent debates (e.g., on niche construction and agency) that stress the active role of the organism in modifying its environment and thus participating in the creation of the conditions for its persistence and the modulation of its evolutionary trajectory (Baedke *et al.*, 2021). In this article, I will focus on a less probed project: (iii) the *organism–biological individual demarcation*.

Now, when the organism concept collides with cognate concepts in the aforementioned dyads, the result lies somewhere between two antithetical perspectives that may be called *essentialism* and *eliminativism*. Sometimes the organism emerges as bearing essential properties that make it stand out as an irreducible special unit. Other times, in turn, continuity between the organism and its neighboring notions is emphasized to the point that their boundaries disappear and typically one of the two concepts in each coupling vanishes altogether. In the demarcation of organisms from non-living systems, essentialism takes the form of vitalism and eliminativism that of reductionist physicalism. Apropos organism-environment segregation, those who disavow the reciprocity between organism and environment and seek for definitive boundaries between the two stick to an essentialist viewpoint, whereas those who claim that there is no boundary between organism and environment vouch for an eliminativist stance. When demarcating the organism from other biological individuals, some authors are committed to finding those properties that are essential to organisms and no other kind of biological individual has, while others utterly blur the distinction between those two concepts to the detriment of one of them. Fortunately, there is enough room between those extremes. Most positions in all of these debates try to recover the organism as a unit worth singling out whilst staying mindful of the fact that sharp distinctions are often artificial and do not make justice to the complexities of the biological world—witness organicism and the nuanced stances on the organism-environment relationship. The real challenge in these cases is finding a good balance between conceptual *narrowness* and *imprecision*.

Why does the organism–biological individual distinction matter? To begin with, this demarcation is not a mere definitional quibble or a matter of terminological taste, but has far-reaching theoretical and practical consequences of which examples abound. For instance, Gawne & Boomsma (2022) suggest that the lack of consistency and conceptual clarity in the way 'organismality', 'individuality', and related terms have been used to describe the so-called 'major transitions in evolution' is to be blamed for the repeated independent "discovery" of those phenomena and the fragmentation of the literature on that topic into parallel traditions. According to Haber (2013), the debates on eusociality have been misguided by the use of the organism concept as a parameter of the extent to which colonies can be regarded as individuals—i.e., 'superorganisms'. Haber argues that the concept is too vague to be able to do any useful work in these debates and that 'individual' should be preferred instead. Finally, Baedke *et al.* (2021) assert that how organisms are marked off from other biological individuals makes a strong difference in how niche construction is conceptualized and ultimately modeled. Niche construction emanates from the reciprocal interaction between organisms and their environments wherein organisms bring about and react to environmental changes most of the times in agential ways. Baedke *et al.* (2021) discuss the interplay between microbiota and host in the transition to herbivory in ruminant holobionts (Chiu & Gilbert, 2020) and show that, depending on which entities are regarded as organisms (i.e., the host, the microbes, or the holobiont as a whole), this case of niche construction can be understood and classified in disparate ways. Thence, adjudicating organismal status dictates who the agent is, what counts as the environment, and what kind of niche-constructing activity is enacted between the two.

More generally, demarcating the organism from other biological individuals is indispensable in every instance where the organism is invoked as a special, autonomous, active, and causally efficacious unit in the biosciences. Without such delineation, we simply do not know to which entities organismal properties and processes such as agency, niche construction, and developmental plasticity refer, and it is not clear whether these properties and processes are exclusive to the organism or can be predicated on other biological individuals as well. This is, I submit, the main reason why this demarcation is warranted and badly needed. All the more so when considering that both the organism-*qua*-living-system and the organism-environment demarcation projects fall short of offering a thorough understanding of what organisms are. The former, because it equates 'organism' with 'living system', overlooking the fact that the category 'organism' conceivably does not exhaust all kinds of living systems that there are (i.e., organisms are living systems, but likely not all living systems are organisms). The latter, because it takes the organism for granted and leaves it unexplained. These projects, though legitimate and sound, can hardly provide answers to questions such as: What is the organismal status of a tissue-forming cell? How is it different from that of a free-living unicellular protist? Or, what is the organism in a siphonophoran—each cell, each zooid, or the whole colony?

In this paper, I aim at fleshing out the problem of the demarcation between 'organism' and 'biological individual'. I start by charting the manifold positions at stake in the relationship between these two concepts. This has not been attempted before and therefore constitutes an important philosophical contribution of this article. I assort the stances into two groups labeled, for the sake of simplicity, 'organism = biological individual' (section 2) and 'organism ≠ biological individual' (section 3). Then, I discuss some of the main topics that stem from the preceding systematization, such as the relationship between evolutionary individuality and the organism concept, and conclude with some suggestions for potential paths through which an organism–biological individual demarcation could be achieved (section 4). A handful of caveats are due at this point. First, I focus solely on those theoretical developments that explicitly pertain to the relationship between 'organism' and 'biological individual', abstaining from comprehensively discussing the countless notions of 'biological individual' and 'organism' that have been put forward (see instead, e.g., Cheung, 2006; 2010; Pepper & Herron, 2008; Wolfe, 2010; Toepfer, 2011; Lidgard & Nyhart, 2017; Bueno *et al.*, 2018). Second, even pursuing this more modest project, I do not claim my list to be complete or definitive. Yet, I believe that, due to its systematic character, it may straightforwardly accommodate additional examples—hopefully without the need for further categories. Third, the stances I compile are not mutually exclusive. Still, they are conceptually distinct, and thus it is worth keeping them separate. Last but not least, I favor breadth over depth for reasons of space. In largely uncharted territories such as this, a map painted with broad brushstrokes is better than having none.

2. Organism = biological individual

When equating 'organism' with 'biological individual', scholars simply use the terms interchangeably (section 2.1) or argue for the elimination of one concept or the other (sections 2.2 and 2.3). Let's briefly unravel the rationale for these positions.

2.1 Coalescence of the terms

It has been noticed several times (e.g., Prévot, 2014; Lidgard & Nyhart, 2017; Okasha, 2022) that 'organism' and 'biological individual' are generally used interchangeably in the literature, without this coalescence being properly argued for or problematized. Presumably, in most cases, it is assumed that the issue is unimportant or merely a semantical issue (e.g., in Kingma, 2020; Kaiser & Trappes, 2021). However, it seems that at least some authors use the term 'organism' as a shortcut for 'biological individual' on the assumption that the debate on individuality is primarily concerned with organisms, which are taken to be the 'paradigmatic' individuals. In this vein, Bueno *et al.* (2018, 5) state that much of the work on biological individuality "focuses on organisms, the paradigmatic biological individuals, and the difficulty of formulating criteria of organismality and, accordingly, biological individuality". Some scholars go a step further and claim that the biological individuality debate has been *de facto* motivated by the question of what organisms are or which entities count as organisms. Pepper & Herron (2008, 622), for instance, affirm that "the question of what constitutes an individual is usually identical with the question of what constitutes an individual organism". As I shall expand in section 4, this position is typical of many evolutionary accounts of individuality (e.g., Gardner & Grafen, 2009; Queller & Strassmann, 2009; Folse & Roughgarden, 2010; Clarke, 2010; 2013; 2016; Bouchard, 2013).

2.2 Biological individual eliminativism

The position according to which the whole debate on biological individuality (or, at least, a substantial part of it) is in fact about organismality, has recently been expounded by Samir Okasha. His main argument reads as follows:

> [T]he expression "biological individual", as used in the literature on biological individuality, really means "individual entity of a certain (biological) sort", where the sort is implicitly determined by the context. And the sort in question, most though not all the time, is "organism". (Okasha, 2022, 11)

The main idea here is that the problem of biological individuality and most of the vast literature around it rest on a category mistake, which consists in the utilization of the expression 'biological individual' as a sortal[1]. Okasha demonstrates that neither 'individual' nor 'biological individual' is a sortal, since questions about counting and persistence—i.e., those that, by the way, figure most prominently in the debates on biological individuality—cannot be answered unless they are specified in terms of a true sortal concept, for they invite the reply "Biological individuals of what sort?." He rightly notices that even though there is a myriad of true sortal terms in biology that refer to *bona fide* biological individuals (i.e., individuals that are biological, such as organs, cellular parts, etc.), in the debates on biological individuality many of them are *a priori* ruled out as candidates. He submits that "[t]he grounds for excluding those entities from the extension of ' biological individual' are obscure, until it is realized that the biological individuality debate is (mostly) about what an organism is" (Okasha, 2022, 11). That is, the sortal term that is customarily implied in the debates on biological individuality is 'organism'. Consequently, Okasha suggests that the term 'organism' be preferred over 'biological individual'.

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[1] Roughly, a sortal is a term—typically a count noun—for which there exist criteria for counting and determining the persistence conditions of the entity it refers to, however vague those criteria might be.

A different approach to biological individuality eliminativism is advanced by Hermida (2021). She starts by defining organisms by the property of 'being alive'. Simple organisms are those that are not composed of other organisms (e.g., bacteria), whereas composite organisms are those composed of other organisms hierarchically. Even though she does not speak of biological individuality, her notion of organism clearly covers living entities that are usually considered biological individuals and not clear-cut organisms (e.g., cells, slime molds, and symbiotic associations).

2.3 Organism eliminativism

In a previous article, Okasha (2011) advanced another interesting argument for the use of the term 'organism' as a synonym of 'biological individual' that draws on the notion of rank freedom from phylogenetic systematics. He analogizes the Linnaean view of fixed ranks with the intuition that organisms are located at a specific level (i.e., constituting a rank) in the hierarchy of nested biological individuals, and that the individuals below and above them are parts and groups of organisms, respectively. He contends that the idea of rank freedom should be applied here, since "[i]t makes no more sense to ask whether a particular biological entity (e.g., an ant colony), occupies the rank of 'organism' than it does to ask whether a particular monophyletic taxon occupies the rank of 'family'" (Okasha, 2011, 59). Adopting this view on the individuality hierarchy implies that all the individuals in the hierarchy are on par, and thus the term 'organism', according to him, "doesn't denote a rank in the ecological hierarchy; rather, *all* entities in that hierarchy, at all levels of inclusiveness, are organisms, or at least approximate that status" (Okasha, 2011, 59).[2]

Okasha's discussions on sortals (section 2.2) and rank freedom (this section) converge on the same outcome: organisms and biological individuals are indistinguishable. But, whereas in the former he concludes that 'organism' should be preferred over 'biological individual', here he remains agnostic as regards which term is to be favored. However, I label his 2011 approach 'organism eliminativism' because, even though he does not propose eliminating the term 'organism' altogether—but rather expanding it to all biological individuals—in practice he turns it inconsequential by stripping it away from any special significance, thus leaving its elimination only a step reach. That extra step is made by Matt Haber:

> Like Okasha (2011), this is a rejection of the rank of organism, but goes one step further … to recognize that *organism* is not simply not doing any work, but instead is obfuscating matters. Rather than worrying about

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[2] Throughout this article no emphasis has been added to quotes.

> whether a particular grouping, be it of cells, multicellular individuals, or cellular parts, constitutes an organism or not, the goal is instead to focus on individuals and features of those individuals. (Haber, 2013, 211-212)

The obfuscated matters Haber refers to are the discussions on the individual or organismal status of animal eusocial colonies. After reviewing the different positions at stake, Haber pinpoints that the concept of 'superorganism' is problematic because it translates the problem of individuality of colonies to the question of whether they are organisms and ultimately to what an organism is, for which there are no good answers. That is why he embraces and extends Okasha's perspective and advances the elimination of the concept of organism in favor of the biological individual.

3. Organism ≠ biological individual

In this section, I cover different positions on how the organism–biological individual distinction has been drawn. These include the claims that organisms are paradigmatic exemplars of biological individuals (section 3.1), limit cases towards which biological individuals tend in evolution and development (section 3.2), or wholes in part-whole hierarchies of biological individuals (section 3.3). They also include the idea that organisms are only a subset of biological individuals writ large, namely physiological individuals (section 3.4), or even a subset of physiological individuals (section 3.5).

3.1 Organism as a 'paradigmatic' biological individual

Organisms are often said to be 'paradigmatic' individuals. But what does it mean? I submit that there are at least three ways of interpreting it. Firstly, one can interpret this statement as implying that the debate on biological individuality is in fact about organismality—which would bring us back to Okasha's argument in section 2.2. In other words, the debate would revolve around the organismal status of biological entities that show certain properties intuitively ascribed to organisms (e.g., cohesiveness, functional integration, reproductive capacity, fitness, etc.) but that are neither clear-cut examples of ('paradigmatic') organisms nor clear-cut examples of non-organisms. Under this interpretation, the idea of 'paradigmatic individuals' would simply mean 'clear-cut examples of organisms' against which "problematic" cases are contrasted.

Secondly, it could mean that the entities traditionally called organisms usually display a high degree of individuality in light of the criteria of biological individuality that have been put forward.[3] A key idea here, which has gained widespread acceptance (Pradeu, 2016a), is that individuality is not an either/or property but comes in degrees. In contrast to the previous interpretation, biological individuality and organismality should not necessarily be understood as synonymous notions in this context. Rather, organisms are a kind of biological individual that rank higher than others, thus epitomizing biological individuality. For instance, Clarke (2010) compares six candidates of biological individuals for six criteria of individuality. Her results perfectly reflect our intuitions about the individuality of those examples. She finds that a puppy—the 'paradigmatic higher metazoan' in her assessment—matches all six criteria followed by the man-o'-war, the bacterium, the bee colony, the aspen grove, and finally the lobster claw. Similarly, Santelices (1999) places metazoans as the best representatives of individuality in terms of genetic homogeneity, genetic uniqueness, and autonomy; Pepper & Herron (2008) locate paradigmatic individuals at the extreme of a continuum of genetic homogeneity and physiological integration; and Godfrey-Smith (2009; 2013) takes humans as paradigmatic Darwinian individuals (i.e., units of selection).

Thirdly, 'paradigmatic' individuals can be interpreted as standards of individuality that suggest what properties define individuality and help characterize other individuals in terms of how closely they approach the paradigm state. Wilson (1999) takes this approach and proposes that the following individuality criteria can be extracted from, and are exemplified by, an adult higher animal: being a particular; spatial-temporal continuity and boundedness; indivisibility; nervous system; allorecognition and immune response; genetic homogeneity; development from a single cell; sexual reproduction; and identity. Whereas in the previous interpretation the paradigmatic cases were purportedly identified after evaluating many cases of biological individuals under some more or less general and objective criteria, here the paradigmatic cases are explicitly used to establish those criteria with which to perform comparisons.

3.2 Organism as a limit state towards which biological individuals tend

The idea of organisms as epitomes of individuality also comes in a diachronic version in which the paradigmatic individuality state is a limit towards which more imperfect or incomplete forms of individuality tend. For instance, Pepper & Herron (2008, 626) speculate that positive feedback loops between functional integration and natural selection lead to increasing individualization towards a paradigmatic state: "In cases where positive feedback has fully

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[3] See Lidgard & Nyhart (2017) for a fairly comprehensive list of individuality criteria.

run its course without interference or complications, we expect the result to be complete functional integration and independence, or in other words, a 'unitary' or 'paradigm' organism".

This notion of progress as the build-up of the individuality hierarchy from groups of individuals to organisms or organism-like individuals during the evolutionary trajectories of multicellular lineages is a central idea of the 'major transitions in evolution' research field (Buss, 1987; Maynard Smith & Szathmáry, 1995). For example, Folse & Roughgarden (2010, 451) explain this kind of transition event, in which organisms at new levels emerge, as "a linear sequence beginning with alignment of fitness by genetic relatedness, the export of fitness by germ-soma specialization, and, finally, functional organization by adaptation at the higher level".

However, this idea has old roots. For example, Julian Huxley (1912/2022) envisions a general pattern of 'life' progressing up towards an ideal 'perfect individual' state. Also, Haeckel (1866) contends that the individuality hierarchy has accrued in the course of evolution as higher levels of individuality have sequentially emerged by aggregation of individuals from preexisting levels, thus giving rise to increasingly complex life forms. Moreover, he maintains that, throughout development, the functional whole ('biont') climbs up the hierarchy of individuality starting from the basal 'plastid' level (i.e., the zygote) to its higher-level mature state (either 'person' or 'colony') as successive levels of lower-level individuals ('morphonts') pile up. That is, development progresses from the bottom-up in the individuality hierarchy, mirroring the evolutionary trajectory—'ontogeny recapitulates phylogeny'.

von Bertalanffy's (1952) standpoint resembles Huxley's in that individuality progresses towards an unreachable ideal state. It also shares with Haeckel's the idea that the process of increasing individuality works at both the ontogenetic and phylogenetic scales. Perfect individuality cannot be attained because it would imply complete indivisibility and thus preclude reproduction, which requires the creation of a new individual out of parts of a previous one. Nonetheless, he argues that individuality is steadily approached in the course of development and evolution through the progressive centralization of biological systems (e.g., through the emergence of circulatory and nervous systems):

> Strictly speaking, there is no biological individuality, but only a progressive individualization, both phylogenetic and ontogenetic, which is based upon the progressive centralization, certain parts gaining a leading role and thus determining the behaviour of the whole. Individuality is a limit which is approached but not reached, either in development or in evolution. (von Bertalanffy, 1952, 49; see also Jeuken, 1952)

3.3 Organism as instantiating the whole in a part-whole hierarchy of biological individuals

There is a leveled and hierarchical understanding of individuality that is related to the notion of organisms as limits and is intimately entangled with the central tenets of the major transitions literature. It envisages organisms as the individuals located at the highest level in hierarchies of nested biological individuals. A way of approaching it is by contrast to Margarida Hermida's eliminativist position (section 2.2). Recall that Hermida equates 'organism' with 'living being' (~biological individual) and discriminates between simple and composite organisms depending on whether they are composed of other organisms or not. She anticipates a counterargument as follows:

> We might … deny that there are composite organisms, by requiring that only the larger living object counts as an organism. However, this seems to be an unprincipled requirement. If we deny that cells in a multicellular organism are themselves organisms, even though they are alive, we must 1) deny that organisms are a natural kind defined by the property "being alive"; and 2) specify a kind "living non-organism" to apply to living beings that are part of composite organisms. (Hermida, 2021, para. 5)

However, Mahner & Bunge (1996, 146-149) do exactly 1) and 2). They define 'biosystems' as concrete (material) systems that have the property of being alive.[4] In their account, an 'elementary biosystem' ('simple organism' *sensu* Hermida) is "any biosystem such that none of its components is a biosystem", and a 'composite biosystem' is "any biosystem composed of (at least two elementary) biosystems". These authors maintain—*contra* Hermida—that not all biosystems are organisms. Rather, an organism is specifically "a biosystem (whether elementary or composite) which is not a proper subsystem of a biosystem". Since all elementary biosystems are cells, "cell and organism are (in metaphorical terms) the smallest and largest units of life, respectively".

In evolutionary terms, some authors conceptualize the organism as the largest adaptation-bearer unit in a compositional hierarchy (Gardner & Grafen, 2009; Queller & Strassmann, 2009; Folse & Roughgarden, 2010). To quote an example, Queller & Strassmann (2009, 3144) affirm that "the organism is the largest unit of near-unanimous design … That is, the organism has adaptations and it is not much disrupted by adaptations at lower levels".

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[4] I take 'biosystems' to be coextensive with 'biological individuals' since Mahner & Bunge (1996, 28, 177) conceptualize them as (biological) individuals belonging to different 'levels of individuality'.

3.4 Organism = physiological individual

Recent debates on biological individuality have focused primarily on ‘evolutionary individuality’, which regards individuals as units of reproduction and evolution and resorts to the theory of evolution by natural selection to ground individuality. The diverse developments grouped under this banner highlight the properties of biological entities that determine or influence their capacity to undergo natural selection (i.e., sexual reproduction, reproductive bottlenecks, germ-soma separation, etc.). More synthetic approaches either weave together several such properties (e.g., Godfrey-Smith, 2009; 2013; Griesemer, 2018), while others focus on the mechanisms that increase the capacity to undergo selection, such as policy and demarcation mechanisms (Clarke 2013; 2016) that result in low conflict and high cooperation between the parts of the individual (Queller & Strassmann, 2009) and thus in the export of fitness from the parts to the whole—i.e., the purported main unit of adaptation (Folse & Roughgarden, 2010).

Instead, ‘physiological individuality’ constructs individuals as cohesive and integrated wholes emerging from the interaction of functionally differentiated and causally interconnected parts. It is a broad and rather vague umbrella term that lumps together a wide variety of concepts and criteria of individuality that emphasize, among others, metabolism (e.g., Dupré & O’Malley, 2009), functional integration (e.g., Wilson 2000), autonomy (e.g., Arnellos 2018), immunology (e.g., Pradeu, 2012), or ecological interactions (e.g., Huneman, 2021) as the kernels of biological individuality, as well as those that construct individuals as ‘interactors’ (e.g., Hull, 1980) or ‘persisters’ (e.g., Godfrey-Smith, 2013; Smith, 2017).

Several authors have stressed the importance of distinguishing physiological from evolutionary individuality on the basis that the organism concept, as it is commonly used, is more akin to physiological than to evolutionary individuality (Pradeu, 2016b). In fact, in most of the viewpoints apropos the organism–biological individual relationship discussed in this paper, the concept of organism involved is essentially physiological. This may explain why the conflation between ‘organism’ and ‘biological individual’ seems plausible in the first place. As claimed by Griesemer (2018, 137), “[m]ost biologists use the term ‘individual’ interchangeably with ‘organism’ except when they are discussing questions of units and levels of evolution”.

This has motivated some authors to synonymize ‘organism’ and ‘physiological individual’. As Thomas Pradeu explains it,

> it is historically much more accurate to use the word “organism” to refer to a physiological individual than to an evolutionary individual … But, in

> addition to being at odds with history and common usage, it is misleading to refer to evolutionary individuals as "organisms", since it suggests, inadequately, that evolutionary individuality and physiological individuality always coincide, which is not true. (Pradeu, 2016b, 807)

According to these authors, the category 'biological individual' would then comprise physiological individuals (=organisms) plus evolutionary individuals (*sensu*, e.g., Pradeu, 2016b) or, equivalently, organisms plus Darwinian individuals (*sensu*, e.g., Godfrey-Smith, 2013). A problem of equating 'organism' with 'physiological individual' is that many entities that fall under the category 'physiological individual' are presumably not organisms but parts (e.g., cells) or groups (e.g., holobionts) of organisms. Thus, the equation implies either an undefined position with respect to all those cases or a restricted form of eliminativism.[5]

The first stance is exemplified by Subrena Smith and John Dupré. Smith tries to clarify the conditions that underlie Godfrey-Smith's (2013) criterion of 'persistence' that supposedly demarcates organisms from Darwinian individuals because she is cognizant that "to say that organisms persist is to say very little about them and does not distinguish organisms from parts of organisms or ecosystems" (Smith, 2017, 6). She finds that differentiation, integration, development, and constitutive embeddedness in an environment are the features that underpin persistence. But, by the end of her paper, she confesses that "[p]erhaps organismality is vague and the dividing line between organism and non-organism is more a function of the parameters of one's explanatory project than it is a fact about the structure of the biological world" (Smith, 2017, 12).

Dupré advocates for a view of living entities as processes intermingling in causal networks. Within this framework, it is humans who draw the (otherwise blurry) boundaries around these processes based on specific practical or theoretical aims. This implies what Dupré brands as 'promiscuous individualism'—there are many ways of dividing the biological word into individuals. Arnellos (2018, 201) impugns Dupré's position, for it "results in a rather vague definition of organisms, as well as in a blurred position in regard to the distinction between organisms and biological individuals". In fact, Dupré's commitment to process ontology and 'promiscuous individualism' compels him to aver that "what is an organism, and whether something is a part of an organism or not, are not questions that necessarily admit of definitive answers" (Dupré, 2012, 153).

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[5] Since there are other kinds of biological individuals besides the physiological, equating organisms with *physiological* individuals does not amount to equating them with *biological* individuals at large. This is why I keep the category 'organism = physiological individual' (this section) apart from 'organism = biological individual' (section 2).

The second alternative is best represented by Jack Wilson, who defines the 'functional individual' as a functional unit made up of causally integrated parts (Wilson, 1999). This kind encompasses, but is not exclusively composed of, organisms. Yet, telling organisms and the rest of functional individuals apart is not an easy task, for the properties that determine functional individuality vary in degree and can be ascribed to different hierarchically organized entities. As Wilson succinctly explains:

> The components of a single cell are well integrated, yet that cell may be a part of a multicellular organism in which all of the cells are also integrated into a collective functional individual. Can we determine that some of those entities are organisms and others are not? I have tried to demarcate organisms from non-organisms within the class of functionally integrated entities but have not found a satisfactory answer. (Wilson, 2000, S302)

Wilson (2000, S301) further argues that such demarcation is ultimately irrelevant for philosophers and biologists alike "because the most important questions about organisms do not depend on this concept".

3.5 Organism as a special kind of physiological individual

If the organism notion is closely linked to physiological individuality, then the problem of demarcating 'organism' and 'biological individual' translates to the organism–*physiological* individual demarcation. Accordingly, some authors have singled out properties that purportedly delineate organisms from other physiological individuals.

Johannes Martens illustrates this standpoint quite neatly:

> The difference [between 'organism' and 'biological individual'] lies in the fact that, in order to identify an entity as a biological individual, you have to decide whether the whole entity is sufficiently cohesive and functionally integrated to impose a common evolutionary fate on its parts, whereas to determine if an entity is an organism …, you must identify a certain *kind* of functional integration, namely the specialization of the parts (different tasks promoting the reproduction of the whole). So, as a consequence, one can perfectly identify in some cases an entity as a biological individual *while* refusing to recognize it as a true organism or superorganism. Such a denial should not be a matter of preference, but should be argued on a theoretical basis. (Martens, 2010, 386)

Thus, organisms constitute a particular kind of physiological individual but do not stand in continuity with other physiological individuals. Rather, they bear certain properties that make them stand out as special units and not merely as paradigmatic cases or as limits towards which other individuals tend. Martens conceives the biological individual as a cohesive and functionally integrated whole and the organism as a biological individual whose functional integration takes a specific form: division of reproductive labor among their parts (i.e., reproductive specialization). Interestingly, Martens also points out that this structural and functional property makes the organism "a true locus of ecological action impacting directly on the causal trajectory of evolution" (Martens, 2010, 397). Thus, the particular form of functional integration and physiological wholeness that organisms display dovetail with their unique capacity to act upon the environment and ultimately bias their own evolution.

Functional integration and wholeness take on a sophisticated form in recent publications within the theoretical framework of biological autonomy.[6] Here, a central notion is 'organizational closure', which Moreno & Mossio (2015, 1) define as "a feature of biological systems by virtue of which their constitutive components and operations depend on each other for their production and maintenance and, moreover, collectively contribute to determining the conditions under which the system itself can exist". This circular, self-recursive causal regime characterizes living beings and determines their identity since it is responsible for the production of the boundary of the system, which in turn materializes the conditions of possibility for its own production. Biological individuality, Moreno & Mossio (2015, 23) suggest, "has much to do with organizational closure, to the extent that one may conjecture that closure in fact defines biological individuality". Therefore, delineating biological individuals would amount to identifying organizationally closed systems. Additionally, some authors have considered the individuality of ecosystems (Nunes-Neto *et al.*, 2014), symbiotic interactions (Bich, 2019), eusocial insect colonies (Canciani *et al.*, 2019), and collective associations of prokaryotes (Militello *et al.*, 2021) not so much in terms of the realization of higher-level closure, but as the result of the integration of organizationally closed systems through regulatory control.

However, the demarcation between organisms and other biological individuals within the organizational framework has only been explicitly addressed in the context of multicellular associations. In a nutshell, to count as an organism, a closed system must additionally be self-regulating and self-determining—i.e., it must be autonomous. In multicellular associations, self-regulation grounds functional integration. That is, the collective of cells imposes regulatory constraints that coordinate the activities and differentiation of each cell, thus making

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[6] I thank an anonymous reviewer for helping me enrich the discussion on this topic and suggesting relevant literature.

the collective behave as a unitary whole (Arnellos *et al.*, 2014; see also Bich *et al.*, 2019). Functional integration through self-regulation—rooted in organizational closure—corresponds to the 'constitutive dimension' of biological autonomy. Nonetheless, there is also an 'interactive dimension' that refers to the interaction of the organism (*qua* agent) with its environment. Climactically, what defines an organism is a reciprocal relation between its constitutive and interactive dimensions (Arnellos & Moreno, 2016; Arnellos, 2018).

4. Discussion

Two patterns crop up from my systematization of the different stances on the organism–biological individual relation (Table 1). The first is that, in most cases, the concept of organism is imprecise. This means that sufficient (or even necessary) criteria for what counts as an organism are seldom offered. Consequently, many stances tend to some form of eliminativism in which organismal status is arbitrarily ascribed (i.e., organism eliminativism) or in which the organism is considered to be the (only) individual the broad notion of biological individuality refers to (i.e., biological individual eliminativism). The exception is to be found in the conceptualizations of the organism as a special kind of physiological individual (section 3.5). But, in those cases, the challenge is that the criteria for organismality seem to be too narrow. For instance, Arnellos (2018, 215) concludes that "the requirements for MC [multicellular] organisms are not satisfied in systems with a lower organizational complexity than that of eumetazoa".

Stance	**Explication**	**Challenge**	**Comparison**	**Examples**
Coalescence of the terms	'Organism' and 'biological individual' are used interchangeably	Imprecision, eliminativism	Horizontal?	10, 11, 13–15, 20, 21, 30, 32, 33
Biological individual eliminativism	Biological individuals are organisms	Eliminativism	Horizontal?	34
			Vertical	31
Organism eliminativism	There is no organism or it is indistinguishable from other biological individuals ('organism' should be replaced by 'biological individual')	Eliminativism	Vertical	17, 23
Organism as a 'paradigmatic' biological individual	'Organism' stands for (a) a clear-cut example of individual, (b) an individual displaying (the) high(est) degree of individuality, or (c) a benchmark for assessing individuality	Imprecision, eliminativism,	Horizontal	7, 8, 10, 12–14, 22
Organism as a limit state towards which biological individuals tend	Individuals progressively become more 'organismal' in the course of evolution…	Imprecision, eliminativism	Horizontal	1–5, 10
	…or development		Vertical	1, 3, 4
Organism as the whole in a part-whole hierarchy of biological individuals	The organism represents the highest level in hierarchies of biological individuals (or units)	Imprecision, elminativism	Vertical	6, 11, 13, 15, 29, 33
Organism = physiological individual	Physiological individuals are organisms (or organisms cannot be distinguished from other physiological individuals)	Imprecision, eliminativism	Horizontal?	18, 19, 22, 27
			Vertical	9
Organism as a special kind of physiological individual	Organisms are physiological individuals but of a special kind (not all physiological individuals are organisms)	Narrowness	Horizontal	16, 24–26, 28

[1]Haeckel (1866); [2]Huxley (1912/2022); [3]Jeuken (1952); [4]von Bertalanffy (1952); [5]Buss (1987); [6]Mahner & Bunge (1996); [7]Santelices (1999); [8]Wilson (1999); [9]Wilson (2000); [10]Pepper & Herron (2008); [11]Gardner & Grafen (2009); [12]Godfrey-Smith (2009); [13]Queller & Strassmann (2009); [14]Clarke (2010); [15]Folse & Roughgarden (2010); [16]Martens (2010); [17]Okasha (2011); [18]Dupré (2012); [19]Pradeu (2012; 2016b); [20]Bouchard (2013); [21]Clarke (2013; 2016); [22]Godfrey-Smith (2013); [23]Haber (2013); [24]Arnellos et al. (2014); [25]Arnellos & Moreno (2016); [26]Moreno & Mossio (2015); [27]Smith (2017); [28]Arnellos (2018); [29]Kaiser (2018); [30]Kingma (2020); [31]Hermida (2021); [32]Kaiser & Trappes (2021); [33]Oderberg (2021); [34]Okasha (2022)

Table 1. Summary of the different stances apropos organism–biological individual demarcation. See details in the text.

The second and most important pattern is that the comparisons between putative biological individuals and organisms have been performed either *horizontally* or *vertically* (Table 1). By 'horizontal' comparisons I mean that the individuals to be compared are typically taken in fully-developed or adult stage, treated as isolated wholes, and put on the same footing even though they usually belong to quite distant branches of the phylogenetic tree and starkly differ in their organizational complexity. These comparisons rely on the idea that individuality is a continuous rather than a discrete property, so different biological entities can be ranked according to their degree of individuality. Occasionally, these comparisons are performed in a principled way by resorting to general theoretical criteria (e.g., autonomy, being a unit of selection). Commonly, however, some notion of paradigmatic individuality is explicitly or tacitly used to establish a metric with which to assess degrees of individuality. In Clarke's (2010) assessment mentioned in section 3.1, for instance, a bacterium 'has more individuality' than a bee colony because it approximates more closely a paradigmatic state.

The problem with the notion of 'paradigmatic' individuals or organisms is that it reflects a strong anthropocentric bias in our understanding of biological individuality and consequently makes horizontally-comparing approaches vulnerable to a circularity objection. Concretely, both the idea of paradigmatic exemplars as individuals displaying a high degree of individuality or as standards for assessing individuality (section 3.1),[7] as well as the notion of organisms as limits (section 3.2), rely on criteria of individuality that have been crafted on the image of our intuitive notion of what an organism is. This image is strongly conditioned by our familiarity with those biological entities we interact more closely with and that are more alike us, particularly the so-called 'higher' metazoans and, of course, humans. Then, it should not come as a surprise that "[h]igher metazoans are in general relatively easy to individuate, most tests agree on their individuation, and give or take a few worries about parthenogenesis or regenerative abilities, there aren't real problems regarding these organisms" (Clarke, 2010, 323), given that most individuality criteria have been made up by drawing inspiration from higher metazoans. More generally, I disagree with Pepper & Herron's (2008, 625) claim that the paradigm individual "is not universal, but neither is it rare, and deviations are often minor". In point of fact, the paradigmatic state falls short for the majority of life forms on Earth (Herron *et al.*, 2013) and is problematic even among mammals if pregnancy (Kingma, 2020; Morgan, 2022) and holobiosis (Dupré & O'Malley, 2009; Gilbert *et al.*, 2012) are considered. The "least problematic" individuality and organismality case, and thus the closest we could get to a 'paradigmatic' individual, would be an entity in which compositionality does not represent a challenge—e.g., a bacterium. But even bacteria perform lateral gene transfer, show collective behavior, form biofilms, etc. (see Ereshefsky & Pedroso, 2016). The moral is that there are no clear-cut, 'easy' individuality cases. The 'paradigmatic' state is a myth.

In 'vertical' comparisons, the idea of individuality as hierarchically structured bears more weight than the idea of individuality as a continuous property and it does not depend on some external, standard paradigm for its assessment. Vertical comparisons are performed between entities belonging to different levels of the same stratified or hierarchical system. Drawing on the aforementioned example,

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[7] These two interpretations can be mapped onto the two variants of what Haber (2013, 199) calls 'the problem of the paradigm', namely, "presuming either that organisms are paradigmatic individuals, or that there is a paradigmatic organism". The underlying anthropocentric bias has been criticized several times (see, e.g., Pradeu, 2016a).

the comparison here would not be performed between the bacterium, the man-o'-war, and the bee colony, because they do not stand in a hierarchical relation to each other. Instead, the comparison would be carried out between each of these entities and their respective lower and higher compositional levels—e.g., between the bacterium and the biofilm it may happen to integrate, between the man-o'-war and each of its zooids, and between each bee and the whole bee colony. Here, no paradigm sets the standard of individuality and the central notion is *wholeness*.

Evidently, the 'vertical' mode of comparison is best represented by the idea of the organism as the largest unit (the whole) within a part-whole hierarchy (section 3.3). Things belonging to levels below the organism level are said to be parts (i.e., they belong to the organism as their *parts*) and things above the organism level are referred to as groups (i.e., they include the organism as a *member*). This means that every biological entity is either (a) an organism, (b) a part of an organism, or (c) a group of organisms.[8] The problem is that, excepting the organism, the *relata* of these part-whole relations are not necessarily biological individuals as they are usually discussed in the biological individuality debates. A bacterial flagellum and my teeth are genuine parts of organisms and (biological) 'individuals' in the sense of (biological) objects that can be individuated, but they are generally dismissed as proper 'biological individuals'—recall Samir Okasha's argument from section 2.2. Mahner & Bunge (1996; section 3.3) and Kaiser (2018) regard (a) and (b) as biological individuals, but not (c). In Hermida's (2021; section 2.2) terms, (a) and (b) are all organisms, but presumably not all (c). Okasha (2011, section 2.3) calls (a)–(c) biological individuals or organisms, indistinctly. And, according to Oderberg (2021), only (a) would be a biological individual.

It is appropriate at this point to explain why I do not include in my systematization a category that specifically relates 'organism' to 'evolutionary individual'. Evolutionary individuality stances are essentially hierarchical. Now, the ambiguity on how (b) and (c) relate to the notion of biological individual explains why 'organism' and 'biological individual' are coalesced in those evolutionary accounts in which the organism is defined as the largest unit that bears adaptations (section 3.3; see also Pepper & Herron, 2008). The organism is deemed not as *an* individual but as *the* individual—hence the idiom 'individual organism'—and normally it is not quite clear whether its lower-level units (e.g., cells) or upper-level units (e.g., populations) are also considered biological individuals

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[8] This has been called "exclusion principle" (Godfrey-Smith, 2013; Morgan, 2022) or "tripartite distinction" (Oderberg, 2021).

in their own right, despite the fact that they may count for fitness assessments and bear adaptations. Therefore, these approaches abut biological individual eliminativism.

The coalescence between 'organism' and 'biological individual' is also pervasive in Clarke's (2013; 2016) evolutionary account, but for different reasons. She understands the evolutionary individual as "a collection of living parts which has some *capacity* for responding to selection at the between-collection level, *because* of the action of individuating mechanisms [i.e., policy and demarcation mechanisms]" (Clarke, 2016, 903). She seems to assign the term 'organism' arbitrarily since her definition bestows no special place to the organism and does not allow discrimination between organisms and other individuals. Thus, her stance adjoins organism eliminativism (see also Bouchard, 2013).

Also close to organism eliminativism is Charles Goodnight's approach, although it is rather unclassifiable. He defines individuality in terms of the level at which fitness is attributed, the lowest level at which natural selection operates, and the lowest level at which evolutionary response to selection occurs. According to Goodnight (2013, 49), individuality is relative to the observer's aims in all three cases, so "there is no one level that can clearly be called 'the individual' to the exclusion of other levels". If individuality is arbitrarily assigned, then the organismal status should *a fortiori* be also arbitrary. Nevertheless, Goodnight nuances his relativism and leaves the door open for the idea that organisms may be special after all, "[b]ecause evolution below the organism level is suppressed, and as a consequence a large amount of selection is focused on the organism".

The last evolutionary individuality approach I shall mention is Godfrey-Smith's (2009; 2013). He understands evolutionary individuals as units of selection but, unlike Ellen Clarke and Charles Goodnight, he thinks that the organism concept cannot be reduced to being a unit of selection. He explains that "[o]ne way to exist, to operate in the world, is as an organism, and physiological unity is relevant to whether an entity has that status. But not all Darwinian individuals have physiological unity—some do not have much in the way of physiology at all". In fact, Darwinian individuals as he defines them "need not even be close to being organisms. Genes, chromosomes, and other fragments of organisms can all form Darwinian populations" (Godfrey-Smith, 2009, 85-86). That is why he prefers to keep evolutionary and physiological individuality apart and define the organism in physiological terms (section 3.4).

Although proposing a solution to the organism–biological individual demarcation problem is beyond the scope of this article, I shall offer in closing some hints on what I think such a solution would require. Assuming, by hypothesis, that there is a special unit at a certain level that deserves the label 'organism', a crucial question needs to be asked: Is that unit present in every *token* hierarchy of biological individuals? I think that, in general, the answer is assumed to be affirmative—"life comes in the form of organisms" (Goodwin & Dawkins, 1995, 47)[9]. If that is the case, then horizontal comparisons are uninformative regarding the organism–biological individual distinction, since differences in the degree of individuality of entities belonging to different *token* hierarchies or the extent to which putative organisms belonging to different hierarchies approximate more or less closely a certain standard of individuality or organismality are irrelevant. Organisms come in extremely diverse forms—some are more 'colony-like', some are more 'paradigm-like'. However, *organismal status is not dictated by the degree of individuality organisms show or by the extent to which organisms resemble a paradigmatic state, but by how they relate to the units above and below in the hierarchy they partake in*. Therefore, the organism–biological individual demarcation problem can be narrowed down to the question: "How do we demarcate organisms from other functionally integrated systems above and below that level of organization?" (Wilson, 2000, S305). In this sense, demarcating the organism amounts to having criteria to decide, when confronted with a living system, at which level the organism is located and thus what counts as its parts and with what entities it groups into higher levels. Or, in evolutionary (or developmental) transitions in individuality, having criteria to decide when an aggregating collective of organisms stops being a group and becomes a new organism or, conversely, when a disaggregating organism stops being an organism and gives rise to a group.

The notion of the organism as a whole in a part-whole hierarchy (section 3.3) is the only one among those I compiled that explicitly deals with the organism–biological individual demarcation problem thus formulated. However, I think the requirement of the whole being the largest unit in the hierarchy is unwarranted. I do not see a clear reason why the organism could not partake in higher-level *biological individuals*, although I am skeptical that an organism can be a part of other *organisms*, as Hermida (2021) contends.

5. Conclusions

The 'organism' and 'biological individual' concepts are central to biology, have an illustrious pedigree and have been among the most intensively discussed notions in the philosophy of biology in the last couple of decades. Moreover, they are so inextricably comingled that they could hardly be spelled out independently from one another. Still, their demarcation has not been sufficiently

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[9] Although there might be cases of biological individuals that are neither organisms nor parts or groups of organisms (e.g., spawned gametes, cells in tissue cultures, or flowers kept alive in a vase).

discussed and, as far as my knowledge goes, the relatively few discussions that explicitly engage with it start from an incomplete view of how these concepts have actually been related.

Here, I reviewed and systematized the different perspectives on this demarcation, and identified eight ways ‘organism’ and ‘biological individual’ have been coupled together in the literature. Each one of them faces conceptual challenges when it comes to demarcating the organism from other biological individuals. Most commonly, they fail in offering precise enough criteria—if any—of what makes organisms a special unit and most of them leave the door open for organism eliminativism.

I also observed that organism–biological individual comparisons have been carried out in two different ways that I labeled ‘horizontally’ and ‘vertically’. I argued that some horizontal comparisons face the problem of relying on an untenable anthropocentric notion of paradigm or limit case individual. More generally, the horizontal comparison mode does not help to demarcate the organism from other biological individuals, for ranking different putative organisms and individuals according to their degree of individuality or how closely they approach a paradigmatic or limit state does not help decide which of the compared entities is an organism and which is not. I also argued that the drawback of the vertical comparison mode is that it is not clear which hierarchically-arranged entities that purportedly are parts and groups of organisms are biological individuals, and thus the organism–biological individual distinction remains obscure.

Finally, I contented that the organism–biological individual demarcation problem requires vertical comparisons to determine at which level in the hierarchy the organism is located—irrespective of how closely it resembles some paradigmatic benchmark. Thus reformulated, I believe the problem becomes tractable, and its solution could yield insights into the notoriously elusive question of what the organism is.

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A Part-Dependent Account of Biological Individuality for Multispecies Consortia

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

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Abstract

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

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

Resumen

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

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

1. Introduction

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

The situation in the biological world does not seem very different from these cases, at least if we think of everyday examples of biological individuals as they are perceived by humans (e.g., dogs, chickens, trees). But the situation in the biological world is not always so simple. For example, take the case of the lichen. From a spatial point of view, or even considering its development, it seems intuitive that the lichen is a single individual. However, the answer changes if we pay attention to its reproduction, since each of the two individuals that compose the lichen (an alga and a fungus) have independent reproductive regimes.[1] Therefore, from a reproductive perspective, it could be said that there are two individuals instead of one.[2] The opposite, however, occurs in the case of a bee colony. Intuitively, it seems that each bee has its own biological development, while the colony does not. But only the queen can reproduce. The rest of the bees in the colony lack this capacity. Therefore, what would be an individual from a developmental perspective, would only be a part of a larger individual from the perspective of reproduction.

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

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

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

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

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

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

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

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

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

These data suggest that all these criteria are ultimately grounded on the existence of intensional properties of biological individuals which are both relevant for scientific practice, and generate extensional conflicts about what counts as an individual. For instance, it seems clear that the histocompatibility criterion is necessary for those interested in studying solid organ transplantation. However, this criterion conflicts with the genetic one, for the very existence of solid organ transplantation relies on the possibility that two individuals who do not share the same genome can ‘easily’ exchange organs with one another. In contrast, self-immune diseases reveal the opposite conflict between these two criteria, since it is sometimes the case that two organs composed of cells sharing the same genome are not histocompatible with one another.

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

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

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

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

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

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

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

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

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

Overall, the key message of this section is the following. On the one hand, the three fields I have analyzed offer specific characterizations of individuality which are linked to three specific research questions: How do organisms evolve? How does their metabolism work? How does their immune system operate? On the other hand, the observation that these three fields require of different criteria linked to the different research questions of each field, and the theories and models guiding these research questions, *does not exclude that each of the criteria used in these fields is ultimately based on metaphysical principles*—even when these are implicit. In this sense, it is basic to distinguish between what Marie Kaiser (2018) calls "biological mereology" and "metaphysical mereology." The first establishes the main biological criteria to determine whether a specific conglomerate satisfies certain biological criteria to be considered a biological individual. The second, in contrast, deals with the fundamental and often implicit metaphysical principles that are required to establish *any* characterization of individuality. In the concrete example of this paper, I follow Vanessa Triviño and Javier Suárez (2020) in their conception that metaphysics, understood as the logical framework of possibilities that are opened due to the research on the constitutive principles of reality (French & McKenzie 2015), is necessary to determine which are the ultimate assumptions underlying biological criteria, as well as the limitations that those assumptions generate in the study of scientific objects (in this case, biological individuals; see also Guay & Pradeu 2016). In the next section, I will reveal what those principles are for later analyzing how the pervasiveness of symbiosis questions their validity.

3. The whole-dependent ontology

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

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

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

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

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

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

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

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

Clarifying this further, let's examine the way how whole-dependent ontology underlies the different conceptions of individuality presented above. Let's start with physiological individuality. Their proponents state that the parts must work *together*, *coherently* and, even claim that "if the parts of a system have a significant amount of metabolic autonomy, and can keep themselves going somewhat independently, this reduces the degree to which the larger system counts as an organism [biological individual]" (Godfrey-Smith 2013, 26), and "[t]he integration of differentiated parts, which allows for phenotypic accommodation, provides the basis for the idea that organisms are in some sense whole systems." (Smith 2017, 2). These are typical demands of those holding a symmetry principle: *G* will be a physiological individual if and only if the parts *a* and *b* that compose *G* mutually depend on one another. But, as soon as *one of the parts* is relatively independent, the *whole* is no more a biological individual, as the requirement of co-dependency is not fulfilled anymore.

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

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

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

Finally, let's examine the immunological criterion. Pradeu claims that they key to delimit the borders of individuals lies on the immunological tolerance/intolerance triggered in response to certain molecular motifs. Those responses would occur in specific immunological receptors, which Pradeu (2012) contends must be in every organism. In his view, given that all cells are individuals—even when they belong to a multicellular organism—then all of them must have a certain type of immunological receptor responsible of the immunological tolerance. Take two random cells from a multicellular organism, and let's evaluate whether the conglomerate formed by both constitutes a biological individual, or it is rather a set of independent biological individuals. To do so, and following Pradeu's criterion, we must evaluate whether the cells tolerate one another. If they do so, they will be. However, if one of the cells does not tolerate the other, even when the later tolerates the former, then the set formed by the two cells will not be a biological individual, as there is not a mutual relationship of tolerance. This lack will manifest because the first cell will generate certain immunological reaction to destroy the second cell, which will in turn compromise the stability of the whole. I think this analysis is perfectly correct. But what concerns me in this paper is analyzing the ontology underlying Pradeu's conception. If the fact that one cell—of a set of two cells—does not tolerate another entails that the set formed by the two cells is *not* a biological individual, then it would seem as if the symmetry principle were necessary to define immunological dependency and, in turn, to define individuality. In other words, Pradeu's criterion would be whole-dependent.

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

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

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

4. Limits of the whole-dependent ontology

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

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

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

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

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

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

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

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

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

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

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

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

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

5. The part-dependent ontology

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

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

However, such criterion does not work. On the one hand, I already said that the relationships between the parts of many individuals are symmetric, something that defenders of whole-dependency have shown and this is a claim they are right about. It seems clear that the dependency relationships between the cells of a multicellular organism are symmetric, especially since the death of some of them usually entails the death of all the others. Taking a principle like the asymmetry principle would lead to erroneously rejecting these cases, and we would be throwing the baby with the bath water.

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

1. $\forall xy\ (Pxy \leftrightarrow \neg Pyx)$

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

2. $\exists xy\ (Pxy \ \&\ Pyx)\ \&\ \exists xy\ (Pxy \ \&\ \neg Pyx)$

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

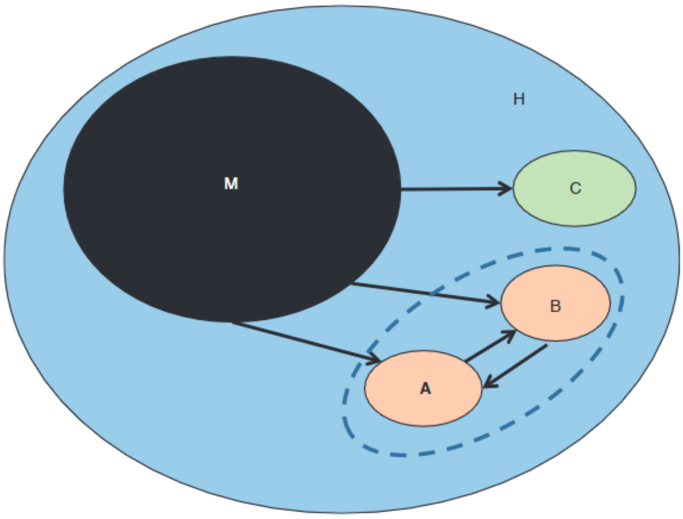

Figure 1. Graphic representation of the contrast between whole-dependent and part-dependent ontology. Let *A*, *B*, *C* and *M* be independent individuals, and let *H* be a higher-level individual. The arrows represent dependency relations (physiological, reproductive or immunological). According to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

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

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

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

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

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

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

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

All these traits have evolved in the squid-*V. fischeri* system, as they are squid adaptations to this specific symbiont. However, the reciprocal is not correct, as most of the engineering adaptations in *V. fischeri* allowing their interaction with the squid either phylogenetically pre-date their symbiotic association, or are a byproduct of traits that evolved to favor their free-living stages. According to Lloyd & Wade (2019), this generates a situation in which an engineering adaptation is produced unidirectionally, so the consortium would be what they call a *demibiont*. However, the evolution concerned is an evolution *of the consortium*. That is, the adaptations, even though they only evolved on the squid-side, would not have evolved in the same or similar way if the squid had not evolved in interaction with *V. fischeri*. Furthermore, any genetic model trying to explain the evolution of bioluminescence in *E. scolopes* must be structured by considering the biological properties of *V. fischeri*: how it can contribute to the consortium, how it can "trick" the squid, how it can penetrate the squid, etc. Otherwise, it is impossible to understand why the Hawaiian bobtail squid has evolved in the way it has done so, as we would be neglecting a part of its evolutionary history. It is therefore necessary to consider the squid-*V. fischeri* system as a biological individual, *even though the evolutionary dependency relationships between the parts are asymmetric*.

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

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

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

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

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

I want to finish the paper with a very brief reflection of the implications of part-dependent ontology to rethink the problem of biological hierarchies (already introduced in Suárez 2019). I use *hierarchies* and not hierarchy since, according to the notion of individuality I have defended, it is always necessary to specify the criterion being used (physiology, evolution, immunology, etc.) before establishing any classification. In general, it is assumed that any hierarchy of biological individuals *must be nested*. That is, the individuals in the higher-level are fully composed by all the individuals at the lower-level, which they include mereologically. For instance, we argue that a lichen is a higher-level individual because its individuality nested-ly comprises the individuality of the alga and the fungi composing it, and as such every part of the fungi and every part of the alga necessarily belongs to the lichen simultaneously. I think this assumption is a logical derivation from the fact that individuality is usually thought as whole-dependent—as I have shown above—and so the biological hierarchy must be so as well. But, is hierarchical nestedness a precondition for thinking of *any* biological hierarchy? Or, to put it differently, is it possible that the hierarchy is sometimes non-nested? By non-nested I mean that higher-level individuals do not need to include as components each of the parts of all the lower-level individuals composing them. That is, there will be at least one part which belongs to the lower-level individual and does not belong to the higher-level individual. Following Suárez (2019), I suspect that the assumption of a part-dependent ontology entails that biological hierarchies are non-nested, as the higher-level individuals generated do not always compromise the individuality of its lower-level counterparts, as at least one part of one of the lower-level components still retains its independency. Another way of seeing this claim more clearly would be this: Let *A* and *B* be two components that establish asymmetric relationships with one another from *A* to *B*. Let *x* and *y* be two parts of *B*. The unilateral dependency results from *A* establishing dependency relationships with *x*, but not with *y*. Therefore, the individuality of *A* is compromised—because, from *A*'s perspective, the individual would be the *A/B* conglomerate—but *B* does not—for at most a part of *B* is compromised, but not *B* as a whole. Note that Suárez's (2020, 2021) stability of traits criterion, according to which not every component in a biological relationship necessarily participates in the relationship, is not but another way of underscoring the same point. The biological hierarchy would thus be non-nested when analyzed from a part-dependent perspective.[12]

7. Conclusion

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

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

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Typology and Organismal Dispositions in Evo-Devo: A Metaphysical Approach

Tipología y disposiciones del organismo en la evo-devo: una aproximación metafísica

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Abstract

In this paper, we address the characterization of the variational tendencies attributed to homologous traits in evo-devo. After arguing that current theories of homology cannot properly explain why traits do, in fact, vary, we propose to characterize them as *disposional natural kinds*. In doing so, we appeal to metaphysical resources regarding the characterization of dispositions. From this metaphysical framework, it is possible to argue that only by attributing dispositions to traits (conceived of as natural kinds), is it possible to make sense of their causal and explanatory power. We argue that this particular case study constitutes an example of a kind of interaction between metaphysics and biology that we label Metaphysics *from* Biology, where the specific demands of a complex reality such as evolution require the development of metaphysical notions that seem to go beyond those present in the literature.

Keywords: metaphysics of biology; homology; natural kinds; causal power; variational tendencies.

Resumen

En este artículo, abordamos el problema de cómo se pueden entender las tendencias variacionales que se atribuyen a los rasgos homólogos en evo-devo. Tras resaltar que las teorías actuales sobre la homología no dan suficiente cuenta de por qué, de hecho, los rasgos varían, proponemos una caracterización de los mismos como *tipos naturales disposicionales*. Para ello, recurrimos a las herramientas que ofrece la metafísica respecto a la caracterización de las propiedades disposicionales. Teniendo en cuenta este marco, consideramos que sólo atribuyendo a los rasgos (entendidos como tipos naturales) la disposición de variar, puede darse cuenta del poder causal y explicativo de los mismos en evo-devo. Este caso de estudio ilustra, además, un tipo de interacción entre metafísica y biología al que denominamos "metafísica *desde* la biología", en que las exigencias específicas de una realidad tan compleja como la evolución demanda unas nociones metafísicas que van más allá de las consideradas en la literatura.

Palabras clave: metafísica de la biología; homología; tipos naturales; poder causal; tendencias variacionales.

1. Introduction

Explanations of biological phenomena vary to a high degree depending on the study subject and the methodology of the discipline from which it is approached (Potochnik, 2013). For some branches of biology, explanations must be causal (e.g., Baedke, 2012); for others, mechanistic (e.g., Brigandt, 2015); for others, statistical (e.g., Walsh et al., 2017); and for many others, topological (e.g, Huneman, 2010), etc. Within this explanatory diversity, however, there are common features that are characteristic of biology. An important one, of increasing philosophical interest, is that biological explanations usually make allusion to dispositional properties: molecular biology refers to the *foldability* of aminoacid sequences, or their capacity to acquire a functional three dimensional structure; cellular biology refers to the *divisibility* of cells; and ecology to the *defensibility* or capacity of organisms to defend themselves from predators (Hüttemann and Kaiser, 2019). The common factor of these properties is that they make reference to a *capacity* to perform a function independently of it being performed. For example, cells are characterized as divisibles, or with a capacity to divide, independently of whether their division has *in fact* taken place or will do so.

The use of dispositions points at the central role of functionality in biology. Biological mechanisms seem to be explained through their functions, providing their dispositions a privileged role when it comes to accounting for their activities (Cummins 1975; DesAutels 2015), leading some authors to claim that such mechanisms must be understood as manifestation processes of biological dispositions (Hüttemann and Kaiser, 2019). Besides explanatory convenience, the use of dispositions unravels a certain way of understanding the biological. To a large degree, the nature of biological dispositions has been approached from a metaphysical point of view (Triviño and Nuño de la Rosa, 2016; Hüttemann and Kaiser, 2019), some scholars pointing out that biology itself exemplifies a *pan-dispositional* metaphysics (Mumford and Anjum, 2011). Metaphysical questions related to the manifestation of dispositions, their individuation, or their causal efficacy, among others, have been recently discussed in the context of biological dispositions, taking general metaphysical debates on the characterization of these properties as reference.

In the case of evolutionary biology, dispositions are used to attribute causal agency to the very systems that undergo evolution. *Variability*, *adaptability*, and *heritability* are among the dispositions of biological entities that are relevant from an evolutionary perspective. The fact that a trait is heritable, for example, is explanatory of its persistence as well as of its variation along its evolutionary history. From a philosophical point of view, the most preeminent evolutionary disposition is *fitness*, or the capacity of individuals to survive and reproduce. This is so because the distinction between this capacity and survival and reproduction itself (that is, the number of offspring that an individual has in fact) sustains the explanatory potential of classical evolutionary biology, saving the Darwinian lemma of *the survival of the fittest* from circularity. Within this context, the philosophy of biology has profusely discussed how this disposition of individual organisms relates to classical population dynamics models that predict evolutionary processes in terms of changes in the genetic composition of populations. For instance, is individual fitness similar to trait fitness as it appears in such models? (Walsh et al., 2017). In particular, a large proportion of the literature has focused on whether fitness must be attributed to organisms (e.g., Pence and Ramsey, 2013), to their traits (e.g., Sober, 2020), or to the populations they compose (e.g., Millstein, 2006).

In this context, it is particularly relevant to account for how the inclusion of an organismal perspective in biology (Etxeberria and Umerez, 2006; Nicholson, 2014; this issue) affects the panorama of evolutionary dispositions. Organisms are in the paradoxical situation of being the central study subject in the life sciences and, at the same time, being erased from the most traditional biological explanations. However, new disciplines and approaches have granted them an increasing explanatory role. In the case of evolution, disciplines and research areas such as niche construction theory or evolutionary developmental biology (hereafter, evo-devo) underline that organismal properties determine the evolutionary fate of species and populations to a large extent, contrasting with the populational and gene-centric approach of classical evolutionary biology (Pigliucci and Müller, 2010).

In particular, evo-devo reveals that the developmental process of organisms is indispensable for accounting not only for how traits reproduce, but also for how the necessary variation for evolution to take place is generated in them. At first sight, it could seem convenient to attribute evo-devo dispositions to organisms themselves and their development. Nonetheless, a look at the recent literature suffices to observe that evo-devo's organismal focus is widely combined with the attribution of dispositions to the *traits* composing different lineages, rather than to the particular individuals carrying those traits. For example, *the tetrapod limb* is variable as a trait, that is, it has the disposition to generate different variants in the course of evolution. In this regard, while part of evo-devo is focused on the dispositions of developing organisms (Austin, 2017), its research agenda has been associated with typological thinking (Brigandt, 2007; Lewens, 2009; Love, 2009). In particular, part of the evo-devo agenda consists in studying homology, or the presence of the same trait in different lineages (Müller, 2003), as based on its developmental properties and their dispositions to vary, or variational tendencies (Wagner, 2014). *Variability*, *robustness*, and *modularity* are some of these variational dispositions of homologous traits under the scope of evo-devo (Austin and Nuño de la Rosa, 2021). But, what is the nature of these evolutionary dispositions predicated on homologous traits, or types, within this discipline?

In this article, we tackle the problem of understanding the causal and explanatory role of dispositions in the organismal view of evo-devo. Specifically, we consider its typological dispositions from the point of view of metaphysics of biology; that is, paying attention to the metaphysical questions that biology itself poses or implies (Triviño, 2019, 2022). Our analysis will lead us to defend that contemporary metaphysical conceptualizations are insufficient to account for the problem of typological dispositions in evo-devo. As a consequence, we propose *dispositional natural kinds* as a metaphysical notion that gives an account of homologous traits and their variational tendencies, as an example of what we will label *metaphysics from biology*.

The structure of the article is as follows. First, we present metaphysics of biology as the framework from which to approach our study subject (§1). Then, we spell out the organismal approach of evo-devo, and we show how it demands to characterize the nature of typological dispositions metaphysically (§2). The next section tackles such a metaphysical characterization and reveals the shortcomings of current positions in accounting for it (§3). Finally, we develop our proposal of characterizing traits as *dispositional natural kinds*, which we consider an example of interaction between metaphysics and biology that we label "metaphysics *from* biology" (§4). As a conclusion, we highlight the main ideas in the article and propose some unsolved questions for future inquiry (§5).

2. Metaphysics of biology

Since the last decade of the 20th century, philosophers of science in general, and of biology in particular, have reemphasized the role of metaphysics, which had been absent from the field since logical positivism (Soto, 2017). Before this renovated emphasis, philosophical approaches to biological theoretical and conceptual problems remained mainly epistemological and methodological (Sober, 1984; Millstein, 2006), sometimes making it difficult to distinguish between philosophy of biology and theoretical biology (Griffiths, 2008). In recent decades, however, many philosophers have turned to metaphysics to address all sorts of conceptual and theoretical issues in the various disciplines of the life sciences, such as evolutionary biology (e.g., Stamos, 2003; Reydon, 2008; Triviño and Cerezo, 2015), evo-devo (e.g., Bapteste and Dupré, 2013; Austin, 2017), developmental biology (e.g., Nuño de la Rosa, 2013), or molecular biology (e.g., Waters, 2017), among others. The appeal to metaphysics has become so common that some authors speak of "Metaphysics of Biology" as a new way of doing philosophy of biology (Guay and Pradeu, 2017; Triviño, 2019). Metaphysics of Biology employs metaphysical resources to address the ontological commitments and implications derived from biological theories and concepts. In doing so, it allows for clarifying such concepts and theories by shedding light on the ontological status of the entities to which they refer. An approach from the metaphysics of biology, therefore, would allow us to approach the variational dispositions of evo-devo beyond its epistemological commitments.

This recourse to metaphysics by philosophers of biology usually takes place in two forms that have been recently referred to as metaphysics *for* and metaphysics *in* biology (Triviño, 2019; 2022). In metaphysics *for* biology, philosophers draw on metaphysical theories and concepts to determine the ontological status of the entity to which a biological concept refers. In doing so, the biological concept itself is also clarified. For example, the dispositional theory of causation (Mumford and Anjum, 2011) is a metaphysical theory that has served to clarify conceptual issues regarding the biological concepts of gene and fitness (Triviño and Nuño de la Rosa, 2016). The metaphysical notion of "emergence" is also recurrent, for example, to characterize both developmental modules (Huneman, 2010; Brigandt, 2015) and the individuality of holobionts (Suárez and Triviño, 2019, 2020). Finally, and as we will see below, the notion of "natural kinds" has been used to shed light on the conceptualization of homology in evo-devo (Rieppel, 2005; Wagner, 2014).

In metaphysics *in* biology, on the other hand, philosophers of biology focus on analyzing the metaphysical commitments and implications that follow from biological theories, practices, and phenomena in order to clarify them. At the level of theories, many discussions have focused on topics related to evolutionary biology, such as the existence of final causes in evolution (Mayr, 1982), or the stochastic or deterministic nature of natural selection (Weber, 2001; Bouchard and Rosenberg, 2004). The idea is that certain theoretical conceptualizations in biology involve specific metaphysical assumptions and commitments. At the level of biological phenomena, the contemporary discussion on whether biological entities should be understood as processes or as substances stands out.

Although substance ontology has predominated in Western philosophy (Seibt, 2016), some biological advances have led to characterizing biological entities as processes (Dupré, 2012; Nicholson and Dupré, 2018). The underlying idea is that some phenomena described by contemporary biology, such as development (Nuño de la Rosa, 2018), can only be understood if this metaphysical framework is assumed. Finally, at the level of biological practice, the lack of laws in experimental evolutionary biology has been taken as a basis for arguing that the very nature of the evolutionary process can only produce contingent regularities (Brandon, 1996; Caponi, 2014). The idea here is that it is possible to access the structure of reality by paying attention to scientific practice itself since ontological reality imposes constraints on it (Waters, 2017).

All these examples highlight how prolific it is to take a metaphysical approach to theoretical and conceptual problems of biology. In particular, concepts that are proper of the metaphysical domain (e.g., causal disposition, emergence, process, contingency, or indeterminism) are either postulated to elucidate a biological problem or derived from its philosophical analysis. In the case we are concerned with in this article, that of the variational dispositions of evo-devo, the task will then be either to find a concrete metaphysical framework that accounts for these dispositions (metaphysics *for* biology, §3), or to study the metaphysical implications of the use made of them in this science (metaphysics *in* biology). Yet, as we will argue, this case illustrates that such implications can transcend existing metaphysical frameworks, which will lead us to propose a distinct type of interaction that we will call "metaphysics *from* biology" (§4).

3. Populational, typological, and organismal thinking

Before metaphysically addressing the variational dispositions of evo-devo, we need to introduce and characterize them. In this section, we present the typological and organismal approach of evo-devo, as well as the use that this discipline makes of variational dispositions or tendencies, in contrast to the classical populational perspective of population and quantitative genetics, which has traditionally served as a framework for much of the philosophical, including metaphysical, discussion of evolution.

So-called "population thinking" considers the properties of populations, particularly the differences in reproductive success among their individuals, as those that make possible and explain evolutionary change. The position of Ernst Mayr (1963) is salient in this regard. Mayr raised population thinking as the main philosophical revolution of Darwinism, as opposed to what he called "typological thinking", associated with the morphological tradition. Mayr identified the latter with an essentialism that, although historiographically erroneous (Winsor, 2006), served as a target for criticism from the trenches of Darwinian evolutionism for decades. It is worth noting the incisive association between typology and pseudoscience, as opposed to the assumed superior status of the populational and statistical approach (Amundson, 2005). Thus, typological notions inherited from the morphological tradition, such as the “unity of type” or “body plan” (Hall, 1999), were relegated to a secondary plane where they were considered causally and explanatorily irrelevant. After all, the populational approach enabled the development of a conceptual and mathematical apparatus that aimed, in principle, to account for both diversity and unity within the biological world through simple generalizable rules.

This classical framework faces harsh criticism not only from the philosophy and historiography of science but from evolutionary biology itself (Pigliucci and Müller, 2010; Huneman and Walsh, 2019). In particular, the agenda of some disciplines within evolutionary biology in a broad sense vindicate the role of typology in evolutionary explanations. This is the case of evo-devo, which inherits some notions from the morphological tradition and gives prominence to the intrinsic properties of traits to explain evolutionary change (Brigandt, 2007; Love, 2009; Wagner, 2014). Evo-devo is interested, for example, in how the tetrapod limb, understood as a trait, has evolved in different lineages, as well as what hypothesized evolutionary changes may occur in its structure. Explaining phenomena of this type not only requires addressing variation beyond the level of individual populations but demands the study of an apparently idealized reality: *the tetrapod limb*.

Tetrapods are vertebrate animals that have four limbs or that come from ancestors that possessed them. The immensity of species belonging to this group shows how a feature such as *the tetrapod limb* is instantiated in very diverse ways. Since their appearance from the lobe fins of some sarcopterygian fishes 400 million years ago, when amphibians initiated terrestrial lifestyles, limbs have diversified in a multiplicity of forms and functions among vertebrates. A human arm, the wing of a sparrow and its hind legs, the leg of a mouse, and that of an elephant are all examples of such a diversification, which, however, present clear common characteristics such as their bone structure (Fig. 1). This highlights the hierarchical nature of traits: bird wings, for example, are a trait in a typological sense since they are instantiated in the wings of sparrows, flamingos, and eagles, among others. But, they are also a *modality* (Wagner, 2014) of a generic trait: *the limb of tetrapods*. If its instantiation is so diverse, how is it possible that to speak of this trait is no more than a mere idealization? Some philosophers, in fact, defend the idealized character of types or traits in evo-devo, in the sense of being abstractions of structural and developmental properties shared by traits of some organisms due to a common evolutionary origin (e.g., Lewens, 2009; Love, 2009).

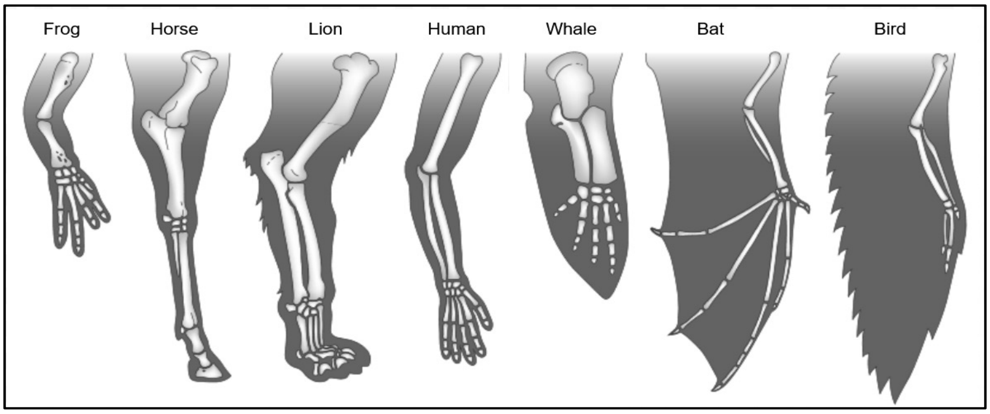

Fig. 1. The tetrapod limb instantiated in various vertebrate species. Modified from: Wagner 2007.

Yet, other authors maintain that traits correspond to a common biological basis responsible for such structural and developmental properties (e.g., Müller, 2003; Rieppel, 2005; Wagner, 2014). According to this perspective, when studying the evolution of a trait or its variational dispositions, such as its modularity or robustness, scientists are not *idealizing* that trait, but understanding it as a *changing evolutionary reality* whose organizational properties affect the course of its own evolution. This idea aligns with the work of some evo-devo biologists in uncovering the biological bases responsible for homologous traits. For example, the theoretical biologist Günter Wagner proposes that the identity of traits is associated with gene regulatory networks that control gene expression in specific cells (2007, 2014). More generally, it seems possible to associate the identity of a trait with some mechanisms responsible for its development in the ontogeny of organisms (DiFrisco et al., 2020). On the other hand, biologists such as Gerd Müller (2003) and Stuart Newman (2006) associate homologous traits with the existence of phenotypic positions of stability, or “attractors”, that remain stable based on their organizational role in organisms, independently of their instantiation in specific developmental mechanisms. With these practices in mind, the position of some philosophers of biology that traits are *natural kinds* (e.g., Rieppel, 2005), and constitute a relatively independent unit of evolution (Amundson, 2005; Brigandt, 2007), makes sense. As pointed out by biologist Brian Hall, evo-devo demands conceiving the trait, not as an idealization, but “as a structural, fundamental, phylogenetic organization that is constantly maintained and preserved because of how ontogeny is structured” (Hall, 1999, 98-99).

This return to typology comes in hand with the organismal turn that the philosophy of biology has undergone in recent decades. Classical populational thinking not only prevents us from talking about traits beyond the level of a population, but it also abstracts statistical properties of populations without considering the complexity of the organisms that compose them. While this may be beneficial for building models of population dynamics, it neglects a whole range of evolutionary phenomena that are best characterized as effects of the causal properties of organisms. The paradigmatic example is niche construction, in which the plastic development and the behavior of organisms affect the very selective pressures they experience (Laland et al., 2016; Casanueva-López and Vergara-Silva 2019). The main idea is that evolutionary and ecological processes affect each other, making it possible to speak of "reciprocal causation" between organisms and selection, which contrasts radically with the received idea that organisms are passive objects of natural selection (Levins and Lewontin, 1985; Laland et al., 2011).

In the case of evo-devo, the organicist view translates into the incorporation of the organizational properties of the development of traits when accounting for their evolutionary course and potential. In evo-devo, there is reciprocal causation between the properties of organisms and the evolutionary causes understood in a classical sense. In particular, the ontogenetic process by which organisms are formed is affected by evolutionary changes and, moreover, influences evolution itself (Müller, 2007; Caponi, 2012). This perspective challenges, on the one hand, the reductionist view of classical genecentrism, according to which the transmission of genes and the existence of mutations are sufficient to account for traits and their variation. In evo-devo, the organizational principles of development and the way in which the parts interact to give rise to the characteristics of the whole become indispensable for explaining phenotypes. On the other hand, this perspective questions populational thinking, and the adaptationism imbricated in it, by understanding the internal functionality of the organism as an agent of change in evolution (Caponi, 2012; Nuño de la Rosa, 2013).

From the perspective of evo-devo, the developmental properties of organisms determine how a trait, in the typological sense introduced above, can vary. Therefore, types in evo-devo are not mere abstractions of phenotypes, since they *refer to the process of generation of the trait*, which implies a look at the functional integration and internal coordination of organisms. A developmental system is neither a phenotype nor a set of genes, but a relatively differentiable module of the developmental process of organisms. Whereas the classical populational approach abstracts traits at the genetic or phenotypic level from the individual as a whole in order to measure them in terms of their fitness—according to their specific contribution to survival and reproduction—, the typological approach understands them as a functional part of a dynamically integrated whole. Thus, for evo-devo, *the tetrapod limb* is not a type in the sense of a series of morphologically or functionally differentiated traits. On the contrary, it is a type in the sense of being a series of processes differentiated by, on the one hand, the role they play in the structure and development of tetrapods and, on the other, the evolutionary history they share.

Developmental processes of organisms, therefore, obey organizational principles that allow us to speak of a modular structure in which traits have different levels of independence and integration with other traits of the organism (Rasskin-Gutman, 2016). This dynamical organization determines the ways in which traits can vary while preserving the functionality of the whole organism. It follows that each trait has a distinct capacity to vary, depending on the mechanisms and processes that generate it and its role in the development of the organism. These different capacities of traits to generate variation, to be robust, or to change modularly in the course of evolution are known as *variational tendencies* of traits (Wagner, 2014). Variational tendencies are dispositions that manifest themselves in evolutionary changes when certain conditions occur in the different lineages that carry the trait, such as selective pressures or mutational changes (Villegas, 2020). Although they are manifested in variation, it is important to separate them from variation itself, since they do not refer to variants, but to their generation (Wagner and Altenberg, 1996; Austin and Nuño de la Rosa, 2021). In fact, these properties are not inferred simply by measuring extant variation, but through different methodologies: paleontological reconstruction, comparative developmental studies, embryological experiments, computational models of the genotype-phenotype map, etc. All of these methodologies lead to postulating different degrees and forms of variability of a trait depending not only on its extant or ancestral instances but also on its potential, inferred from its dynamic properties and experimental behavior. For example, dynamical models of limb development in vertebrates predict the variational tendency to lose or gain a given number of digits in evolution (Lange et al., 2018). Of course, some changes modify the very structure of the trait in a way that they are better understood as evolutionary novelties. Thus, the appearance of limbs is a novelty with respect to fish fins. In this sense, traits are generated in evolutionary history and can give rise to other traits with new variational tendencies.

In order to include these realities in the explanatory framework of evolution, it is necessary to allude to the *dispositions* that developmental systems present. In the philosophy of biology, there is a large consensus that the biological notion of fitness is a disposition of individuals (Triviño and Nuño de la Rosa, 2016). The classic work of Mills and Beatty (1979) introduced the idea that, in order to save the causal and explanatory role of fitness within evolutionary biology, it should be understood as a propensity or disposition of individuals, i.e., as a dispositional property responsible for their survival and reproduction. In general terms, the dispositional nature of fitness enables us to base possible evolutionary changes on the ecological capabilities of the individuals that constitute a population. In the case of evo-devo, and pursuing the same explanatory framework, the evolutionary potential of traits has also begun to be considered in dispositional terms (variability, robustness, modularity, and evolvability), which has led some philosophers to highlight the importance of the dispositional nature of these properties (Austin, 2017; Villegas 2020; Nuño de la Rosa and Villegas, 2022; Brigandt et al., 2023).

However, as we have seen, the predication of these dispositions is primarily understood in a typological sense. It is *the limb of tetrapods* that exhibits *variability*, or *the eye of vertebrates* that exhibits *robustness* (Nuño de la Rosa and Villegas, 2022). In particular, although individual organisms instantiate the mechanisms that confer identity to a trait (DiFrisco et al., 2020), they do not manifest the variational dispositions of these mechanisms. Only through the *reproduction* of the trait is it possible to speak of the manifestation of its variability, robustness, and variational modularity, which places such a manifestation beyond individual organisms.

4. Metaphysics for dispositional tendencies: *types* and *tokens*

The peculiar situation of variational tendencies in evo-devo raises the question about the kind of relation that holds between the developmental dispositions of organisms and the evolutionary dispositions of traits as *types*. Is this relation assimilable to that which holds between the fitness of individuals and the fitness of traits in a given population (Sober, 2020)? What needs to bear evo-devo dispositions to be considered causally effective rather than mere idealizations? To answer these questions, we turn to the tools of metaphysics.

4.1 Variational tendencies are dispositions

In metaphysics, the ontological characterization of properties is usually divided into categorical and dispositional (Mumford, 1998; Bird, 2007). Dispositional properties are those that allow their bearer to manifest a certain behavior when the proper circumstances are met. A classic example in the literature is *solubility*. A sugar cube is soluble, i.e., it possesses the dispositional property of *solubility*, if, given the right circumstances (e.g., the cube is introduced into water), it would dissolve. In this case, dissolution is the *manifestation* of *solubility*. Categorical properties, on the other hand, are properties that continuously manifest themselves. They do not require specific circumstances to manifest. “Being red” or “being octagonal”, for instance, are categorical properties. The stop sign on the street manifests the property of being octagonal regardless of its surrounding circumstances.

By taking this metaphysical distinction into account, we can say that the variational tendencies of traits (Wagner, 2014) are dispositional properties: they are identified in terms of their manifestation. *Variability* is the disposition to produce *variants* of the same trait; *robustness* is the disposition to reproduce the same trait in the face of mutational perturbations; *variational modularity* is the disposition to produce localized variation in one module independently of others; and *evolvability* is the disposition to produce potentially adaptive variation. None of these properties is categorical, as they only manifest themselves in the face of specific triggers. A variable trait, such as the pigmentation patterns in butterfly wings, has the capacity to generate new instances of pattern in response to different stimuli, such as the occurrence of mutations in a specific lineage or changes in selective pressures in a particular population.

Dispositional properties have been strongly questioned by philosophical traditions like logical positivism, which considers that this kind of properties are not real because they are not directly observable: it is not possible to know that an entity has a disposition until it manifests itself. Thus, we cannot know that the sugar cube is soluble until it is introduced into water and, in fact, dissolves, just as we cannot know whether the pigmentation pattern of butterfly wings or the limb of tetrapods are variable traits unless there are specific changes in the lineages that instantiate those traits. From the positivist framework, only categorical properties are causally relevant. Thus, what explains the dissolution of the lump of sugar when introduced into water is not *solubility*, but the possession of certain categorical properties, such as a chemical composition or structure, which acts according to natural laws (Armstrong, 1969). Similarly, the pigmentation of butterfly wings would vary more than other traits not as a function of its *variability*, but of categorical properties such as its physical composition, together with the laws of nature.

This criticism of dispositions, however, generates additional metaphysical problems, such as the need to clarify the ontological status of natural laws (Mumford, 2004). For the purposes of this article, it is sufficient to note that more recent positions claim for the ontological nature of dispositions, either considering that they coexist with categorical properties (Mumford, 1998) or defending that, in fact, all properties are dispositional (Mellor, 1974; Mumford and Anjum, 2011). In the case at hand, this would imply that variational tendencies or dispositions are actual properties, despite the fact that their *manifestation* is not present as long as the specific circumstances are not given (Molnar, 2003). Dispositions such as *variability* and *modularity* would therefore be real properties of biological traits, responsible for the variation that they manifest in the course of evolution (Austin and Nuño de la Rosa, 2021).

4.2 Typology as abstraction

Although dispositions such as *variability* are identified with a *type* of manifestation, it is only through their instantiation in an entity that they can be causally effective, giving rise to concrete manifestations. Thus, when we speak of *variability* as the disposition to generate diverse variants in the course of evolution, we are referring to *variability* as a *type* of disposition. Concrete biological systems, however, exhibit *instantiated* variability (hereafter *token*). The distinction between *type* and *token* is common in the field of properties. Roughly speaking, *types* refer to the kind of property something is. Thus, we have the *type* “redness” or “circularity,” for instance. These are properties that are not instantiated in any particular entity and therefore do not occur in any particular spatiotemporal location. In this sense, *variability* is a *type* of disposition. *Tokens*, on the other hand, refer to a concrete property that is instantiated in a given entity in a specific spatiotemporal location. For example, "the red color of my neighbor's car", or "the circularity of my cousin's ball". The variability of a particular biological system is a *token* disposition.

Token-dispositions are always relative to a context, which implies the possibility for some circumstances to prevent (Johnston, 1992) or alter (Mumford and Anjum, 2011) their manifestation. For example, a biological trait may be variable in the face of mutations, yet not generate a new phenotypic variant due to environmental factors. In *type-dispositions*, this kind of context-relative aspects are not relevant. The manifestation of the disposition is not a concrete effect, but what confers identity to the disposition itself.

The causal power of dispositions, therefore, is always attributed to their *tokens*, not to *types*. In metaphysics, *token-dispositions* have the causal power to allow the entity that bears them given to behave in certain ways when particular circumstances are met (Wilson, 2002). *Type-dispositions*, on the other hand, are relevant in an epistemic sense and possess no causal power. That the manifestation of *solubility* is dissolution does not cause this lump of sugar on my table to dissolve when I put it into water. It is the *token-disposition* of *solubility* that characterizes this particular lump of sugar that causes it to, in fact, dissolve when I do so (assuming there are no contextual factors that might prevent this from happening). This distinction is clearly seen in the epistemological approach of philosophy of science. Authors such as Cartwright (1989) or Fetzer (1974) introduced the idea that causal generalizations can be understood in dispositional rather than nomological terms. In this sense, *type* dispositions seem to play an *explanatory* role in patterns of generalization. Thus, a particular glass, such as that of an office window, may be characterized as having the disposition to break even though it has never suffered a mishap, by virtue of belonging to the *class* "glass". This type of attribution is considered to be explanatory. Conversely, effective causation is considered to exist only in particular cases, spatiotemporally localized, in which, in fact, the fragility of the object has contributed to its breaking.

This standard view of causality leads us to understand variational dispositions as abstractions derived from the dispositions of particular organisms. The organicism embedded in evo-devo, and the idea that there is reciprocal causation between the properties of organisms and evolution, seem, in fact, to be in line with this perspective. In this sense, the causal efficacy of variational dispositions would be exerted on individual organisms in development. Thus, a particular mouse would instantiate in its legs the variational tendencies of the tetrapod limb. Following the polydactyly model developed by evo-devo biologists (Lange et al., 2018), we could say that a particular mouse has the disposition to develop 6 digits instead of 5 under certain conditions, e.g., environmental, as shown by some experimental results. From this individual developmental disposition, we would infer that the limb, as a trait, has a variability or tendency to develop a different number of digits under different conditions.

Something similar occurs in classical population dynamics models when the fitness of a trait is inferred as a function of the fitness of the individuals that carry it. Although there is some discussion about the kind of relationship there is between the fitness of traits and that of individuals (Walsh et al., 2017; Sober, 2020), in general, the populational properties of classical evolutionary genetics obey an abstraction scheme. Thus, they can be assimilated into the classical metaphysical framework in which only *token* arrangements are causally efficient. Even those positions that defend that evolutionary causes act at the level of populations, and not of individuals, consider that idealization is an essential part of causal attributions in evolution, assuming their explanatory value without reference to ontological commitments (e.g., Millstein, 2006).

This abstraction model, however, presents specific difficulties in the case of evo-devo. In the classical case of fitness, the organisms that instantiate this disposition are the ones that also manifest it—in their increased survival and reproductive success. In this sense, the greater reproductive success of a *trait-type,* such as the light fur of mammals in snowy landscapes, derives, necessarily, from the manifestation of the fitness of the light-furred *mammal-token* in these landscapes. In the case of variational tendencies, however, *token-organisms* do not seem to be the ones that manifest them: although organismal traits have the capacity to evolve different variants in ontogeny through phenotypic plasticity (Pigliucci, 2001), manifesting this capacity implies a type of change in the *trait-token* that differs from that which occurs when homologous traits vary in the evolutionary sense. In particular, a trait that develops as a function of an environmental variable does not usually manifest a variation in the *trait-token* itself. Rather, that trait develops differently than how another *trait-token* does under different environmental circumstances. Phenotypic plasticity is a disposition of *tokens* to manifest a different phenotype depending on the circumstances, whereas a variational tendency is the disposition to generate new *trait-tokens* with different properties. Thus, the variability of a trait such as the pigmentation pattern in butterfly wings, is a disposition that is instantiated in *reproduction* but not in the ontogeny of particular organisms. That is, although developmental properties determine the changes that are possible in evolution, these changes, in principle, do not manifest themselves in an individual *token*, but in the successive *reproduction* of *tokens*.

This brings us to the main problem of understanding variational tendencies as abstractions, namely, that it is in direct conflict with the typological perspective which, as we have seen, is an essential aspect of the evo-devo agenda. In this sense, conceiving variational dispositions as abstractions necessarily implies understanding traits-as-types also as abstractions. If variational dispositions are predicated on traits but instantiated in individual organisms, then traits are abstracted from individual organisms. However, as we have already advanced (§2), there is a strong tendency in evo-devo to understand traits as *evolutionary units* that change and whose properties are evolutionary determinants. What this shows is that there is a tension between considering the variational tendencies of evo-devo as causally effective and explanatory dispositions, on the one hand, and considering traits as natural types, on the other. Classical metaphysical approaches, therefore, seem unable to account for all the ontological commitments that follow from explanations in evo-devo.

5. Dispositional types: causal efficacy of type dispositions in evo-devo

The ontology of types in evo-devo has been addressed using resources from metaphysics (§1 and 2). Some authors have studied the ontological implications and commitments that follow from the theories developed in this discipline, which constitutes a case of metaphysics *in* biology. One of the ontological implications that have been considered about typology in evo-devo is that traits seem to refer to *individuals* (Brigandt, 2009), in the same sense that biological species are characterized as such (Hull, 1978; Reydon, 2008). These individuals would be units of evolutionary change that form a material continuity of lineages of living beings (Wagner, 2014). In the case of traits, this would translate into characterizing them as a phylogenetic lineage of the mechanisms responsible for their development in organisms. Such mechanisms would be constituent parts of the trait as an individual. In this kind of proposal, traits would no longer be types, but *tokens*, since, as individuals, they would refer to spatiotemporally localized entities. This position has the apparent advantage that it allows for understanding variational dispositions as properties of *tokens*, making their causal efficacy possible. Thus, one could understand that the trait is an individual possessing the disposition to vary and that this same individual manifests this disposition when the trait in question evolves. This seems to account for an aspect that was absent from the characterization of traits as abstractions (§3), namely the causal power of variational dispositions. At the same time, it fits within the metaphysical characterization of dispositions, in which dispositions have causal power only insofar as they are instantiated in *tokens*.

However, from our perspective, the consideration of phylogenetic lineages of traits as individuals does not completely solve the problem of typology in evo-devo. On the one hand, in this position the traits of individuals come to be understood as parts of a trait instantiated at the historical level, contradicting the intuitive idea that such traits are *tokens* in their own right. Importantly, this characterization also underestimates the relevance of organisms in evo-devo by assuming that they are *parts* of the evolutionarily relevant individual (i.e., the lineage), rather than authentic agents of evolution. On the other hand, the attribution of dispositions to a phylogenetic lineage is problematic since a lineage refers to the *outcome* of an evolutionary process. Phylogenetic lineages are the object of study of systematic biology, which is responsible for reconstructing the evolutionary history of species (Reydon, 2008). Lineages, therefore, are static entities for which it makes no sense to predicate dispositions. Any change or any causal power that the disposition (e.g., *variability*) can attribute to the lineage, has already taken place. Lineages refer, precisely, to the result of that manifestation. This can also be seen in "lineage explanations" (Calcott, 2013), which are common in evo-devo, where lineages of developmental mechanisms that vary gradually to give rise to phenotypic changes are postulated. For example, to explain the appearance of feathers in birds, some evo-devo models propose gradual modifications in the follicle, which is part of the developmental mechanism that produces both the feathers and the filaments that preceded them in evolution. If this lineage of mechanisms were understood as a single individual, it would not make sense to attribute variability to it, since it would simply be an individual that has *de facto* varied, without belonging to a class of individuals that vary. Understanding traits as individuals, therefore, would lead us to consider them as static entities whose properties lack causal power. Thus, again, what we have in phylogenetic lineages is a trait with variations composed of a historical succession of organisms, but we do not have the disposition of the trait to vary. This contrasts with the evo-devo idea that variational trends are not reducible to extant variation of a trait nor to its phylogenetic history of change. Instead, they are understood as the *potential* for dynamic developmental properties of the trait. In this sense, as dispositions, it is not their historicity that confers their identity, but their *potential manifestation*.

Given this tension between the static character of phylogenetic lineages understood as individuals and the dynamism implied by dispositions, in this article we want to explore a different solution that aligns with other positions in the evo-devo literature where traits are considered *natural kinds* (Wilson et al., 2007; Assis and Brigandt, 2009). These evo-devo natural kinds, or types, evolve and vary, in contrast to the tendency in metaphysics to define "type" and "typology" "in such a way that [they] cannot evolve" (Brigandt, 2007, 713). Considering traits as natural kinds avoids identifying them with the traits instantiated in the organisms of a taxon and in phylogenetic lineages understood as individuals. However, this characterization raises the problem of how we can account for the changeable and evolutionary aspects of traits. In the literature, these positions have resorted either to the idea of *homeostatic property clusters* (Boyd, 1991) or to that of *historical kinds* (Wagner, 2014) to eliminate the rigidity of the metaphysical notion of type, understanding it not as something permanent and immutable, but as something that can change.

This position, although correct in recognizing traits as natural kinds, seems to fail in explaining how these kinds change. Downgrading the metaphysical rigidity of types does not solve the problem of their variability and evolution, insofar as the type is allowed to change without an explanation of how or why, in fact, it changes. Our proposal is to characterize traits as natural kinds in such a way that is explanatory of change. To this end, we propose that evo-devo homologous traits be understood as *dispositional natural kinds*.

In our view, the typological character of traits is only compatible with their changing and evolvable nature if we can attribute to them a causal power responsible for their own change. In this sense, for a trait to have causal and explanatory power regarding its different variations, as it seems to follow from evo-devo, it is necessary that it possesses dispositions. Thus, biological traits would be natural kinds possessing variational dispositions, such as *variability*, *modularity,* or *robustness*. In this way, we can explain that it is the trait as a type the one that changes, rather than the token traits of the organisms. That is, it is the type itself that has the capacity to change and, in fact, the one that manifests changes in the course of evolution.

Yet, as we have seen, individual organisms are the ones that instantiate the traits. For example, a swallow instantiates the type of the tetrapod limb both in its legs and in its wings. However, as we noted (§2), it does so by instantiating a specific *modality* of that type (Wagner, 2014; DiFrisco et al., 2020). In this particular case, swallow wings and legs instantiate distinct limb modalities: evolutionarily originating independently, they share structural features with each other, but diverge in the way they can give rise to specific variations of the type-trait. Thus, although both legs and wings are variations of the same trait, they cannot, for example, give rise to each other. This occurs because the instantiation of the trait is done following the developmental process that (re-)produces the specific modality from which it derives. These developmental properties of the specific organisms *determine* the possible changes of the modalities of the traits but do not themselves instantiate the variational dispositions of the *trait-type*.

How then do variational dispositions *manifest themselves*? Every disposition needs specific conditions that allow them to manifest. In the case of variational dispositions, it is the *reproductive connections* between the organisms of a species that make it possible for them to manifest. These reproductive connections allow variational dispositions to be activated by changes in the conditions of the generation of the trait, whether mutational, environmental, or derived from recombination in sexual reproduction. Without reproductive connections between the *organisms-token*, the trait cannot vary in an evolutionary sense and, therefore, the variational disposition cannot manifest itself. These connections are understood as causal processes, and not as concrete entities. Thus, although individual organisms may instantiate traits through the mechanisms that confer their identity (DiFrisco et al., 2020), as particular entities they cannot manifest their variational dispositions. In this case, it can be said that the manifestation of trait variation is *observed* by studying and attending to the phylogenetic lineages themselves. However, these lineages do not instantiate the trait nor manifest the variation; it is the trait itself, understood as a natural kind, that varies because it possesses the disposition to do so.

Considering natural kinds to be dispositional seems to have the potential to address some of the shortcomings of the metaphysical positions developed for evo-devo. From a metaphysical standpoint, however, characterizing these kinds may be problematic because of the nature of natural kinds and of dispositions. However, we believe that the field of evo-devo demands a reconceptualization of kinds that can account not only for their changing nature but also for their own causal role in such a change, which involves considering their dispositions.

This is why we consider that addressing the problem of trait homology in evo-devo with the tools of metaphysics requires a type of interaction between metaphysics and biology that had not yet been contemplated in the literature on metaphysics of biology. Instead of speaking of "metaphysics *in* biology" or "metaphysics *for* biology", where metaphysical tools present in the literature are used, our proposal illustrates a case of "metaphysics *from* biology", where metaphysical tools must be adjusted considerably to account for the ontological commitments of biology. The very complexity of the evolutionary process and of evolving entities demands metaphysical notions that transcend the conceptualizations considered in standard metaphysics. In the particular case of evo-devo, the constant recourse to natural kinds, dispositional properties, and organismal agency, makes these metaphysical and ontological demands even stronger.

6. Conclusions

In this paper, we have addressed the problem of how to understand variational tendencies of traits in evo-devo from a metaphysical perspective. After pointing out the limitations posed by some proposals given in the literature, we propose to consider homologous traits as *dispositional natural kinds*. As we have argued, only by attributing dispositions to traits understood as natural kinds can their ability to vary be accounted for.

In our view, the particular case of homology in evo-devo also illustrates a particular interaction between metaphysics and biology that we have labeled metaphysics *from* biology. The complexity of the biological reality to be accounted for demands metaphysical tools that are not present in the current literature, which is why we consider that the interactions of metaphysics *in* and metaphysics *for* biology cannot account for this case.

This characterization is tentative and requires further development in future works, particularly regarding the type of concrete commitments it makes on natural kinds. However, we consider this proposal as an exploratory path that would overcome some current limitations of understanding traits as abstractions, as individuals, or as natural kinds without causal or explanatory power. Moreover, our proposal reconciles the seemingly contradictory ontologies of evo-devo by combining the causal and explanatory power of types with that of the individual organisms that instantiate them. In this sense, the organicism imbricated in the introduction of development into evolution, and the consequent reciprocal causation between organisms and evolutionary forces, such as natural selection, would represent the necessary condition for the potential change of types to manifest itself. This position opens new exploratory avenues regarding the relationship between *token* individuals and *dispositional natural kinds* in evo-devo.

Our work also makes it possible to ask whether the challenges that organicism poses to classical population thinking in evolution relates to typology and to the role of dispositions. While we consider that in evo-devo these issues do go together, it remains an open question whether other organicist approaches, would also benefit from an ontology of dispositional natural kinds.

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The Concept of Organism in the Philosophy of Hans Jonas

El concepto de organismo en la filosofía de Hans Jonas

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Abstract

The current philosophy of biology, having overcome reductionist temptations, has focused its attention on the concept of organism. Hans Jonas' thought will be useful in this new context, since it deals with this concept in a profound way. From this conviction, the present text intends to explore precisely the notion of organism in Jonas' work. To do this, I will begin by exposing the motivations that lead the author towards the concept of organism (section 1). He turns to it as a way out of the dualistic difficulties that, in his opinion, threatened to suffocate philosophical research. In a second step, I will specifically present the idea of organism that Jonas proposes with its most conspicuous features, among them, a close link with the notion of metabolism (section 2). After that, I will look for the connections of the concept of organism with other areas of Jonas' thought: ontology, anthropology, ethics and theology (section 3). I will then outline some criticisms on Jonas's ideas, especially regarding the application of the term "freedom" to organisms, as well as the absence of references to biological reproduction (section 4), and end with a concluding summary (section 5).

Keywords: organism; dualism; materialism; existentialism; metabolism; freedom.

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[1] I am very grateful for the valuable comments I received from Alejandro Fábregas and Mariano Martín, as well as from two anonymous reviewers.

Resumen

La actual filosofía de la biología, superada ya la tentación reduccionista, ha centrado su atención en el concepto de organismo. El pensamiento de Hans Jonas resultará de utilidad en este nuevo contexto, pues aborda de modo profundo dicho concepto. Desde esta convicción, el presente texto se propone explorar precisamente la noción de organismo en el pensamiento de Jonas. Para ello, comenzaré por exponer las motivaciones que conducen al autor hacia el concepto de organismo (sección 1). Acude a este como vía de salida de las aporías dualistas que, a su parecer, amenazaban con asfixiar la investigación filosófica. En un segundo paso, presentaré ya en concreto la idea de organismo que propone Jonas, con sus rasgos más conspicuos, entre los que consta un estrecho vínculo con la noción de metabolismo (sección 2). Tras ello, buscaré las conexiones del concepto de organismo con otras áreas del pensamiento de Jonas: ontología, antropología, ética y teología (sección 3). Esbozaré, a continuación, algunas críticas a las ideas de Jonas, en especial en lo que hace a la aplicación a los organismos del término “libertad”, así como a la ausencia de referencias a la reproducción biológica (sección 4), para finalizar con un resumen conclusivo (sección 5).

Palabras clave: organismo; dualismo; materialismo; existencialismo; metabolismo; libertad.

1. Introduction: dualism (and its sequels) as a problem, the organism as a solution

In his youth, still in Germany, Hans Jonas became interested in ancient thought. He worked on the ideas of St. Augustine and the Gnostics (1958). As a disciple of Heidegger, he relied on existential analytics as an interpretative method for the study of the Gnostics. It was his detailed history of Gnosticism that first made him known as a philosopher. However, because of his Jewish background and Zionist convictions, his academic career in his native country was to prove brief. Needless to say, his relationship with his teacher was severely damaged because of the political positions adopted by the latter. Jonas soon went into exile in Palestine, to return to Europe alone as a member of the British army and fight in World War II. With the end of the war, and after finding about the death of his mother in Auschwitz, he left Germany for good, worked for five years in Canada and finally settled in New York. It was during his Canadian period that he became more directly involved with the concept of the organism. He then produced what he himself called “an ‘existential’ interpretation of biological facts” (1966, ix). Already in the USA, his philosophical interests shifted towards questions of ethics and philosophy of technology that would make him world-renowned with the publication of his book—already a classic—*The Imperative of Responsibility* (1984). Here we are mainly interested in his philosophy of the organism, but we could not grasp its meaning without showing the path that Jonas followed to reach it. That is to say, we must take into account the influence that Jonas received from Heidegger, as well as the knowledge he attained about ancient gnosis.

Hans Jonas arrives at the reflection on the organism through a peculiar intellectual route.[2] We could reconstruct it more or less in the following terms. For Jonas: "When man first began to interpret the nature of things [...] life was to him everywhere, and being the same as being alive" (1966, 7). Pan-vitalism dominated the conception of the world at the dawn of humanity. Thus, what stood before human beings as an enigma was death and not life. When experiencing the strange stillness of the corpse, the question arose as to the reality of death. How had such a thing entered the world, a world flooded with life? This gave rise to the first forms of dualistic thought, which put on one side the inert matter of the corpse and on the other the living soul, which may even pre-exist and subsist. Life is the rule, the familiar, the given; death is the exception, the strange, that which requires explanation. Ancient dualism has taken root in various forms of myth and philosophical thought, from the *Epic of Gilgamesh*, through the Egyptian *Book of the Dead*, to Orphism, Platonic philosophy and Gnostic thought. In any case, it is a pan-vitalist dualism whose objective is to deal theoretically and practically with the enigma of death.

Perhaps the most radical version of ancient dualism is found by Jonas among the Gnostics: "At the peak of the dualistic development, in Gnosticism, the soma-sema simile, in its origin purely human, had come to extend to the physical universe. The whole world is tomb (prison house, place of exile, etc.) to the soul or spirit" (1966, 14). A human being falls only circumstantially on a body, but his or her most authentic reality is spiritual. Moreover, the world as a whole becomes inert matter, dead and disenchanted, through which the spirit hardly passes. If ancient dualism sprouts in a pan-vitalist landscape, with the aim of accommodating death in it, the reality it leaves us with as an inheritance consists, on the one hand, of a devitalized world and, on the other, of a disembodied spiritual sphere. In other words, the basis for a new dualism—a modern one, in this case—and for a new post-dualism. We can be more concrete at the cost of simplifying things: by dividing reality in two, the foundations are laid for modern dualism, that is, Cartesian, and also for the post-dualist residues that derive from it, those of materialist affiliation and those of idealist affiliation, both with identical nihilistic consequences.

Perhaps now one of Jonas's cryptic statements about Heidegger can be understood. For the former, his teacher's thinking itself "also represented a sort of present-day gnostic phenomenon" (Jonas, 2008, 66). If Heidegger initially gave

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[2] It is worth mentioning here the connections between the thought of Jonas and that of Ludwig von Bertalanffy. According to Roberto Franzini Tibaldeo, the epistolary exchanges between Bertalanffy and Jonas were fundamental for the latter to draw parallels between Gnosticism and interwar philosophy (Tibaldeo, 2012).

him the methodological keys to read the Gnostics, it is now the Gnostics who provide Jonas with the best perspective to understand the existentialist Heidegger. It is not that Heidegger is in some sense a contemporary Gnostic, but that his thought is one of the sequels of a dualistic approach similar to that of the Gnostics. Similar, yes, but not identical.

The main difference can be seen in the background landscape. Ancient dualism is outlined against the background of an animate universe, while modern dualism does so on an inert basis. The former seeks to explain death, the latter takes it for granted, it emerges already bathed in inert matter; its problem consists, therefore, in accounting for a pair of tiny and extravagant, capricious, almost maddening, cosmic details: life and consciousness. Cartesian dualism dawns already looking towards the new physics of Galileo, whose method empties matter of life. Descartes transformed what, in principle, was only innocuous methodology into a whole ontology of the *res extensa*, that is, of dead things. Nonetheless, what the corpse was for ancestral pan-vitalism, was consciousness for modern pan-mechanism. An undeniable nuisance that somehow has to be accommodated. And Descartes appealed to the other substance, the *res cogitans*.

We already have inert matter on one side and consciousness on the other. The human being is properly res cogitans, but his or her material body can hardly be ignored, which raises the never well solved problem of the connection between the two substances. What about the rest of the living? As is well known, they pass forthwith to the side of matter. They are machines. The mechanistic theory of the organism will try to explain life from the conceptual categories of the non-living. Not surprisingly, this whole dualistic enmeshment turned out to be unstable. It immediately suffered an inclination towards the materialist side, from which it was proposed to dispense even with *res cogitans* as substance, in order to undertake repeated attempts to explain it in terms of matter and motion. Had any of these attempts been successful, the transition from the archaic monism of life to the modern monism of death would have been completed through a long dualistic detour. But what is certain is that the contrary tendencies, towards the sphere of consciousness, with the consequent forgetting of the body, and even the negation of matter, were also present from very early on. In this second line Jonas situates the existentialist anthropology of the first Heidegger, who denies the human being all remnants of nature and conceives him as freedom thrown into a strange world in which he must constantly invent himself. “In *Being and Time*,” writes Jonas, “the body was omitted and nature was relegated as the merely existent” (2001, 144; quoted in Gutierro, 2021, 85).

As Jonas summarizes, in the current “postdualistic situation there are, on principle, not one but two possibilities of monism, represented by modern materialism and modern idealism respectively. [...] We would then have a phenomenology of consciousness and a physics of extension” (1966, 16-17). We already know that neither one nor the other, separately, are fully satisfactory. Nor would a juxtaposition of the two, a division of the work on two separate fields of reality, be valid as a compromise. Within Jonas' line of argument, this is the exact point at which the notion of organism is inserted. His familiarity with Heideggerian existentialism as well as with Gnostic dualism leads him to recognize, with all the historical nuances one may wish, that the former is to be interpreted as a residue of modern dualism, together with the other complementary residue, the materialist one. Both residual approaches fail in the face of the reality of the organism (for reasons we shall see immediately). And, of course, so does any form of dualism. For Jonas, the organism functions up to this point as a touchstone. The organism will also function, from here on, as way out of the aporia of dualism and its aftermath.

2. Profiles of the organism concept in Hans Jonas

The materialistic approach comes up against the interiority of the organism, which is insurmountable to us through our own self-experience.[3] Every living being possesses a certain intimacy that distinguishes it from its environment, and, especially, every animal is capable of feeling, willing and moving with what Jonas has come to call *freedom*. From the categories of the extensive, which, let us remember, neither feels nor suffers, the explanation of the living is an unapproachable enterprise. When we think of the organism in a mechanistic way, we inexorably leave out the very condition of organism, its interiority, its capacity to feel, to desire, to behave. And at this point, I would like to add, it is customary to invoke epiphenomena, emergence or simple elimination, meager nominal consolations for our explanatory indigence.

Nevertheless, from the side of the philosophy of consciousness, we also do not have frank access to the organism, which is still a bodily entity and, therefore, a spatio-temporal one, subject, of course, to the laws that govern matter. The body must be understood, then, as one more of the ideas that are given to consciousness, and, with this, it is completely distorted. If the materialistic explanation of the living body leaves out the living, the idealistic explanation disregards the genuinely bodily.

Nor is a return to dualism possible by means of some agreement of peaceful coexistence along the following lines: the natural sciences, with their methodology,

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[3] I am aware that the use of the first-person phenomenological perspective is open to criticism from a naturalistic vantage point. However, this use is perfectly compatible with a moderate or pluralistic naturalism, which admits cooperation between different methods. And it is this type of collaboration that Jonas proposes and practices. On the current debate on the advantages and limitations of naturalisms, see Pérez (2021).

become concerned with the bodily aspects of the organism, while the sciences of the spirit gain access to its undefined interiority. It is not feasible because, according to Jonas:

> [...] our living body constitutes the very self-transcendence in either direction and thereby makes the methodological epochē founder on its rock. It must be described as extended and inert, but equally as feeling and willing—and neither of the two descriptions can be carried to its end without trespass into the sphere of the other and without prejudging it (1966, 18).

In short: in Jonas' assessment, the very reality of the organism challenges both dualism and its monistic residues. In a complementary way, the author will glimpse a genuine ontology of the organism as a way out of the modern labyrinth:

> Perhaps being physically exposed—Jonas recalls from his war experiences—, with which the destiny of the body imposes itself forcefully [...], contributed to the new reflection [...] [and thus] the idealistic partiality of the philosophical tradition became completely evident to me. Its secret dualism, a millenary legacy, seemed to me to be contradicted in the organism, whose forms of being we share with all living beings. Its ontological understanding would close the crack that separated the self-understanding of the soul from the knowledge of physics (2001, 145).

And what is an organism for Jonas? According to him, life is, first of all, a metabolic phenomenon. This is the keystone of his ontology of the organism (Gutierro, 2022, 82-90). Thanks to metabolic activity, each living being, without ever abandoning its material condition, without leaving space-time for an instant of its life, is capable of moving through matter without losing its identity. The organism thus depends on *matter*, but not on *this matter* in particular. Moreover, its very survival depends on its being able to constantly renew the matter of which it is composed. This capacity of the organism to keep itself alive without depending on any concrete part of matter is seen by Jonas as a first glimpse of freedom, albeit a "needful freedom" (see Jonas, 1966, 80). And he immediately places this notion of freedom in continuity with that of *form*. That is to say: with life, the real difference between matter and form enters the world.

This approach recalls a crucial passage from Aristotle's biology, located in his treatise *On the Parts of Animals* (643a, 24): "The difference is the form in the matter" (Bartolomé and Marcos, 2018, 172). Although Jonas does not mention it explicitly, one cannot but foretaste these words of the Greek thinker in the background of his ontology of the organism. In fact, in line with Aristotelian hylomorphism, Jonas argues that the concrete unity of matter and form holds also in the case of organisms, in which there is coincidence "with their actual collection at the instant" (1966, 80). That is, in organisms always "the material contents in their succession are phases of transit for the self-continuation of the form" (1966, 80). But, just as in the realm of the non-living the separation between matter and form is a mere abstraction operated by us, in the living "the ontological relationship is reversed: form becomes the essence, matter the accident" (1966, 80). In the case of an organism, the instantaneous identity between matter and form is a mere abstraction; the concrete is the continuous temporal course of the organism, throughout which, thanks to metabolic processes, matter changes, while form is maintained and, with it, the identity of the organism itself.

From this conception of the living follows other features or characteristics of organisms. The first of these is their interiority. If in the metabolic processes we see how matter enters and leaves the organism, it is clear that this delimits an inner and an outer zone, opens an inner space, an intimacy and, correspondingly, delimits its surroundings, an environment, an outer world. The point of life itself, Jonas compiles, is "its being self-centered individuality, being for itself and in contraposition to all the rest of the world, with an essential boundary dividing 'inside' and 'outside'—notwithstanding, nay, on the very basis of the actual exchange." (Jonas, 1966, 79).

Every organism divides the world into two zones, one internal and the other external; and also puts them in communication. Interiority, environment and intercommunication are distinctive notes of the living. "But if inwardness is coextensive with life, a purely mechanistic account of life, i.e., one in outward terms alone, cannot be sufficient" (1966, 58).

With what has been said, we have already hinted at other derived traits that, according to Jonas, characterize the organism, and which we will not go into here. These are features such as the unity and individuality of the living being, the organic totality that each one forms, so that it does not coincide exactly with the mere sum of its parts, its condition of center of its own activities, that is to say, its functional and teleological aspect, its dynamism and plasticity (cf. Gutierro, 2021, 143-44). It does seem opportune, however, to make a separate mention of gradualness. It is this feature of the living that will allow Jonas to raise his gaze from metabolism, already present in the simplest of living beings and, of course, in all plants, to sensibility, emotions and behavior, which come into the world through animal life, and so on until we reach the self-consciousness, will and freedom proper to humans. What appears as gradual in the whole scale is precisely what Jonas calls *freedom*, the autonomy of the living being with respect to its environment, from whose dependence, ultimately, it can never completely detach itself.

In the plant there is no distance between the nutrients it metabolizes and its own limits. The metabolic exchange has an immediate chemical nature. Roots and leaves are in contact with the nutrients that they eventually internalize. For its part, the animal opens a space between the nutrients and its own body. Sensation establishes a certain distance between it and the food. Emotions give it the impetus to get going and movement eventually fills the gap. In addition, before the chemical assimilation of nutrients, there is in many cases a mechanical processing, e.g., by chewing, which is a mediating action. In this way, the animal has gained degrees of freedom, since it can choose this or that source of nutrients, something that is not given to the plant. In the case of humans, obviously, the space grows and the mediations become enormously complex, as well as the degrees of freedom, even to select vital objectives much more differentiated than mere survival.

From these last remarks we can already surmise that the concept of organism will influence many other areas of Hans Jonas' thought. Let us see it in detail.

3. Connections of the concept of organism with other areas of Jonas' thought

The concept of organism is at the heart of Jonas' philosophy. We have already seen how it arises from the struggle that the thinker maintains with dualistic tendencies, ancient and modern, as well as with the materialistic and existentialist sequels of modern dualism. Thus, the question of the organism is clearly linked to the studies on Gnosticism and to the positions adopted by Jonas with respect to his teacher, Heidegger.

However, in addition, the notion of organism, once installed in Jonas' thought, is projected onto his ontology, anthropology, ethics and theology, and is decisive for the development of all these issues. To begin with, Jonas' ontology starts from the undeniable reality of the organism, to which we have access in a double way, both through the perception of living bodies, including our own, and of their movement in space, and through the sensation and thought that serve as open windows into the interiority of the organism that each one of us is. We see the organism—so to speak—from the outside and from the inside, but what we see is a single entity, not two distinct substances. Doing ontology implies taking note of this primary unity that is the living organism. The dualistic disintegration of it only propitiates what Jonas calls "ontology of death" (1966, 20), because "pure consciousness is as little alive as the pure matter confronting it" (1966, 21). Our thinker proposes to start from life as it presents itself to us, that is, in living organisms, in order to end up explaining the whole ontology of the universe. Any ontology that pretends to start from matter or from pure consciousness, that is, any ontology of death, will fail to account for the living, it will distort or deny it. Jonas understands the two phases of dualism, matter and consciousness, as abstractions formulated from the experience of the living and, he states, "abstractions themselves do not live" (1966, 22).

There are many Aristotelian reminiscences in all this eagerness to maintain the unity and concreteness of the organism, as well as its focal position for all ontology. From the organism, matter has to be explained, as *matter-of*, and always as something relative. From the very interiority and freedom of the living, which already dawn with metabolism, the problem of sensation and thought must be approached. Here, the ideas of matter, form, difference and substance, which come from the Aristotelian tradition, will be crucial supports. The very Aristotelian metaphor of the wax and the shape, so present in *De Anima*, comes to mind again and again in reading Jonas. "Les us consider further this new element of *freedom*," Jonas recommends, "that appears in organism, with special reference to *form*" (1966, 80; italics in original). Jonas refers to form as a "real, that is, efficacious, characteristic of life" (1966, 80). In addition, the Aristotelian distinction between the physical (*physikós*) and the logical (*logikós*) perspective is relevant here. Jonas speaks to us, no doubt, of form in the physical sense, as a reality in the world, not as a simple concept or idea. He asserted that it is only with life that "the difference of matter and form, in respect to lifeless things an abstract distinction, emerges as a concrete reality" (1966, 80). In the world of the non-living, the separation between matter and form is a mere abstraction, whereas in every living "the difference between the two is the concrete" (2000, 124). Again, we sense here an implicit quotation from the text of Aristotle reproduced above, contained in *On the Parts of Animals*. Jonas expands on this idea and connects it in a very suggestive way with the question of time. According to him, when we split the existence of an organism into instants, we are proceeding by abstraction. Such a splitting of what is physically one does not exist in reality, only in our mind. "The reality of its form is in the succession of instantaneous materialities, which it converts into its duration" (2000, 125).

In the interplay between matter, form and difference appears what is proper to life, its paradoxical and indigent aspect. With the emancipation of form, which can roll, thanks to metabolism, on matter, life becomes extremely dangerous, continually dependent on the obtaining, never guaranteed, of new matter. Life is a mode of being that, by abandoning identity and devoting itself to difference, becomes an adventure with the risk—and the sentence—of death. Life abandons the identity between matter and form, and with it security, and enters "boldly into the world of difference" (2000, 149). It might seem that the shadow of dualism looms again here, but this is not the case. The organism whose form is emancipated from matter does not become less material, but more. It does not diminish here "the overall computation of the materiality of the form detached from the fixed material equation, and in this sense 'liberated,' but on the contrary makes that materiality increase" (2000, 149). In the course of its life, any organism processes far more matter than is required for its constitution at any current instant. Moreover, it is continually engaged in the attainment of new matter. The entire matter of the universe thus becomes, for an organism, a possibility. The concepts of actuality and potentiality are here assumed. And the teleological character of organisms, which tend to survival through the progressive renewal of their matter, is also pointed out.

Allow me to expand somewhat on this last point, because of its obvious importance and its conflictuality. All modern science seems to be anchored in the elimination of finality. However, the teleological orientation of each organism towards its own life is an indispensable datum of our experience. The reduction of everything biological to pure efficient cause, to mechanism, is frustrating. It always leaves us with half an explanation. It is perfectly legitimate, from the methodological point of view, to put finality in parentheses in order to be able to better study other aspects of reality. But with this we cannot pretend that purposiveness itself has been eliminated from reality. Every organism manifests the opposite. And the scholar of the living, he or she himself or herself, turns out to be an organism, with access to his or her tendential interiority, to his or her emotions and volitions, to the finalistic ordering of his or her action. From this vital position, we could hardly deny the teleological condition to our body and to the rest of the living. “However complete the physicochemical analysis of the composition of the eye and of the processes attending its stimulation may be,” Jonas reminds us, “no account of its construction and functioning is meaningful without relating it to seeing” (1966, 90). Finalism and mechanical causality coexist. It must be recognized that there is something enigmatic in this, an unresolved problem, but it cannot be denied that such coexistence occurs, and even less so when the student of life is a living being, who by his own condition has access to the evidence of both dynamisms. “Life,” says Jonas, “can only be known by life” (1966, 91). The problem before us “cannot be denied either is a problem not to be ‘solved’ by sacrificing an evidence (purposiveness) to a theorem (exclusiveness of *causa efficiens*)” (1966, 90).

If Jonas’ ontology, as we see, springs from the idea of organism, so does his anthropology, since the human being is an organism and can only be understood as such. Anti-dualism now becomes especially peremptory. There are not two substances in us, but each human being is precisely a substance, an organism, in which the traits that we had already seen appear in the simplest of living beings are manifested in a particularly clear way. It is this position of the human being that makes him so apt to understand what other organisms are and to structure from there a whole cosmovision. The most elementary of the entities capable of metabolism already separates reality into two zones, one interior and the other exterior, already puts them in communication, already makes its form take distance from matter, not because it can dispense with it in general terms, but because it does not identify itself with any particular part of it, already indicates tendencies in its mere structure and seeks in each of its actions its own subsistence. All this is applicable to a simple bacterium and, of course, to plants. With animal life, freedom gains ground, as we have seen, thanks to sensation, emotion and movement. And in this line of gradual gain of distance, of interiority, of self-reference, of degrees of freedom, in short, we must situate the human being. Jonas himself establishes this transition in one of the chapters of *The Phenomenon of Life*, entitled “From the Philosophy of the Organism to the Philosophy of Man” (1966, 183-187). The author suggests that the animal organism is building around itself a world, which is already something more than a simple environment, like that which surrounds plants. A world implies a certain distance, and, with it, a certain representation. "'World' confronts the subject with discrete, self-contained objects, whereas the plant-environment consists of adjacent matter and impinging forces" (1966, 183). The next step in the same direction places us definitively in the anthropological terrain: "In the image-faculty of man a further degree of mediacy is reached, and the distance between organism and environment is widened by a further step. [...] This new degree lies in the ideative extension of *perception* [...]. The new mediacy consists in the interposition of the abstracted and mentally manipulable *eidos* between sense and actual object" (1966, 184). In fact, the closest we have in Jonas to a definition of the human being is the expression *Homo pictor* (1966, Seventh Essay). The human being thus converts things into images and language, he distances himself from them in order to be able to manipulate them more freely before returning to them.[4] At this new level, a maximum is reached with respect to the tendency to separation, which already began with simple metabolism.

On the other hand, the tendency to goals is also present in all organisms; in animal life it is specified as drive, effort, pleasure and fear, which finally take the form of "reaching self-transparency in consciousness, will and thought of man" (1966, 90; cf. also Jonas, 1976). The human being ends up being understood by Jonas not only as an organism, but as the seat of the organism's knowledge. Thus, a philosophy of life has to deal "with the organic facts of life, and also with the self-interpretation of life in man" (1966, 6).

As a whole, with the appearance of the human being, a range of purposes never before given appears in the universe. Each of us, as an organism, seeks survival, but we do so in a much more complex, sophisticated and free way than the simplest organisms. In addition, we seek not only life, but a good life, with the aspiration to happiness, which is fulfilled in very different ways depending on the person. In other words, human beings open up new purposes that would be unthinkable without them, open up new areas of value in the universe. And with this observation we begin the transition from anthropology to ethics. The whole of Jonas' (1984) ethics of responsibility is based on these considerations. Given the value assigned to human life, the universe would be seriously impoverished by its loss. The range of possible ends would be drastically diminished, and the possibilities of value would thereby be reduced. Here is the insertion of the concept of organism into ethics. It is organisms that possess ends, ends open up possibilities of value, and these are maximized by the presence of human beings on Earth. There would be, then, "something absolutely inadmissible, namely, that man destroys himself (for example by ruining the biosphere)" (2000, 322). From this follows the principle of responsibility itself, which, in one of its statements,

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[4] There are interesting parallels between Jonas' ideas and those of Helmuth Plessner (see, for instance, Michelini, Wunsch & Stederoth (2018) and Greene (1966)).

goes as follows: "Act in such a way that you do not threaten the conditions for the indefinite continuity of human existence on Earth" (1984, 36). It is a principle of respect and care for life in general and human life in particular.

Jonas' ethics proposes to go to the root of the question, that is, to the question of the primacy of being over non-being. It asks why being has value, why it is better than non-being. The answer is that only in what *is* can there be value, so that this mere possibility of value is already a value that makes being preferable to nothingness, that is, that makes it better and therefore preferable. In other words, there can only be something good if there is something. As he put it, "[...] the mere fact of value (with its opposite) being *predicable* at all of anything in the world, whether of many things or few, is enough to decide the superiority of being, which harbors that possibility within its manifold, over nothingness, of which nothing whatever, neither worth nor worthlessness, can be predicated" (1984, 48-49; italics in original). Now, this value of being does not occur equally in all entities. Some can *be* more fully than others, and consequently their value will vary by the variation of their mere possibility of sustaining values. Jonas formulates this idea in terms of the capacity of every substance to have ends, and in the case of humans also to propose ends to themselves: "We can regard the mere *capacity* to *have* any purposes at all as a good-in-itself, of which we grasp with intuitive certainty that it is infinitely superior to ay purposelessness of being" (1984, 80; italics in original). We have the profound moral intuition that being is worth more than non-being, that organisms are worth more than non-living things, and that not all living things are worth the same, and, consequently, that not all deserve the same treatment. The just gradation of the same is in close connection with the very idea of organism that we have been presenting.

In closing this section, I will make two brief observations regarding the impact that the idea of organism has on Jonas' theology. To begin with, this idea owes much to a mental experiment, of a theological nature, which our author develops in chapter five of his book *The Phenomenon of Life*. The title of the chapter is highly significant, since it connects from the outset the biological with the theological: "Is God a Mathematician? (The Meaning of Metabolism)" (1966, 64-98). I cannot expand in the exposition of the ideas it contains, but I will try to summarize the core of its meaning. Frequently, especially since the beginning of modernity, the idea of a mathematical God, who designs the universe so that it works by itself according to precise laws, has been advanced. The saying attributed to Galileo, according to which the book of nature is written in mathematical characters, points in this direction. God would have spoken to us of himself through the Bible and through the mathematics implicit in nature. According to Jonas, a mathematical God would be blind to see such a ubiquitous phenomenon in our environment as metabolism. God's famous point of view would be of little use to us now. Not even for elementary biology. "The mathematical God in his homogeneous analytical view misses the decisive point," writes Jonas, "the point of life itself: its being self-centered individuality, being for itself and in contraposition to all the rest of the world, with an essential boundary dividing 'inside' and 'outside'" (1966, 79). This blindness of the mathematical God to life is due to "the invisibility of life to the analysis of the extensive" (2000, 135). In this we have an advantage over the mathematical God "we poor mortals [...] [are] happening to be living material things ourselves, we have in our self-experience, as it were, peepholes into the inwardness of substance" (1966, 91).

The second observation refers to a connection that no longer depends on a mere mental experiment, but is given in terms of the deep theological convictions of Jonas. These are expounded in the manner of a myth, that of the face or image of God, but a myth, says Jonas, "which I would like to believe 'true'—in the sense in which myth may happen to adumbrate a truth which of necessity is unknowable and even, in direct concepts, ineffable, yet which, by intimations to our deepest experience, lay claim upon our powers of giving indirect account of it in revocable, anthropomorphic images" (1966, 278). This myth says that the human being is not created in the image of God, but *for* the image of God, that is, that he has the mission to create, to produce with his actions, the very face of God. He thus becomes a kind of "cosmic adventurer" who places his fate entirely, in a surrendered manner, in our hands, for good... or for evil. There is no need for the world to exist, but by "foregoing its own inviolateness the eternal ground allowed the world to be" (1966, 279). Through the emergence of organisms, with all the characteristics that Jonas recognizes in them (most notably freedom), and with the intensification of these to the human extreme, the "divine adventurer" stakes his own face without remission. And, Jonas concludes, "it is not licit for us to leave him in the lurch, not even if we would like to leave ourselves in the lurch" (2000, 323).

4. Some critical reflections

After the expository and interpretative phase of this article, I will now formulate some critical reflections on Jonas' ideas. Simplifying things, I can mention that these reflections refer (i) to the use of the notions of freedom and life; (ii) to the lack of distinction between science and scientism; (iii) to the sparse treatment of the phenomenon of biological reproduction; and (iv) to the doubts that may be generated today by the characterization of plant life provided by Jonas.

(i) The concept of freedom appears very frequently in the texts that Jonas devotes to thinking about the organism. It is, for him, a key notion. However, the use he makes of the very notion of freedom is, if I may be allowed the redundancy, too liberal. He employs it already in relation to plants and even to the simplest forms of life. We could say that for Jonas there is freedom as long as there is life. It is true that on some occasions he typographically indicates the term with quotation marks or italics, but not always, and on others he reserves for the human the expression "freedom of the spirit." In any case, by attributing freedom to any metabolic organism, Jonas makes things too easy for the explanation of human freedom. Perhaps there is little in common between the possibility that any organism has to metabolize this or any other matter and the freedom of action and will that we humans experience. Each of these phenomena could be given, in all tranquility and perhaps with a gain in precision, a different name. Conceivably it would be more rigorous to speak of metabolic autonomy in the case of metabolism and of authentic freedom in the case of human action. The expression "metabolic autonomy" could perhaps serve to bring Jonas's positions closer to those of the more current enactivism or organizational approach,[5] or at least facilitate a possible dialogue with them. This need not be the best terminological choice, of course, but Jonas' generous use of the concept of freedom somewhat distorts his explanation of the organism in general and the human being in particular. Interestingly, the author himself is critical of analogous rhetorical maneuvers. For example, he states—rightly, I believe—that "cybernetics is not as innocent" when selecting certain terminology: "The use of an intentionally ambiguous and metaphorical terminology facilitates this transfer back and forth between the artifact and its maker." That is, when we metaphorically describe cybernetic control artifacts as "perceptive, responsive, adaptive, purposive, retentive, [having] learning, decision-making, [being] intelligent, and sometimes even [as] emotional" (1966, 110), we are rhetorically facilitating the subsequent conception of human beings as mere cybernetic systems, as complex robots, as well as the assignment of intelligence to the artifact. Something analogous could be said to be done by Jonas in already endorsing freedom to any metabolic organism, item more so when in his own text we can read, separated by a few pages, the two statements that follow. "Let us consider further this new element of *freedom* that appears in organism" (1966, 80; italics in original); and "The advent of man means the advent of knowledge and freedom" (1966, 277). It is true that in the former the term in question appears in italics, but will there not be here, consciously or not, an ambiguous and metaphorical use of it?

Regarding the notion of life, it should be said that sometimes it could be replaced with advantage by that of living being. Jonas usually refers to organisms, to each one of them, as a concrete entity. This reference is better indicated by the concept of living being than by that of life. Life can only be an abstraction formulated on the basis of what living beings have in common, or else the activity proper to a living being. In any case, before life there is the concrete living being, that is, the organism. The whole spirit of Jonas' philosophy points in this direction, confusion is not easy, but it would be even less so if in numerous passages he were to replace life by living being, for example—one among many that we could bring up—when he affirms that form is an "efficacious, characteristic of life" (1966, 80).

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[5] See, in this regard, Etxeberria & Moreno (2007), Barandiaran & Moreno (2008) and Moreno & Mossio (2015).

(ii) Another objection that we could interpose concerns the distinction between natural sciences and scientistic mentality. It is not clear to me whether this is a terminological question in Jonas, like the previous ones, or whether it goes to the heart of his thought, so I treat it separately. I refer here to programmatic statements such as this: "[...] the following investigations seek to break through the anthropocentric confines of idealist and existentialist philosophy as well as through the materialist confines of natural science" (1966, ix). Here one would expect Jonas to contrast two antagonistic philosophical ranges, on the one hand that which encompasses idealism, existentialism, perhaps nihilism, and, on the other, that which includes materialism, radical naturalism, and scientism. But what he does is to oppose philosophical ideas to natural sciences, the latter implicitly linked to a materialist philosophy. From my point of view, this is an error of expression. I understand that, at bottom, what Jonas is looking for is the opposition of philosophies, but as he says it, the question is not clear. In our days it is already evident to everyone that science is something different from scientism, that the natural sciences do not imply a radical naturalism and that the scientific study of matter does not have to lead to materialism. I avoid here the work of giving argumentative support to these claims, for such work has already been successfully done by many contemporary authors. In this regard, let me cite only, and in honor of its clarity, Francisco Soler Gil's book entitled *Materialist Mythology of Science* (*Mitología materialista de la ciencia*, 2013). With its underlying message I believe that Jonas himself could agree, despite the doubts that may be generated by textual quotations such as the preceding one.

(iii) With the third objection we clearly leave the realm of terminology and enter into the heart of the matter. When characterizing the organism, Jonas appeals directly to the biological phenomenon of metabolism. But living beings are distinguished by at least two very conspicuous features: one is, in fact, metabolism, the other is reproduction with inheritance. From some living things others are generated, and these retain some of the traits of their progenitors. Theories of the origin of life have to deal with this dichotomy if they do not want to appeal to a simultaneous debut of both phenomena: either they focus on the origin of metabolism or on the origin of reproduction. Then it will be necessary to explain how the one is produced from the other. But "an 'existential' interpretation of biological facts," such as the one proposed by Jonas, would in principle not have to do without one of the two phenomena that mark the living, neither metabolism nor reproduction. It is surprising, therefore, the almost complete absence of references to the latter that we detect in Jonas' texts, where the exclusive attention is placed on the former. It is obvious that given the biological importance of reproduction, as well as its immediate connection with the evolutionary process, any philosophy of life that does not pay attention to it will be incomplete. As I have been arguing, the Jonasian reflection on life is of enormous value, but it would be even more so if it contemplated, together with metabolism, reproduction. The same Aristotelian inspiration that we find in Jonas' thought could have led him to the phenomenon of reproduction, to which the Greek thinker dedicated a specific treatise.

(iv) Finally, I would like to point out a refinement on the vision that Jonas presents us of the life of plants. In this case, no fault can be attributed to the author, since the botanical research to which I would like to refer has had its impact on the academic community after the death of the German-Jewish thinker. I refer to the research carried out by Stefano Mancuso and his team (2015), according to which it would be appropriate to assign to plants a certain type of intelligence and sensitivity, which Jonas reserved, according to tradition, for animals. Mancuso detects phenomena of communication between plants, behavioral strategies that even involve mutual aid. His positions have triggered an interesting debate in the world of botany (Calderón, 2021). But, regardless of its evolutionary background, it seems clear to me that the sharp distinction we used to make between plant life and animal life needs to be reconsidered. If Jonas's ideas about what an organism is are to be rescued for contemporary debates, they will have to be done under this nuanced tone.

5. Concluding Remarks

Both biology and the philosophy of biology have now placed the organism at the center of their agenda. It is no longer an issue of reducing it to the categories of inert matter, but of understanding it in its own terms. For this task, recourse to the ideas of Hans Jonas, who thought of the organism in an original and profound way, will undoubtedly prove useful. As we have seen, Jonas approached this subject from his rejection of dualism and as a way out of the aporias to which it condemns us, both in its ancient versions and in its modern variants. Neither are the systems derived from the mutilation of dualism by the negation of one of its terms operative for conceptualizing the organism. Neither the appeal to pure consciousness, nor the reduction to crass matter will serve to understand what a living being is. This is Jonas's diagnosis, and many of us agree with its wisdom.

As an alternative, the German-Jewish thinker proposes that we start from our own experience of the organism, either seen as something spatial and external, or lived from within, since each one of us is an organism. This is a double perspective projected on a single concrete substance. Through this methodology, we aspire to understand the reality of the living. According to Jonas, this is built on metabolism.

It is this biological phenomenon that opens up new metaphysical spaces, that introduces an initial difference between matter and form, that allows the identity of form to roll, so to speak, over matter without ever ceasing to constitute a material entity. Metabolism goes hand in hand with the introduction into the world of an enclosure of interiority, of a frontier between the organism itself and the rest of reality. There is no living without metabolism and there is no metabolism without the distinction between a zone of intimacy and an environment which, moreover, the organism puts in continuous communication. This is what its life consists of, without it—without interiority and communication—it could not subsist. But the distance, the autonomy, the—let us say it, in spite of everything, in the words of Jonas—*freedom* of the organism with respect to the environment is growing. It is already a being in itself, a substance, and a being for itself, teleologically oriented towards its own life. In addition, a space is opening up there, between the organism and its environment, which will allow, in the course of time, the emergence of sensation, emotion and movement.

The plant is in continuous and immediate contiguity with its nutrients, it takes them from the air or from the soil directly, by contact, as well as the solar energy that puts everything into operation. It does not have to scrutinize, stalk, jump on them, but they simply arrive and knock at its door. For the animal, in contrast, it is necessary to search, to look, to listen from a distance, to move to the source of matter and energy for its subsistence, and with it fear and desire, attack and flight. It is *freer*, yes, and at the same time lives a more needy and risky life than the plant, which already constituted as a way of being a mortal risk with respect to the non-living.

This philosophy of the organism gives Jonas the key to build his entire ontology, since the entire universe becomes illuminated by the life of organisms. It is also easy to intuit how the reflection on the human is inserted in the economy of his thought from what is found in the organism. Open space, distance, freedom—now yes, in the full sense and without italics—, interiority, sensation, even self-referential thought, tension converted into will and emotions educated by reason flourish fully in human life, in the biography of each person.

And the value that we can assign to this adventure of the living, the new range of purposes and functions that each organism unfolds in the universe, will serve Hans Jonas to found his ethics of responsibility. It is the human being who has to bear the burden of responsibility, who is responsible for the destiny of the living on Earth. With this, according to the theological myth that Jonas wants to believe to be true, he traces, from time and forever, the face, the image, of the divine adventurer.

All this architecture, full of meaning and beauty, is not, however, without cracks, perhaps merely cosmetic, typical of the coating, or perhaps more nuclear and dangerous for the balance of the whole. We have pointed out some of them, those that concern the concepts of freedom and life, those that refer to the distinction between science and scientism, those that affect the (absent) treatment of the biological phenomenon of reproduction or those that ask to be updated according to the findings of new botanical research. Nevertheless, the initial estimate, in my opinion, is maintained and reinforced after the journey we have made: biology and the philosophy of biology today have in the work of Hans Jonas a very valuable source of inspiration for thinking about the organism.

Text translated into English by Alejandro Fábregas-Tejeda and Mariano Martín-Villuendas.

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From Mechanistic Biomedicine to Organismal Systems Medicine

De la biomedicina mecanicista a la medicina de sistemas organismales

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Abstract

Biomedicine, the predominant medical model that emerged during the twentieth century, is founded conceptually on mechanism and reductionism, especially in terms of portraying the patient as a machine reducible to its component parts. Systems medicine, in contrast, has emerged during the early part of the twenty-first century to address problems arising from biomedicine's failure to cure diseases such as cancer. In this paper, a conceptual framework is provided for shifting from mechanistic biomedicine to organismal systems medicine. Specifically, organicism and holism provide the necessary foundation for viewing the patient not simply as a diseased or dysfunctional body part but as a whole person embedded within a biological, psychological, social, and environmental framework. Although biomedicine's approach has identified many of the physiological and pathological components of health and disease, a shift to organismal systems medicine promises to deliver the principles and rules by which these components relate and interact with one another in a holistic rather than simply in a reductive mechanistic fashion.

Keywords: holism; mechanism; medicine; organicism; reductionism.

Resumen

La biomedicina, el modelo médico predominante surgido en el siglo XX, se basa conceptualmente en el mecanicismo y el reduccionismo, sobre todo en lo que respecta a la descripción del paciente como una máquina reducible a sus componentes. La medicina sistémica, en cambio, ha surgido a principios del siglo XXI para abordar los problemas derivados de la incapacidad de la biomedicina para curar enfermedades como el cáncer. En este artículo se ofrece un marco conceptual para pasar de la biomedicina mecanicista a la medicina sistémica organismal. En concreto, el organicismo y el holismo proporcionan la base necesaria para considerar al paciente no sólo como poseedor de una parte del cuerpo enferma o disfuncional, sino como una persona completa integrada en un marco biológico, psicológico, social y ambiental. Aunque el planteamiento de la biomedicina ha identificado muchos de los componentes fisiológicos y patológicos de la salud y la enfermedad, el paso a la medicina de sistemas organismales promete ofrecer los principios y reglas por los que estos componentes se relacionan e interactúan entre sí de forma holística y no simplemente de un modo mecanicista reductor.

Palabras clave: holismo; mecanismo; medicina; organicismo; reduccionismo.

1. Introduction

During the twentieth century, biomedicine was the predominant medical model in terms of both basic and clinical research, as well as clinical practice (De Chadarevian and Kamminga, 1998, Lock and Gordon, 1988, Löwy, 2011). Two of the fundamental concepts grounding biomedicine are mechanism and reductionism (Andersen, 2017, Clarke and Russo, 2018, Illari, 2017). According to these concepts, the patient's body is a machine reducible to its individual parts with respect to its functioning and/or malfunctioning. Biomedicine's success depended on mechanical philosophy, which has a rather long history in western medicine (Glennan, 2017, Sheldrake, 1980, Westfall, 1977). And much of that success relied on reducing disease to its mechanistic parts (Darden, et al., 2018). For example, hemophilia and von Willebrand disease are bleeding disorders that were explained and eventually treated through the isolation of clotting factors from human blood (Federici, et al., 2006, Green, 2018). Indeed, as hemostasis or blood coagulation was reduced to various clotting factors, eventually a hemostatic model or cascade was assembled in the second half of the twentieth century and used to investigate and treat other coagulation disorders (Owen, 2001). And this approach to understanding and treating disease led to the prevalent "magic bullet" approach closely associated with the biomedical model (Brandt and Gardner, 2000). Unfortunately, this approach failed to cure complex chronic diseases, like cancer (Cutter, 2018, Keating and Cambrosio, 2012, Mukherjee, 2011), resulting in a situation that resembles a Kuhnian paradigmatic crisis (Kuhn, 1970).

During the first-half of the twentieth century, systems theory and science were used to tackle apparent anomalies in the biological and biomedical sciences in which the traditional mechanistic approach was unable to provide adequate solutions (Bertalanffy, 1974, Hanson, 1995, Skyttner, 2005). Two important fundamental concepts grounding systems theory and science, especially the biological sciences, are organicism and holism (Botz-Bornstein, 2021, Döring, et al., 2015, Capra and Luisi, 2014, Sheldrake, 1981). And these concepts have been incorporated into systems medicine to address problems for treating complex diseases like cancer, diabetes, and cardiovascular diseases (Rosslenbroich, 2016, Tretter, 2019). For example, cancer throughout the twentieth century did not succumb to biomedicine's straightforward "magic bullet" approach to produce a cure; and even then US President Richard Nixon's 1971 "war on cancer," which promised that cancer would be cured by the US 1976 bicentennial, failed to deliver on its promise (Surh, 2021)—although limited success was achieved but it has been costly (Cutler, 2008, Sporn, 1997). Moreover, the military terminology or metaphor of this approach to cancer has been criticized as unproductive and inappropriate (Haines, 2014). In place of the biomedical approach, a systems medicine approach has emerged, especially during the early part of the twenty-first century with the completion of the Human Genome Project, which promises to cure cancer and other complex diseases (Roukos, 2010, Karimi, et al., 2022).

In this paper, the concepts of organicism and holism are used to construct a conceptual framework for the shift from mechanistic biomedicine to organismal systems medicine. Specifically, organicism and holism provide the theoretical foundation for viewing the patient as a whole person, especially in terms of personal health, and not simply as a diseased body part—as is often common in the biomedical sciences. And these concepts are contrasted to the concepts of mechanism and reductionism associated with the traditional biomedical model, as well as with a molecular systems medicine (Tretter, 2019). Although mechanism and reductionism have been instrumental in biomedicine to identify many of the components that compose pathophysiological states, a shift to organismal systems medicine within the twenty-first century promises to deliver the principles and rules by which the components of the organism relate and interact with one another at a holistic level, including the social and environmental levels (Wolkenhauer, et al., 2013, Rosslenbroich, 2016). To that end, the concepts of mechanism and reductionism associated with the biomedical model are examined in the next section, followed in a subsequent section by a discussion of organicism and holism associated with systems medicine. In a concluding section, the relationship between mechanistic biomedicine and organismal systems medicine is explored.

2. Biomedicine: Mechanism and Reductionism

The success of the biomedical model throughout the twentieth century was certainly impressive, especially in terms of the molecularization of physiological and pathological processes (De Chadarevian and Kamminga, 1998, Grote et al., 2021). As already mentioned, hemostasis was reduced to various blood clotting factors that could not only explain the coagulation mechanism but also provide the knowledge and understanding for developing therapeutic agents to treat clotting disorders. In addition, other diseases were explained and treated using knowledge obtained from the biomedical model, such as insulin for type 1 diabetes (Bliss, 1982, Vecchio, et al., 2018), antibiotics for numerous infectious diseases (Hutchings, et al., 2019, Rosen, 2017), and even cancer itself was thought to be explained in terms of reducing it to various molecular entities, especially mutated genes, responsible for regulating the mechanisms responsible for the cell cycle and cellular proliferation (Bertram, 2000, Knowles and Selby, 2005, Pecorino, 2021). Mechanism and reductionism, then, are the underlying concepts of the biomedical model and sciences, and mechanical philosophy in general is the founding metaphysics upon which the medical universe is explained simply in terms of matter and motion. In this section, mechanism is initially examined, followed by reductionism, and then both concepts are illustrated with the examples of hemostasis and carcinogenesis.

2.1 Mechanism

The rise of modern western science reflects the history of mechanism, especially in terms of the analogy between machines or automata and natural phenomena (Berryman, 2003, De Solla Price, 1964). In general, a machine is defined as “a contrivance, with organized parts whose interconnected workings can be easily understood” (Craver and Darden, 2005, 234). The machine analogy was important in the establishment of mechanistic philosophy, since the analogy’s heuristic promise is that natural scientists could control and manipulate natural phenomena qua machines via their component parts. The analogy was also apt because the functions of machines are often deterministic and follow straightforwardly fundamental engineering principles and rules. One of the chief presumptions for the analogy between machines and natural phenomena is the inherent intelligibility of nature itself. A major part of that intelligibility centers on temporally and spatially extended causal processes. In other words, mechanisms are processes that connect within particular locations and between temporal sequences: "a cause (or beginning state) to an effect (or end state)" (Craver and Darden, 2005, 236). Mechanical philosophy, then, had a profound impact historically on both biology and medicine; and its greatest impact was the development of molecular biology in the twentieth century, which was to convert contemporary medicine into a molecular discipline and practice (Bechtel, 2006, Darden, 2006, Tretter, 2019).

Peter Machamer, Lindley Darden, and Carl Craver (hereafter MDC) introduced a popular articulation of mechanism in which they stress a mechanism's process-like nature. "Mechanisms," according to MDC, "are entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions" (2000, 3). They illustrate the concept as follows: "A->B->C" (2000, 3). The letters A, B, and C, represent entities, while the arrows represent activities. Whereas activities are the processes involved in an orderly change, entities are the agents responsible for that change. MDC claim that their concept of mechanism exhibits ontic, descriptive, and epistemic adequacy. As for ontic adequacy, their concept combines both substantive and process ontologies such that ontology is neither eliminable nor reducible to the other. MDC's concept also exhibits a descriptive adequacy by illuminating the initial and final conditions, as well as the intermediate conditions, for progressive routine change. Finally, their concept of mechanism is epistemically adequate since it renders complex phenomena intelligible in terms of mechanistic explanations.

Although many examples of mechanism are available from the biomedical sciences, such as intermediate metabolism, MDC cite the central dogma of molecular biology as the prime example for their concept of mechanism. The central dogma is the fundamental paradigm of molecular biology, and molecular biologists have used it to guide their research since its introduction in the late 1950s, when Francis Crick (1958) announced the central dogma publicly at a symposium in London. According to Crick's version of the dogma, a polymerase transcribes DNA into RNA, which is then translated into protein, and both DNA and RNA can replicate themselves. In MDC's terms, DNA, RNA, and protein, are entities; while transcription, translation, and duplication are activities which the entities cause and through which predictable change occurs. Importantly, DNA contains the genetic information that shapes living organisms through the production of proteins, i.e., genotype dictates phenotype.

2.2 Reductionism

The central dogma relies not only on mechanism but also on reductionism, which enjoys a privileged position—along with mechanism—in the development of the twentieth-century biomedical sciences (Andersen, 2017, Brigandt and Love, 2017, Jones, 2000, Van Regenmortel and Hull, 2002). The chief idea behind reductionism is that scientists can investigate and explain natural mechanisms with respect to their component parts and properties. And contemporary biological scientists assert that through reductionism "the complete determination of a biological system becomes a concrete, achievable goal" (Selinger, et al., 2003, 254). According to reductionism, then, natural mechanisms can be investigated, described, and explained entirely in terms of their component parts and properties. As John Dupré elucidates, reductionism is "the view that the ultimate scientific understanding of a range of phenomena is to be gained exclusively from looking at the constituents of those phenomena and their properties" (1993, 88). In other words, the whole and its properties are equal to the analysis and sum of its individual parts and their properties.

Reductionism, especially in the biomedical sciences, can be divided into at least three types: ontological, methodological, and epistemological (Boogerd, et al., 2007, Brigandt and Love, 2017). Ontological reductionism claims that material or physical components make up natural mechanisms, in that the material composition of complex mechanisms are reducible to simpler material components. For example, the heart is composed chiefly of cardiac cells, which are the basic unit of the organ (Litviňuková, et al., 2020). Methodological reductionism involves the strategy or method and protocols or techniques by which to investigate and model higher-level mechanisms with respect to lower-level mechanisms. For example, the heart can be investigated in terms of its cellular function such that cardiac cells contract in unison to form a pump (Trayanova, 2011). Epistemological reductionism asserts that higher-level mechanisms can be described and explained in theoretical terms and laws used to describe and explain lower-level mechanisms. For example, the heart and its regulation can be explained theoretically with respect to its contractile proteins (Winegrad, 1984).

Moreover, the relationship among these three types of reductionisms is important. Ontological reductionism espouses that material components make up natural mechanisms. For the biomedical sciences, it is claimed that the body is composed of basic parts, such as macromolecules, cells, and tissues. Based on that claim, biomedical scientists devise and develop methods and technology to investigate these mechanisms in terms of their elemental components. Of course, the development of the microscope was very instrumental in identifying the body's cellular composition (Wilson, 1995). In turn, these scientists then utilize the observations and results obtained from these investigations to reduce theoretical explanations for complex mechanisms to the theoretical explanations for the elemental components constituting complex mechanisms, such as blood coagulation or tumor formation. Finally, these three types of reductionisms are related in the sense that ontological reductionism serves as a guiding principle for conducting biomedical investigations, and the results from those investigations serve to explain higher-level mechanisms with respect to lower-level mechanisms.

2.3 Examples of Mechanistic Biomedicine

The following two examples illustrate the power of the concepts of mechanism and reductionism for advancing the biomedical agenda. The first example is the biochemical mechanism responsible for hemostasis. According to the standard cascade model of blood coagulation, the formation of a fibrin clot begins with the activation of clotting factors associated with either the extrinsic or intrinsic pathway (Davie, 1995, Mann and Lorand, 1993). The extrinsic pathway is activated through tissue factor or factor VII, while the intrinsic pathway through Hageman factor or factor XII. Both pathways converge onto Stuart factor of factor X, which is then activated and results in the activation of prothrombin or factor II to thrombin. Thrombin is responsible for the enzymatic cleavage of fibrinogen or factor I to fibrin, which is finally stabilized to form a fibrin clot. This cascade model for the clotting mechanism has been the foundation for explaining and developing treatment regimens for numerous bleeding disorders (Ratnoff and Forbes, 1996). Although platelets and other blood and tissue cells were known to be important in blood coagulation, their role was not fully appreciated or included into clotting theories until the end of the twentieth and the beginning of the twenty-first centuries (Hoffman, 2003, Riddel et al., 2007, Roberts, et al., 1998). And although the molecular reductive approach to the mechanism of blood coagulation is still critical for understanding and treating hemostatic disorders, it is challenged by several anomalies such as abnormalities of blood clotting in cancer patients (Hamza and Mousa, 2020).

The second example is from oncology and involves the biochemical and genetic mechanisms responsible for tumorigenesis. As for the biological sciences, so the biomedical sciences also adopted the central dogma as its fundamental paradigm for explaining diseases such as cancer, especially as biomedicine became an information science within the postgenomic era (Lenoir, 1999). The cancer phenotype could now be explained reductively in terms of a dysfunctional or mutated genotype. The mechanism of carcinogenesis involves the mutation of genes responsible for regulating the cell cycle, which leads to uncontrolled cell proliferation and growth and ultimately to metastasis (Bertram, 2000, Knowles and Selby, 2005, Pecorino, 2021). Cancer, then, is reduced to mutated genes, such as oncogenes and tumor suppressor genes, that control cellular division and proliferation. But as with blood clotting, theories of carcinogenesis also began to incorporate the role of cells into tumorigenesis. Douglas Hanahan and Robert Weinberg (2000), for example, published probably the most influential article on the mechanism of tumor formation called the somatic mutation theory. The mechanism consisted of six hallmarks or capabilities of tumors, each of which was reduced to biochemical and cellular mechanisms. Hallmarks like sustained angiogenesis or limitless replicative potential represented the outcome of mutated genes that regulate angiogenesis or cellular proliferation. Importantly, Hanahan and Weinberg contrasted their model, which they called heterotypic cell biology, with a model in which cancer cells are uniform or homogenous in that each cancer cell contains a standard set of mutated genes. In sum, a reductive strategy was instrumental in identifying the molecular entities, whether genes or cells, involved in the mechanisms of tumorigenesis and thereby explaining tumor formation, which is comparable in a variety of—if not all—organisms (Marcum, 2005). Thus, during the second half of the twentieth century a method of reductive analysis and synthesis was thought to be adequate for investigating and explaining complex mechanisms like carcinogenesis.

Finally, the biomedical community accepts and promotes mechanism and reductionism, as illustrated by the two examples above, for several reasons. The first is that reductionism is remarkably successful for identifying the mechanisms and their parts underlying biological phenomena (Brigandt and Love, 2017, Robinson, 1992). Part of the success of mechanism and reductionism is their simplification and analysis of complex processes into their constitutive parts and how those parts are structured. By isolating and identifying the various components of complex entities and their properties, biomedical scientists can then piece together or synthesize the underlying mechanisms, especially for diseases. For example, coagulation disorders are the result of dysfunctional or absent clotting factors, while cancer involves mutated genes. Moreover, reductionism provides the opportunity to construct a simple and consistent account for natural mechanisms, which allows biomedical scientists to manipulate and control such mechanisms. In addition, it provides a causal relationship between higher-level mechanisms and their component parts such that "causality entails reductionism" (Dupré, 1993, 99). In other words, lower-level mechanisms and their properties are thought to be causally necessary and sufficient for producing higher-level mechanisms and their properties. So a hemostatic disorder like von Willebrand disease can be explained by the absence of the von Willebrand factor and cured by replacing the factor. In short, reductionistic biomedicine provides universal statements about complex mechanisms constituting physiological and pathological processes.

3. Systems Medicine: Organicism and Holism

Just as mechanism and reductionism are the foundational concepts for biomedicine, so are organicism and holism for systems medicine. And so organicism and holism are critical for fully transitioning from mechanistic biomedicine to organismal systems medicine. While mechanism and reductionism focus on lower levels of organization—such as macromolecules and cells—to investigate and explain a patient's pathophysiology, organicism and holism include not only these but also higher levels of organization—such as the tissue, organ, or organism—to examine and explain a patient's pathophysiology while maintaining the patient's integrity as a whole rather than reducing the whole to its isolated parts. Besides the boundaries of mechanistic biomedicine and organismal systems medicine, hybrid models populate the area between these two boundaries, such as molecular systems medicine.[1] However, for these hybrid models the patient is still reduced to individual molecular parts that are generally considered sufficient for investigating and explaining higher levels of functioning. For organismal systems medicine, the patient is treated as a whole in which parts from different levels or sales are interrelated or entangled with one another. Moreover, several systems biologists utilize mechanistic explanations to account for systems phenomena (Brigandt, et al., 2018, Richardson and Stephan, 2007). Although mechanistic systems biology represents a legitimate approach to medical research, some commentators argue that without a holistic context, a system cannot be adequately or sufficiently explained since the isolated parts, especially at lower levels, do not provide sufficient relevant information to explain the system (Soto and Sonnenschein, 2018, Tretter, 2019). In this section, organicism is initially discussed followed by holism, and the section concludes with exploring from an organismal systems medicine perspective the blood clotting and cancer examples discussed in the previous section.

3.1 Organicism

According to organicists, mechanical parts alone, as advocated by mechanists, are insufficient ontologically to investigate adequately or to manipulate effectively living organisms (Botz-Bornstein, 2020, Henning and Scarfe, 2013). What mechanists fail to consider when causally explaining biological or biomedical phenomena from a reductionistic stance is what Daniel Nicholson calls the "*organismic context*" (2012, 159). As Nicholson elaborates, "mechanistic explanations specify

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[1] Felix Tretter (2019) contrasts organismal systems medicine, which he bases on Ludwig von Bertalanffy's organismal biology, to a molecular systems medicine in that the former takes into consideration the patient's developmental stage within an ecological and environmental context, which includes the molecular or omics data, while the latter considers only the molecular data.

only those features of the underlying causal networks that biologists deem *most relevant* for manipulating and controlling the phenomena whilst at the same time presupposing a great deal of the organismic context that makes them possible" (2012, 159, original emphasis). Moreover, mechanism represents a metaphor that, according to Lenny Moss, has "run out of steam" with respect to accounting for living processes (2012, 170), even though during most of the twentieth century, the mechanistic view of life eclipsed the organicist view (Nicholson and Gawne, 2015, Peterson, 2016).

What was problematic for twentieth-century advocates of organicism was an inability to develop the requisite technology and methodology to investigate living organisms as intact entities, and so organicism was eventually obscured by mechanistic biomedicine during the second half of the twentieth century. However, at the beginning of the twenty-first century organicism has had a revival, especially after the completion of the Human Genome Project (Botz-Bornstein, 2020, Nicholson, 2014). An important reason for its revival in the postgenomic era is the development of omics technology, which has permitted clinicians to gather substantial amounts of data on patients, to use these data to treat patients specifically as individuals, and finally to predict diseases to which patients are susceptible based on their omics data (Chen and Snyder, 2013, Loscalzo and Barabasi, 2011, Montévil, 2020).

According to contemporary organicists, a system's properties are independent of its isolated parts and the properties of those isolated parts. For example, Gagliasso contends that for a living organism

> the particular properties are given by the relationships between the parts and the characteristics considered as defining of any living entity (an organ, an organism, an organic and environmental system) and are determined by all the relationships that interconnect the diverse entities and that transform both the entities and the relations. (2003, 344)

As a concept, organicism envisions just a single whole of which all other levels within that whole are interrelated or integrated parts, but the properties of the whole are independent of the parts' properties. For example, Morton Beckner advocates a form of organicism in which "higher level processes…are autonomous with respect to lower levels" (1974, 171). And according to Robert Wilson (2005), the world of organisms is well structured and sufficiently complex to defy reductionistic mechanism.

Contemporary organicism, then, is a relational concept and depends on the organized interactions of the parts that make up the organic whole (Beckner, 2006, Elsassar, 1998). Further, an organism's composition is not necessarily what determines it; rather, an organism depends upon the organization or structure of its components (Brooks, et al., 2021). For the organism's structure is critical for promoting and regulating specific interactions of the components. As Michel Morange observes, the organism's ontological complexities "lay not in the nature of the macromolecular components, but in the way these components associate and interact to generate complex [and ontological distinct] structures and functions" (2006, 357). And Ernst Mayr makes a similar observation:

> The basis for organicism is the fact that living beings have organization. They are not just piles of characters or molecules, because their function depends entirely on their organization, their mutual interrelations, interactions, and interdependencies (1998, 19).

For contemporary organicism, the structure-function relationship—not just its resultant material composition—is what defines the organism. In other words, life can be made of various materials as long as it reflects living processes that are governed by specific principles and rules.[2]

While mechanistic biomedicine is founded on the central dogma of molecular biology and the principles and rules that regulate information flow from genotype to phenotype, organismal systems medicine is founded on the central dogma of systems biology, i.e., "it is system dynamics and organizing principles of complex biological phenomena that give rise to the functioning and function of cells" (Wolkenhauer and Mesarović, 2005, 14). The information flow within organismal systems medicine includes not just the flow dictated by the central dogma of molecular biology but also the flow of information among dynamic modular processes involved in a patient's pathophysiology. In other words, just as genetic information within cells follows particular pathways, so organismic information within biological systems follows certain dynamical pathways. For example, carcinogenesis involves not just the central dogma of molecular biology in terms of information flow between genes and proteins but also the organizational information of the chromosomes in which those genes are located, which includes, for example, epigenetic information (Marcum, 2019).

Just as mechanistic biomedicine's goal is to work out the principles and rules that govern the flow of genetic information within cells, so organismal systems medicine's goal is to work out the general principles and rules that govern information flow within organisms. Mihajlo Mesarović and colleagues, for instance, demarcate between controlling and coordinating principles for organic organization and function (Mesarović, et al., 2004). Controlling principles govern

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[2] Unfortunately, what constitutes the fundamental properties or processes of life or what is life is a highly contested issue (Weber, 2018). Although this might appear problematic for organismal systems medicine, such medicine provides the means for identifying not just the fundamental processes but more importantly the principles and rules by which these processes are regulated.

an organism's fixed behavior, while coordinating principles govern its flexible behavior. Moreover, Ana Soto and Carlos Sonnenschein (2018) identify three principles that center around an organism's agency. The first principle of proliferation involves the rules that regulate organismal growth and reproduction, while the next principle pertains to the rules governing variation within organisms. The final principle includes the rules that are responsible for an organism's organization and function.

Sara Green and colleagues also explore the general characteristics of organismic principles (Green and Wolkenhauer 2013, Green 2015, Green et al. 2018). Their principles are divided into four categories. The first is composed of organizing principles, including the principle of control and adaptation of dynamical systems, the principle of feedback control, the principle of closure to efficient causation, and the coordination principles like bounded autonomy of levels. Design principles composed the next category, including the principle of network motifs, the principle of modularity, the principle of bi-stable switching, and the principle of robustness, along with design principles involved in evolutionary change. The third category includes optimality principles, such as the branching angle principle (as in vasculogenesis) and the demand principle for gene regulation. The last category contains isomorphic principles, which pertain to open systems principles, exponential growth and decay principles, and the principle of allometric scaling relations. And as Green summarizes, these principles represent a need "to understand what generic features characterize pattern-producing systems in biology and beyond, and why we should expect particular organizational patterns in evolution" (2015, p. 649).

Finally, Bernd Rosslenbroich (2016) incorporates organismal biology into medicine in terms of five principles, especially to define the nature of health.[3] The first principle is that the patient qua organism is organized on different systems levels, while the next two principles are closely related to one another in that each system level is regulated by rules specific for that level and that the various levels are interdependent with respect to causation. The final two principles pertain first to organismic autonomy, i.e., the patient *qua* organism is self-regulatory, robust, independent, and flexible, and secondly to phenotypic plasticity, i.e., changes are in response to perturbations to the patient *qua* system. "Health," as Rosslenbroich concludes, "can be described in medicine and psychology as the

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[3] These principles owe their inspiration to Denis Noble's ten principles of systems biology (Nobel 2006), which both Soto and Sonnenschein (2018) and Tretter (2019) also use to ground their organismal systems medicine.

capacity for dynamically balanced systems autonomy" (2016, 10). And its such health that is one of organismal systems medicine's chief goals rather than simply treating or even preventing disease.

3.2 Holism

Although reductionism is a popular concept among biomedical scientists and clinicians, it has its limits and critics (Brigandt and Love, 2017, Kaiser, 2015); and various holistic concepts have been espoused to replace it (Verschuuren, 2017, Wolfe, 2012). Contemporary versions of holism are explicated in naturalist or physicalist terms and not in a reductionist sense since the parts of the whole are necessary but not sufficient for constituting or determining the whole; and agency, i.e., the capacity to bring about change, is embedded or entangled within the material or matter itself qua whole (Chong and Ray, 2002, Placek, 2004, Woods, 2017). What constitutes holism is unpacked in the remainder of this section by initially defining holism and then by examining it with respect to its metaphysical, methodological, epistemological, and ontological dimensions (Esfeld, 2009). The sequence of these dimensions is important in that holism functions metaphysically by which methodological questions concerning natural phenomena are addressed experimentally and theoretically. Through this process the whole is understood and explained epistemically, and its ontological nature is categorized in terms of integrated levels. Finally, from an organismal systems medicine perspective, the nature of the patient, especially with respect to personal health, is discussed throughout the section in contrast to the biomedical model's reductionist approach.

Holism relies on the notion of wholeness, which entails an irreducible and a dynamical totality that is complete and undivided (Piechocinska, 2004). The main idea behind holism is that the investigation and explanation of natural phenomena or systems and their properties only with respect to their component parts and properties are deficient and incomplete; rather, the whole must be investigated and explained on its own terms. In other words, "the whole is fundamental, not any one [part]" (Jones, 2000, 337). As Denis Noble (2006) claims, no one part is privileged causally. In short, the whole and its properties are greater than the sum of its parts and their properties (McDaniel, 2010). Although the component parts that constitute natural phenomena do provide the basis from which phenomena at higher levels materialize or emerge (Findlay and Thagard, 2012), the component parts do not entirely cause or account for the whole (Boogerd, et al., 2007). Consequently, natural phenomena at lower levels must be investigated and explained with respect to phenomena at higher levels, since phenomena at higher levels regulate or control phenomena at the lower levels.

Philosophically, holism has important metaphysical, methodological, epistemological, and ontological implications for organismal systems medicine. Metaphysically, patients in terms of wholeness are viewed and understood with respect to their totality as holistic agents. To investigate their totality at higher-levels requires a methodology that does not simply reduce or fragment them into isolated component parts, as in the case for reductionist biomedicine, but maintains the integrity of the whole. Epistemically, holism implies that patients as higher-level phenomena are to be understood in terms appropriate for that level and not just in terms for explaining lower-level phenomena. Finally, patients qua higher-level or whole phenomena are ontologically distinct from their lower-level parts. In other words, as higher-level entities they are not just composites of lower-level parts; rather, they are entities in their own right, with their own unique properties. In sum, holism pertains to the integral structure of the material components that make up patients as natural entities and agents; and, consequently, methods and technology must be employed to investigate them with respect to their ontological integrity. However, the observations and results obtained from these investigations must be used to formulate and confirm explanations of complex, higher-level phenomena like health and disease and what they are ontologically.

Conceptually, then, holism is crucial for moving from a mechanistic approach and understanding of patients to an organismal approach and understanding (Sturmberg, 2016, Vogt, et al., 2016). Through holism, the integrity of the patient's personal health from an organismal systems medicine perspective depends on the robustness and interaction of the biological, psychological, social, and environmental factors, composing it. In contrast, reductionistic biomedicine suffers from a myopic and fragmented view of the patient qua machine. And such a view can often result in medical errors, especially in terms of making the wrong diagnosis and then prescribing the wrong medication, that can either harm or even kill the patient (Levins, 2014). Indeed, reductionism can even blind the clinician to obvious clinical facts and prevent an accurate diagnosis. Finally, holism undergirds the healthcare profession by promoting healing as a return to an integral whole or as close to achieving wholeness as possible or even creating a new wholeness. For wholeness denotes a sense of soundness in the body as good health or wellbeing.

3.3 Examples of Organismal Systems Medicine

Both hemostasis and carcinogenesis provide excellent examples for exploring the potential of organismal systems medicine to address the problems arising from mechanistic biomedicine's failure to treat effectively or to cure various pathological conditions and diseases. For blood coagulation, systems theory is used to model clot formation or thrombosis and clot dissolution or fibrinolysis in a test tube or under *in vitro* conditions (Diamond, 2016). Such modeling depends on "bottom-up systems biology" in which blood clotting factors and their rates of interactions are computed to determine clot formation or dissolution (Diamond, 2013). Such models also include the participation of blood cells such as platelets and fluid dynamics, especially under *in vivo* conditions (Chen, et al., 2014, Colace, et al., 2013). However, blood coagulation remains hard to predict "due to nonlinearity, sensitivity to initial conditions, network complexity, feedback regulation, and biorheological/transport influence" (Diamond, 2013, 224). In other words, the future of blood coagulation vis-à-vis organismal systems medicine will require a top-down systems biology in which the integrity of the organism is maintained as clotting parameters are varied. For example, the role of heparan sulfate proteoglycans in the non-thrombogenic properties of the vascular endothelium was determined using a systems biology approach (Marcum and Rosenberg, 1987). However, the question remains as to how this system interacts with other regulatory mechanisms of blood coagulation such as protein C and thrombomodulin (Weiler and Isermann, 2003). Finally, systems medicine is currently being employed to treat, especially with respect to personalized or precision medicine, clotting disorders. For example, studies have been conducted to simulate the impact of low-molecular weight heparin on coagulation pathologies, especially in terms of a patient's blood clotting profile (Pisaryuk, et al., 2022).

For carcinogenesis, Hanahan and Weinberg's original six hallmarks of cancer are expanded and repositioned within a systems biology approach to carcinogenesis, both in terms of basic research and clinical practice (Bertolaso, 2016, Bizzarri et al., 2008, Fouad and Aanei, 2017, Malaterre, 2007, Paul, 2020, Plutynski, 2018). In reflecting on their 2000 article in which they introduced the hallmarks, Hanahan and Weinberg (2011) acknowledge two more hallmarks consisting of reprogramming the cell's energy metabolism and the tumor's evasion of an immune response, as well as the tumor's microenvironment, in tumorigenesis. However, they still advocate a strictly somatic mutation theory for carcinogenesis. In response to Hanahan and Weinberg's original somatic mutation theory, Carlos Sonnenschein and Ana Soto (2000) proposed a tissue organization field theory of carcinogenesis. The theory claims that the default state of normal cells is not quiescence but rather proliferation and that tumorigenesis is the result of changes in the structural organization of the tissue such that cellular proliferation is no longer regulated adequately. Recently, Soto and Sonnenschein (2021) have turned to organicism to advance their theory. Specifically, they argue that besides the bottom-up causation exhibited by mutated genes responsible for many of the hallmarks of cancer, top-down causation, especially in terms of the structural organization of the tissue, is also critical. In support of their theory, they cite studies in which malignant cells when exposed to a normal tissue organization do not express their malignant phenotype. Soto and Sonnenschein conclude that carcinogenesis needs to be situated with respect to the intact organism and not simply reduced to mutated genes.

Finally, an organismal systems medicine can also be used to combine both hemostasis and carcinogenesis, not only with respect to basic research but also in terms of treating of patients clinically (Buller, et al., 2007, Goubran, et al., 2012, Sharma, et al., 2019, Wang, et al., 2018). Experimentally, for example, "data from basic research indicate that the hemostatic components and the cancer biology are interconnected in multiple ways. Notably, while cancer cells are able to activate the coagulation system, the hemostatic factors play a role in tumor progression" (Falanga, et al., 2013, 223). In terms of the activation of thrombosis, many cancer patients exhibit hypercoagulable states that involve increased levels of clotting factors such as tissue factor or factor VII and suffer from both arterial and venous thrombi (Khorana, 2012, Zwicker, et al., 2007). As for tumor progression, again, clotting factors such as tissue factor are correlated with reshaping the tumor's microenvironment, especially in terms of promoting metastasis (Falanga and Marchetti, 2018, Lima and Monteiro, 2013). Moreover, blood coagulation plays an important role in terms of tumor progression and growth with respect to promoting angiogenesis (Nash, et al., 2001, Tsopanoglou and Maragoudakis, 2004). In sum, organismal systems medicine provides a means and an approach for integrating the various specialties in medicine, as exemplified with hemostasis and carcinogenesis, in order to maintain the patient's integrity and to treat the patient efficaciously and safely.

4. Conclusion

The main conceptual foundation for organismal systems medicine, then, consists of organicism and holism. Organicism, indeed, captures the patient's organic vitality and agency, especially as the biological, psychological, social, and environmental components entangle to give rise to personal health or disease; and it expresses the necessary agency to participate actively in requisite treatment, as well as to promote a healthful lifestyle. In contrast, biomedicine's concept of mechanism can at times imprison and dehumanize the patient as a machine, which when broken is simply fixed by repairing the broken part or by replacing it. The patient's materiality or physicality is often simply passive. Although mechanistic biomedicine can identify important components that constitute the patient, especially as exemplified by hemostasis and carcinogenesis discussed above, organismal systems medicine provides the principles and rules concerning not simply *how* the components interact but also *what*, as Dupré (2020) insists, to expect from those interactions. The interaction of thrombosis and tumorigenesis certainly illustrates the importance of maintaining a system's integrity, particularly in organismal terms. In other words, multimorbidity is an important issue in treating patients given the complexity of many pathophysiological processes (Sturmberg, et al., 2017), as illustrated with hemostasis and carcinogenesis.

Finally, some advocates for a systems approach to the biomedical sciences argue for a paradigm that combines or integrates both reductionism and holism (Latterich, 2005, O'Malley and Dupré, 2005, Woods, 2017). According to Francisco Ayala, for example, the majority of these advocates "agree that the study of problems at a given level of complexity of the living world must proceed by exploring lower as well as higher levels of organization" (1974, ix). In other words, both reductionism and holism represent opposite poles on a continuum in which possible intermediate positions are available between "microscopic 'nothing but' statements" and "macroscopic 'all or nothing' statements" (Boogerd, et al., 2007, 12). And these advocates claim that such intermediate positions provide a comprehensive picture of the natural world. "In order to understand Nature," writes Peter Schuster, "we can neither dispense from the reductionist's program and its results nor can we totally abolish the holistic view" (2007, 12). Moreover, for other advocates of systems medicine, both reductionism and holism are critical concepts for practicing clinical medicine (Berlin, et al., 2017, Federoff and Gostin, 2009). This approach is pluralistic and opportunistic in its nature and takes its cue from the problem at hand. "The consensus view," suggest Marc Van Regenmortel and David Hull, "leads to pluralism: both reductionist methods and a more holistic approach to biological complexity are required, depending on the questions being asked" (2002, 13). But the questions being asked currently in twenty-first century medicine, especially in terms of big-data and discovery science, are outstripping the reductionist approach of mechanistic biomedicine and calling for a holistic approach of organismal systems medicine.

In conclusion, although the proposed organismal systems medicine does appear to rely on integrating its conceptual foundation of organicism with biomedicine's mechanistic approach, still its approach is strictly organismal in the sense that the patient has agency inherent within its embodied and entangled state, especially with respect to participating in the healing process. Certainly, biomedicine's mechanistic approach, with its associated reductionism, is important for a robust organismal systems medicine at the current time, still the concept of organicism drives the conceptual framework for twenty-first century organismal systems medicine. In other words, mechanistic biomedicine with its associated reductionism has provided several of the entities and activities involved in various physiological and pathological processes; but as the examples from hemostasis and carcinogenesis illustrate, organismal integrity is vital for identifying the principles and rules by which those entities and activities are involved in health and disease. Indeed, the power and potential of organismal systems medicine should eclipse the mechanistic biomedicine as the twenty-first century continues to unfold.

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La construcción de un mundo: la importancia del juego en la evolución

The Construction of a World: The Importance of Play in Evolution

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Resumen

Comprender que los organismos multicelulares no son entes pasivos es esencial, por una parte, para ampliar nuestro entendimiento sobre la evolución de las especies y, por otra, para esclarecer cómo percibimos e interactuamos en el mundo. Lo anterior se debe a que, a través de múltiples procesos y mecanismos ontogenéticos y filogenéticos, los organismos navegan activamente el ambiente en el que están inmersos. Sin embargo, a pesar del énfasis que actualmente se ha puesto en esta visión académica, una conducta que ha recibido poca atención en este debate, en el caso de los homínidos y particularmente en *Homo sapiens*, es el *juego*. En este trabajo contribuimos a dilucidar la importancia del juego en el proceso de construcción de nicho y la emergencia de la cognición, dos áreas fundamentales para la discusión contemporánea del pensamiento evolucionista y de las ciencias cognitivas corporizadas. Sostenemos que esta tarea es relevante debido a que el juego es un camino a través del cual diferentes organismos multicelulares pertenecientes a un enorme número de especies indagan, conocen, construyen y transforman el mundo. En la primera sección, situamos la discusión y puntualizamos la estructura de nuestros argumentos. Enseguida, exponemos la importancia de la teoría de construcción de nicho, y las definiciones de nicho cultural y nicho ontogenético. Lo anterior subraya el rol activo de los organismos en la modificación de los ambientes (selectivos y ontogenéticos). Luego, explicamos los principales supuestos del enactivismo y sus implicaciones para comprender las propiedades dinámicas, corporizadas y situadas de los organismos en el estudio de la cognición. Después esclarecemos el rol del juego para robustecer el análisis de este vasto entramado de conceptos evolutivos y enactivistas. Finalmente, presentamos conclusiones sobre las implicaciones que este tipo de investigaciones pueden tener para diferentes campos del conocimiento —p. ej., la antropología biológica, las ciencias cognitivas, la filosofía de la biología o la pedagogía—.

Palabras clave: construcción de nicho; nicho ontogenético; enactivismo; herencia inclusiva; organismo.

Abstract

Multicellular organisms are not passive entities. Understanding this is important to increase our knowledge about the evolution of species, and to clarify how we perceive and interact in the world. Through multiple mechanisms and processes involving developmental as well as phylogenetic dimensions, these organisms actively navigate their environments. Despite current academic interest in these viewpoints, though, play has not been a central topic in this discussion, particularly in hominids and specifically in *Homo sapiens*. In this work, we contribute to elucidate the importance of play for niche construction processes and for the emergence of cognition, two fundamental fields within contemporary debates in evolutionary thinking and embodied cognitive science. We claim this is relevant because play is a path through which a very large number of multicellular species inquire, know, build, and transform the world. In the first section, we situate the discussion, and we describe the structure of our arguments. Then, we present the importance of niche construction theory, and the definitions of cultural and developmental niches, to highlight the active role of organisms in modifying (selective and ontogenetic) environments. Later we explain the enactivist perspective and its implications concerning the dynamics, and the embodied and situated properties of organisms for the study of cognition. Afterward we highlight the value of play in this wideview of evolutionary and enactivist frameworks. Finally, we offer conclusions on the implications that this kind of research could have for diverse disciplines —e. g., biological anthropology, cognitive science, philosophy of biology or pedagogy.

Keywords: niche construction; developmental niche; enactivism; inclusive inheritance; organism.

1. Introducción

> *No dejamos de jugar porque envejecemos; envejecemos porque dejamos de jugar.*
>
> Patrick Bateson y Paul Martin

En la actualidad existe una amplia discusión en la que se ha enfatizado la importancia de incluir el concepto de *organismo* en las explicaciones provenientes, principalmente, del campo de las ciencias cognitivas corporizadas y de la filosofía de la biología (Thompson, 2007; Nicholson, 2014). Durante la segunda mitad del siglo pasado, en el auge de la Síntesis Evolutiva y el cognitivismo, esta noción teórica desapareció de la agenda científica y los diferentes *explanantia* estuvieron centrados en esclarecer los mecanismos implicados en el estudio de los genes, en la dinámica de poblaciones y en las computaciones llevadas a cabo por diversas áreas cerebrales. Sin embargo, especialistas provenientes de distintas áreas del conocimiento han considerado que esta forma de entender la interacción entre el ambiente y las variadas formas de vida es insuficiente —concretamente, porque los organismos no son entes que se adaptan o perciben los mundos pasivamente—. Para comprender las implicaciones que se siguen de esta idea, es necesario retomar los principales supuestos teóricos de dos programas de investigación que dentro de sus campos están replanteando la forma en que entendemos la evolución y la cognición. Por una parte, la Teoría de Construcción de Nicho (TCN) enfatiza el rol activo de las interacciones entre organismos y su entorno en la reconfiguración de los ambientes selectivos (Laland y Sterelny, 2006; Stotz, 2010; Laland y O'Brien, 2011) mientras que, por su parte, el enactivismo se enfoca en las propiedades dinámicas, corporizadas y situadas de los organismos en el estudio de la cognición (Thompson, 2007; Hutto y Myin, 2012; Varela, et al., 2016). Ambas visiones convergen en la importancia de investigar los elementos implicados en la ontogenia y la filogenia, para robustecer nuestra comprensión respecto al carácter dinámico de los organismos en sus ambientes. En este contexto, una conducta que no ha sido centralmente estudiada, particularmente en el caso de los seres humanos y los homínidos en general, es el *juego*.

Existen dos razones principales que justifican la necesidad de indagar sobre el juego, y sus consecuencias para robustecer nuestro entendimiento al respecto de la relación entre organismos y ambientes. En primer lugar, en esta actividad cada organismo individual está indagando, construyendo y transformando el mundo activamente. En segundo lugar, el juego es una característica prevalente en diferentes especies, y constituye un componente importante durante el proceso evolutivo. Además, esta actividad podría ser entendida como conducta y como comportamiento. Por una parte, es conducta dado que está presente en muchas ramas del árbol filogenético —por ejemplo, en los mamíferos y en las aves— y, posiblemente, ha funcionado para preparar a los organismos en el desarrollo de habilidades motoras para enfrentar diversas situaciones en las que podrían encontrarse en su vida (Di Paolo et al., 2010; Bateson y Martin, 2013). Por otra parte, es comportamiento, si lo consideramos como una característica observable en diferentes sociedades humanas, que tiene un componente cultural y simbólico, y que constituye parte fundamental del proceso de construcción del nicho cultural. En otras palabras, el juego en los seres humanos también refleja una forma de comprender y ordenar el mundo. Por ejemplo, en el México prehispánico muchas clases de juegos estaban vinculados con un contexto ritual o profético (López, 1967; Johansson, 2013).

A partir de lo anterior, se puede plantear que en estos dos ámbitos en los que podemos identificar al juego —conducta y comportamiento— intervienen procesos ontogenéticos, filogenéticos, sociales y culturales. No obstante, este fenómeno tan complejo ha desembocado en un desacuerdo entre los investigadores para delimitar su estatus epistémico y ontológico. En palabras de Bateson y Martin (2013, vii), "los diferentes significados que ha tenido el término juego han creado mucha confusión, y han contribuido a la visión de que el juego es enigmático y está más allá de los límites de la ciencia". Esta cita es un claro ejemplo que ilustra las diferentes problemáticas a las que se pueden enfrentar las comunidades de investigación cuando estudian diversos aspectos sobre el juego. Por lo anterior, se hace evidente la importancia de prestar más atención a este comportamiento ya que, a través de su análisis en los términos investigativos aquí propuestos, podríamos generar nuevas hipótesis que no han sido parte nuclear de trabajos académicos previos, y que podrían ayudar a responder la cuestión de cuál es la potencial importancia que el juego podría tener para comprender la evolución y la cognición humana.

El objetivo de este texto es contribuir a dilucidar la relevancia del juego en el proceso de construcción de nicho y la emergencia de la cognición, dos áreas de elaboración teórica fundamental para la discusión contemporánea en el pensamiento evolucionista y en las ciencias cognitivas. Las interacciones entre las herramientas conceptuales provenientes del campo de las así llamadas 'Síntesis Evolutiva Extendida' y 'Cognición 4E' son fundamentales para la elaboración de puentes interdisciplinares y la creación de oportunidades de colaboración entre especialistas de distintas áreas del conocimiento. Algunos esfuerzos recientes para consolidar estas conexiones han desembocado, por ejemplo, en debates internacionales acerca del lugar de las *affordances* en la evolución (Heras-Escribano, 2020), la relevancia de incluir la biología evolutiva del desarrollo (evo-devo) en la construcción de sistemas emocionales artificiales (Hernández-Ochoa y Vergara-Silva, 2022), o para comprender la profunda continuidad entre la vida y la mente defendida por los científicos y filósofos enactivistas (Corris, 2022). Entonces, en el contexto de las discusiones sobre las relaciones entre TCN y enactivismo, la aportación de este trabajo tiene dos vertientes. Por un lado, busca complementar las explicaciones previas sobre el juego que, en ocasiones, han estado sustetandas en mecanismos evolutivos como la depredación, el sexo o la agresión (veáse Pellis y Pellis, 2023); por el otro, intenta fortalecer exploraciones basadas en el enfoque enactivo (Di Paolo, 2010), así como otras investigaciones existentes que han estado dirigidas a perspectivas no relacionadas directamente con nuestros intereses (p. ej., los trabajos sobre *pretend play* de Rucińska y Reijmers, 2015; ver también Rucińska, 2017).

Si bien reconocemos que esta amplia exploración no puede ser agotada en este artículo, ofreceremos un conjunto de elementos para abrir el debate y regresar a lo que Humberto Maturana (1993) nombró "el camino desdeñado" en la evolución. Las ideas maturaneanas son relevantes, en este contexto, debido a que nos guían a incluir un conjunto de nociones teóricas que no han sido parte nuclear de las investigaciones evolucionistas-enactivistas en el estudio de la cognición. En lo que sigue, expondremos la importancia de la teoría de construcción de nicho, el nicho cultural y el nicho ontogenético. Lo anterior nos permite subrayar el rol activo de los organismos en la modificación de los ambientes selectivos. Luego explicamos los principales supuestos del enactivismo, y sus implicaciones para comprender las propiedades dinámicas, corporizadas y situadas de los organismos en el estudio de la cognición. Después esclarecemos el rol que puede tener el juego para robustecer la comprensión de este vasto entramado de conceptos evolucionistas y enactivistas. Finalmente, presentamos nuestras conclusiones acerca de las implicaciones que podrían seguirse de esta investigación para diferentes campos del conocimiento —p. ej., la antropología biológica, las ciencias cognitivas, la filosofía de la biología o la pedagogía—.

2. Una relación de causalidad recíproca entre organismo y ambiente. La construcción de nicho y la plasticidad ontogenética: sus relaciones y sus variantes

La Teoría de Construcción de Nicho (TCN) fue presentada de manera exhaustiva en el tratamiento monográfico de F. John Odling-Smee, Kevin Laland y Marcus W. Feldman (2003). Los antecedentes de esta propuesta son múltiples, pero entre ellos destacan, sin lugar a dudas, los trabajos de Conrad Hal Waddington (1959), Richard Lewontin (1983), Odling-Smee (1988) y Laland, Odling-Smee y Feldman (1996). Una de las características más importantes de esta corriente teórica es, justamente, la importancia que le atribuye al ambiente para explicar la adaptación de los organismos. En palabras de Laland, en un trabajo colaborativo con el filósofo de la ciencia, Kim Sterelny:

> La teoría de la construcción de nicho contrasta con las conceptualizaciones convencionales de la evolución. En los modelos estándar, haciendo a un lado complicaciones como la coevolución y la selección del hábitat, la adaptación es un proceso mediante el cual la selección natural forma a los

> organismos para que se ajusten a las “plantillas” ambientales preexistentes. La flecha causal apunta sólo en una dirección: determinar las características de las criaturas vivientes. (Laland y Sterelny, 2006, 2)

En la cita anterior se puede observar que los defensores de la TCN representan una postura antagónica ante la denominada ‘teoría estándar de la evolución’ (TSE; es decir, la ‘Síntesis Moderna’ o ´Teoría Sintética de la Evolución’).[1] Desde aquella perspectiva teórica, más antigua, los organismos se adaptan al entorno, sin embargo, el entorno no se reconoce como afectado por los organismos a través de alguna modificación causada por éstos. Para tal marco teórico evolucionista, la selección natural es el factor adaptativo por excelencia. En cambio, la TCN plantea que la construcción de nicho es un proceso que está a la par de la selección natural. En este caso, la flecha causal que conecta organismos y ambientes es bidireccional, lo cual implica que éstos se adaptan conjuntamente. La construcción de nicho puede ser entendida, entonces, como *el proceso mediante el cual los organismos, a través de sus actividades y elecciones, modifican su nicho y otros nichos* (Laland y O’Brien, 2011). Algunos ejemplos típicos que se usan para destacar la importancia de esta relación bidireccional entre organismos y ambientes hacen referencia a especies de hormigas constructoras de nidos, o bien a especies de castores que elaboran de presas. En los dos casos mencionados, existe una modificación que es guiada por los organismos e influye en diferentes aspectos del entorno —por ejemplo, en las propiedades del suelo o la distribución de agua, lo que repercute en la creación de diferentes nichos para las diversas especies que coexisten con ellos—. Es imprescindible subrayar que, una vez que los organismos modifican el ambiente, éste difícilmente regresará al estado previo a la alteración: los ambientes modificados se heredarán a la siguiente generación de animales. A esta noción se le conoce dentro de la TCN como *herencia ecológica*.

La construcción de nicho es relevante en el evolucionismo biológico contemporáneo, pero también en las aproximaciones antropológicas y cognitivas de hoy, porque “un nicho es la suma total de las maneras que tiene un organismo de ser en el mundo” (Fuentes, 2017, 17). Lo anterior involucra un conjunto clave de elementos que es necesario señalar y esclarecer para comprender el alcance explicativo del proceso de construcción de nicho, en general, de todos los organismos y, en particular, de los seres humanos. Fuentes (2017) ha sugerido que la interacción de cada organismo animal en el mundo está constreñida por los elementos físicos y biológicos con los que cada individuo interactúa en su ambiente. En efecto, un nicho es el lugar de un organismo en el mundo natural

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[1] El análisis detallado desde la filosofía de la biología acerca de la compleja relación existente entre los conceptos de ‘organismo’ y ‘ambiente’ en el evolucionismo de la Síntesis Moderna original y la TSE, con respecto al papel de esos dos importantes conceptos dentro de la TCN y de la así llamada ‘Síntesis Evolutiva Extendida’ (SEE) va más allá de los propósitos de este trabajo. Laland et al. (2015) constituye una excelente introducción a los debates correspondientes a dicho análisis.

(Laland y Uller, 2021), y en función del marco teórico ofrecido por la TCN es lógico afirmar que dicho lugar se ha construido activamente a través de diferentes mecanismos y procesos que están inmersos en la ontogenia de todos los seres vivos. Particularmente para los seres humanos, la *construcción de nicho cultural* y las diferentes maneras en que se despliega la herencia, han tenido un lugar central en la forma en que interactuamos y comprendemos el mundo. Ahondaremos a continuación en ello.

2.1 Nicho cultural, plasticidad fenotípica y sesgo ontogenético: un bucle de interacciones en la construcción de nicho

En los párrafos anteriores se puede notar que la importancia de la TCN es que los organismos no son sólo entes pasivos que se adaptan al ambiente, como lo proclama hoy la TSE, con base en el discurso canónico de la Síntesis Moderna. Los organismos tienen un rol activo, que es vital en su propio proceso adaptativo. Es en ese sentido que se habla de *relaciones de causalidad recíproca entre los organismos y el ambiente*. Sin embargo, en el caso de los mamíferos primates y, en particular, los seres humanos, además de los mecanismos esbozados con anterioridad, la cultura ha potencializado nuestra capacidad para construir nichos y también para modificar los ambientes selectivos (Laland, Odling-Smee y Feldman, 2001).

En este contexto, el 'factor cultural' se entiende como *los elementos de la herencia no-genética, los cuales suelen definirse como 'conocimiento' o 'cultura material' desde el punto de vista de las teorías antropológicas y de las ciencias sociales*. En palabras de Odling-Smee y Laland (2011, 226), puede denominarse "*construcción de nicho cultural* a ese subconjunto de construcción de nicho que es la expresión del conocimiento culturalmente aprendido y transmitido (en oposición a la información genética o aprendida individualmente)". Siguiendo esta línea, el estudio de la construcción de nicho humano se ha enfocado en tres dominios: genético, ontogenético y cultural. Estas tres dimensiones son de suma importancia para dilucidar cómo construimos nichos los seres humanos, debido a que existe una constante interacción entre ellas. A partir de estas ideas, podemos notar que hay una heterogeneidad subyacente en las diferentes vías de herencia —genética, epigenética, comportamental y simbólica— postuladas por la TCN, y así como por elaboraciones teóricas afines (ver, p. ej., Bonduriansky y Day, 2018; Jablonka y Lamb, 2007; Fuentes, 2016, 2017). Un contexto de interacciones y procesos que intentaremos vincular con estos elementos hereditarios que rebasan las fronteras somáticas es, precisamente, el caso del juego.

El dinamismo que entrelaza estos mecanismos de herencia es una característica importante del proceso de construcción de nicho y, en el caso de los homínidos, particularmente *Homo sapiens*, del proceso de construcción de nicho humano. Para Fuentes, "las culturas humanas son más que percepciones, creencias y comportamientos: también son reglas, organizaciones, etc., con estructuras concretas y consecuencias específicas. Los sistemas culturales están entrelazados con patrones de constricción y facilitación social, y esto es potencialmente una fuerza evolutiva" (Fuentes, 2016, 17). La reflexión de Fuentes (2016) es importante porque nos induce a pensar sobre las redes de interacción y retroalimentación, en las cuales están involucrados los mecanismos evolutivos que van desde el individuo al grupo social y la comunidad. En la Figura 1 es posible analizar gráficamente estos supuestos. Así podemos pensar en que, a partir de comportamientos innovadores, los grupos humanos adoptan artefactos (u otros elementos externos a lo estrictamente corporal) y posteriormente emergen un conjunto de normas, reglas y creencias asociadas con la validación de su uso en la comunidad. Eso suele ocurrir con muchas innovaciones que se van incorporando en los nichos a lo largo de la historia.

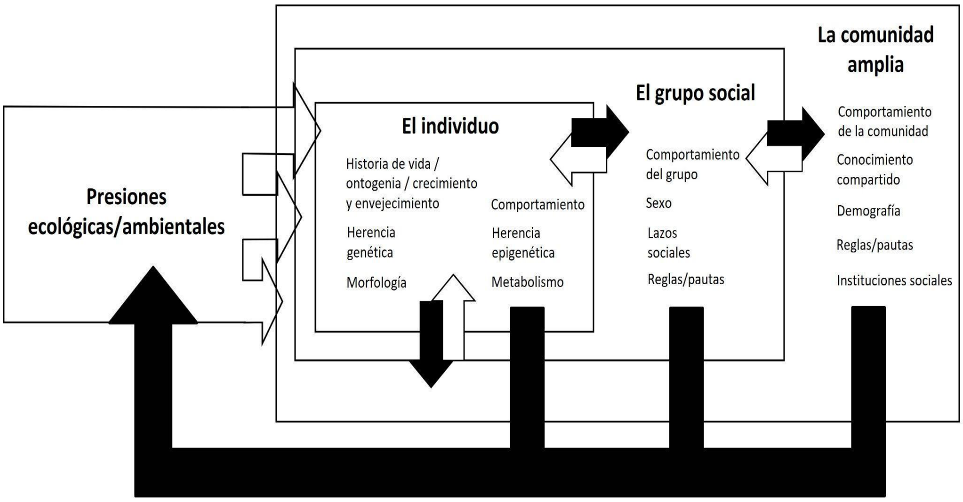

Figura 1. Redes de interacción y bucles de retroalimentación en la construcción del nicho humano. En la imagen se pueden observar las interacciones de los diferentes elementos situados e inmersos en el proceso de construcción de nicho humano. Por un lado, están las presiones selectivas procedentes del ambiente. Por otro lado, se encuentran el individuo (caracterizado por diversos rasgos involucrados en su conformación), el grupo social (que se refiere a la red central y más próxima al individuo), y la comunidad extendida (que indica "una colección de individuos/grupos con 'parentesco' e historias sociales y ecológicas compartidas"; Fuentes, 2016, 18), p. ej. una nación o un estado. Extraído y modificado de Prince-Buitenhuys et al. (2020).

Siguiendo esta línea argumentativa, es importante señalar la importancia de dos mecanismos evolutivos que posibilitan la interacción de los humanos con el mundo, y que han sido analizados en varios análisis derivados de la TCN, en su aplicación a los nichos humanos. En primer lugar, tenemos a la *plasticidad fenotípica,* que puede ser explicada como una propiedad inherente al proceso de desarrollo que contribuye e impulsa el cambio evolutivo (West-Eberhard, 2003; Laland, et al., 2015; Stearns, 2015; Stotz, 2017). En segundo término, está el *sesgo ontogenético* que, desde el punto de vista de la biología evolutiva, restringe las variantes fenotípicas que pueden ser expresadas en un organismo (Parsons et al., 2020).[2] Las condiciones o propiedades organísmicas caracterizadas por estas nociones teóricas son útiles para comprender por qué somos sensibles a ciertos estímulos ambientales y a otros no. Además, en el caso de los seres humanos, tales disposiciones del organismo están fuertemente ligadas a la cultura, pues ésta también constriñe las respuestas plásticas y sesgadas ante una situación. En otras palabras, los mecanismos de plasticidad y sesgo contribuyen a normar las maneras en que percibimos e interactuamos en el mundo. Investigar y reflexionar sobre esta cuestión es pertinente por su apoyo en el esclarecimiento de los elementos constitutivos del proceso biológico y cultural del cual es producto la cognición humana.

Con lo expuesto previamente, se hace notoria la relevancia de enfatizar que estas formas de actuar y ser en el mundo son parte de la *herencia inclusiva* en la que diversos grupos de nuestra especie están inmersos —es decir, diferentes configuraciones de herencia que coexisten e interactúan en la construcción de los nichos humanos correspondientes—. En la constitución de tales nichos humanos podemos observar un conjunto de elementos que son parte de nuestro legado, y que éstos se construyen y reconstruyen, por diversas vías, durante el desarrollo ontogenético humano. Asimismo, la incorporación de los mecanismos —relacionados con los diferentes canales de herencia— que están involucrados en la ontogenia humana posibilita una transformación profunda y radical de la comprensión que tiene la comunidad científica de las condiciones ecológicas en que ocurre la evolución en nuestra especie: “la similitud entre padres e hijos se produce no solo por la transmisión del ADN, sino porque los padres transfieren una variedad de recursos de desarrollo que permiten la reconstrucción de *nichos ontogenéticos*” (Laland et al., 2015, 4; cursivas añadidas). En lo que sigue, profundizaremos en las principales características del concepto de ‘nicho ontogenético’ y en sus relaciones con el marco TCN aplicado a los ámbitos de construcción de nichos humanos.

2.2 Añadiendo el nicho ontogenético al bucle

El concepto de *nicho ontogenético* fue defendido por West y King (1987) para señalar la importancia de la herencia ecológica y social. Esta propuesta resulta esencial para comprender cómo se desarrollan los sistemas cognitivos, principal-

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[2] Estos conceptos son muy importantes para el contexto evolutivo-enactivo. Por una parte, la plasticidad fenotípica es una característica de los seres vivos para responder a los cambios en sus entornos (West-Eberhard, 2003). Por ejemplo, los diferentes grupos humanos estamos adaptados a particularidades culturales, sociales, afectivas y ambientales. Por otra parte, el sesgo ontogenético es una propiedad que limita las respuestas plásticas (Stotz, 2017), p. ej., los simios no podemos interactuar a través del olor como lo hacen los perros, ni tampoco podemos percibir el aire como un ave.

mente, en los seres humanos. La razón de lo anterior es debido a que, si reflexionamos respecto a las implicaciones de tener y compartir una herencia inclusiva con los miembros de nuestra especie, nos encontramos con el cruce de diversas nociones extrasómaticas —una instancia de este cruce es el conjunto de creencias y costumbres que comparten los miembros de una sociedad humana, transmitidos y/o reconstruidos de generación en generación—[3].

Esta clase de herencia lleva consigo los saberes de la utilización de alguna herramienta o el uso de alguna palabra. Sin embargo, es esencial puntualizar algunas de las principales diferencias entre la clase de nicho que está involucrado en la noción estándar de la TCN —que es el nicho selectivo (NS)— y el nicho ontogenético (NO). Al inicio del apartado 1 explicamos, puntualmente, que una de las principales características de la TCN es el énfasis en considerar al ambiente selectivo como la fuente de la construcción de nicho; es por eso que se le comprende y define como un mecanismo evolutivo paralelo a la selección natural. Sin embargo, "mientras que la construcción de nicho selectivo (CNS) explica el rol activo del organismo en su entorno selectivo, la construcción de nicho ontogenético (CNO) indica el rol activo del organismo en su entorno de desarrollo" (Stotz, 2017, 2). Comprender lo anterior es muy importante debido a que, a través del dinamismo de la CNO y su relación con diferentes fuentes ambientales en las que está inmerso un organismo, se produce nueva variación que podría ser adaptativa. Además, tomar en cuenta la CNO permite analizar mejor la plasticidad fenotípica —la cual es entendida, en este contexto, como una propiedad inherente al proceso ontogenético de los organismos, que potencialmente optimiza la habilidad de éstos para adaptarse a su ambiente—.

Las etapas ontogenéticas en las cuales se desenvuelven los bebés humanos pueden ilustrar la importancia de la CNO. Como señaló Stotz (2017), a diferencia de otros primates, gran parte del desarrollo del cerebro humano se lleva a cabo en un período posnatal. Esto tiene como consecuencia que, para garantizar la supervivencia de los humanos en sus primeros años de vida, a través de la historia evolutiva de la especie humana los cuidados tuvieron que intensificarse y transmitirse a la siguiente generación con el propósito de garantizar la supervivencia de éstos. Por ejemplo, las prácticas occidentales que se tienen respecto al cuidado de los bebés: ponerlos en cierta posición para evitar que se ahoguen después de la ingesta de comida, guiar y supervisar su capacidad de locomoción bípeda, entre otros. Estos cuidados son parte del nicho ontogenético en el que los humanos estamos sumergidos. *El estudio de la CNO resalta que parte de la naturaleza humana proviene del entramado emergente en el contexto de desarrollo ontogenético*. Para la

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[3] Hablar de 'transmisión' y de 'construcción' en este contexto nos conduce directamente a contrastar las visiones tradicionalistas versus críticas contemporáneas sobre 'evolución cultural'. Nuevamente, esta importante discusión filosófica no puede ser abordada aquí con detalle; el tratamiento del filósofo de la ciencia Tim Lewens (2015) es altamente recomendable para introducir al lector a estos temas.

comprensión de la condición humana es vital, por lo tanto, ahondar en cómo se construye el nicho ontogenético. Y por supuesto, entender y enfatizar también que este proceso de interacciones inicia desde la formación del feto hasta los ritos de paso característicos de cada cultura (Fuentes y Wiessner, 2016). En la Figura 2 mostramos una aproximación que refleja el carácter dinámico de los elementos conceptuales trazados en este apartado.

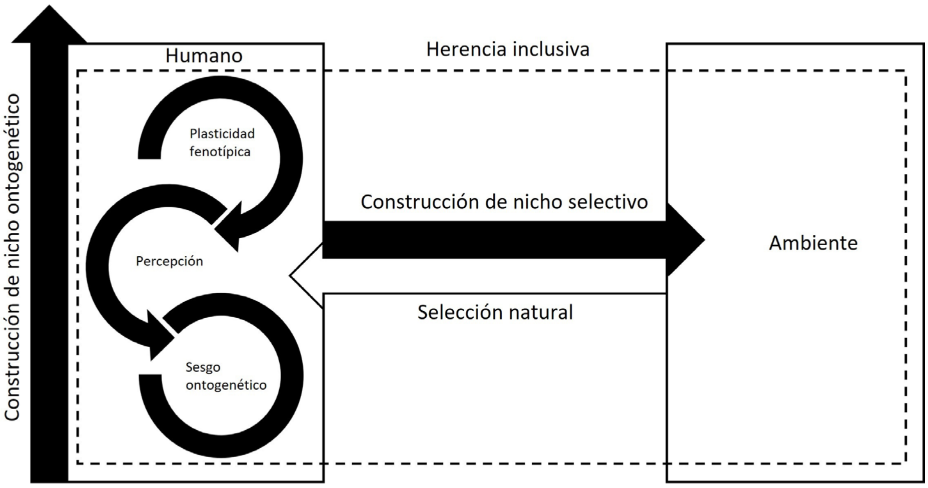

Figura 2. Entrelazamiento de los procesos involucrados en la construcción de nicho ontogenético. La flecha bidireccional en el centro indica la causalidad recíproca entre el organismo y su ambiente. Es sustancial observar cómo el sesgo ontogenético y la plasticidad fenotípica influyen en la manera en la que un organismo, en este caso un humano, percibe el mundo. Estos mecanismos serán permeados por los diferentes canales de herencia durante el proceso de construcción del nicho cultural. Además, siguiendo a Stotz (2017) es relevante destacar la direccionalidad del nicho selectivo (flecha negra horizontal) y del nicho ontogenético (flecha negra vertical).

El estudio del nicho ontogenético y los elementos involucrados en su conformación es esencial debido a que de esta manera podremos esclarecer “el origen de la variación fenotípica potencialmente adaptativa y heredable” (Stotz, 2017, 2). Por lo anterior, podemos corroborar la gran importancia que tiene comprender las diversas fuentes con las que interactúa un organismo a lo largo de su vida, ya que éstas permearán su forma de ser y estar en el mundo. Con el objetivo de analizar desde otra teoría la importancia de este último enunciado, en el siguiente apartado expondremos las características centrales del enactivismo y sus implicaciones para entender la cognición. Este ejercicio nos llevará a comprender el juego desde un quiasma entre ellas (ver Sección 4).

3. Generando sentidos en el mundo: el enactivismo y la emergencia de la cognición

El enactivismo es un programa de investigación antagónico al pensamiento ortodoxo en ciencias cognitivas. Esto quiere decir que, para los investigadores suscritos a éste, no es necesario postular el uso y manipulación de representaciones para explicar las bases de la cognición, algo defendido por el cognitivismo. En otras palabras, "el enactivismo se inspira en la idea de que la actividad situada y corporizada de los seres vivos proporciona el modelo correcto para entender las mentes" (Hutto y Myin, 2012, 4). Para dichos autores, y otros que han trabajado dentro de la misma tradición, es necesario explicar la historia de acoplamiento e interacción entre los organismos y sus ambientes. Lo anterior se debe a que de esta forma podremos estudiar los aspectos fenomenológicos y biológicos:

> Sostenemos, con Merleau-Ponty, que la cultura científica occidental requiere que veamos nuestros cuerpos no sólo como estructuras físicas sino como estructuras vividas y experienciales, es decir como "externos" e "internos", como biológicos y fenomenológicos. Es obvio que ambos aspectos de la corporalidad no se oponen, sino que, por el contrario, circulamos continuamente de un aspecto al otro. (Varela, Thompson y Rosch, 2016, 62)

Al igual que Merleau-Ponty, Francisco Varela y colaboradores conceptualizan el cuerpo humano en dos dimensiones. Por un lado, la experiencia corporizada es esencial para otorgarle sentido y significado al mundo que nos rodea; a través de la experiencia vivida, el cuerpo establece una relación directa y significativa con los objetos, colores y formas que percibimos. Por otro lado, es el organismo biológico el que facilita y constriñe las experiencias de un cuerpo con su medio ambiente. Entonces, para el enfoque enactivo, la cognición en su sentido más amplio se convierte en la historia corporal de la cual emerge un mundo a partir de las interacciones con el entorno. En otras palabras, "lo endógeno y lo exógeno se definen mutuamente a lo largo de una cronología prolongada" (Houdé et al., 2003, 102). En este apartado explicaremos cuál ha sido una de sus principales vertientes y sus implicaciones en el estudio de la cognición: a saber, el *enactivismo sensoriomotor*.

3.1 Enactivismo sensoriomotor

Los defensores del enactivismo sensoriomotor sostienen que la percepción, la acción y la experiencia perceptual están conectadas inexorablemente (Noë, 2004; Hutto y Myin, 2012). Esto es muy importante, entre otras razones, por el contraste con la forma tradicional de entender la percepción; esta última ha sido explicada como la capacidad de los organismos para extraer datos del entorno, procesarlos y, posteriormente, responder a ellos. Por ejemplo, al respecto de la percepción espacial:

> Percibir una característica determinada de la disposición espacial, como el tamaño de un objeto, puede ser útil en una amplia gama de actividades. Por lo anterior, se ha defendido que esta percepción se produce de forma algo independiente de la actividad particular del momento. Por lo tanto, se puede pensar que una roca en un campo tiene un tamaño percibido particular que es más o menos *independiente* de si uno se va a sentar o saltar sobre ella. (Sedgwink, 2005, 129; cursivas añadidas)

A partir de esta cita podemos extraer, por una parte, que el propósito de la percepción espacial es proporcionar información sobre *qué* es lo que está en el espacio y, por otra parte, *dónde* se encuentra para ejecutar una acción sobre el mundo (Kandel et al., 2013). Además, resalta la división entre lo interno (el acto de percibir la roca) y lo externo (ejecutar una acción sobre ella). En otras palabras, es notoria la dicotomía entre lo que hay en el mundo y las acciones que un organismo puede ejecutar sobre él. Aunque es verdad que los órganos sensoriales son necesarios para detectar cierta clase de estímulos, no son suficientes para explicar nuestra experiencia perceptual y la cognición; hay más elementos involucrados. Es decir, ¿podemos percibir una piedra exclusivamente con una modalidad sensorial?

Para los enactivistas, el acto de percibir es un proceso de interacción en el cual el organismo navega y actúa en un ambiente (Hutto, 2005). En otras palabras, a través de este ejercicio de movilidad generamos la fuente de *hacer sentido* en el mundo (Sheets-Johnstone, 2011). Esto ocurre debido principalmente a las actividades recurrentes, realizadas a través de la historia evolutiva, entre los organismos y sus ambientes relacionadas con su autoproducción y supervivencia (Di Paolo, 2005), y a los procesos sensoriomotores inmersos en la ontogenia. Pensar de esta manera la interacción de los organismos en el mundo ha llamado la atención y ha influido en otras áreas importantes de las ciencias cognitivas. Por ejemplo, Brooks (1990) resaltó la importancia de analizar, en términos evolutivos, la capacidad de los organismos para moverse en un entorno dinámico, sobrevivir y reproducirse. Según este autor, comprender las características ecológicas del movimiento será clave para dilucidar cómo percibimos y conocemos el mundo. Por lo tanto, siguiendo lo anterior, es importante centrar las investigaciones en el entendimiento de cómo surgió este *saber hacer* que compartimos con todos los miembros del árbol de la vida. Los murciélagos saben desplazarse por medio de la ecolocalización (Dawson, 2014); las arañas saben tejer sofisticadas telarañas (Japyassú y Laland, 2017); los humanos sabemos utilizar nuestras extremidades para realizar diversas actividades como braquiar, desplazarnos bípedamente o jugar de una forma particular. Según los enactivistas, la habilidad de percibir e interactuar en el mundo está constitutivamente anclada al conocimiento sensoriomotor. ¿Qué pasaría si un organismo no tuviera un conjunto de fenotipos típicos de su especie?

Otro ejemplo que nos lleva a reflexionar sobre la importancia de la experiencia sensoriomotora lo podemos encontrar en el trabajo de Wood y Stuart (2009). En ese artículo se ofreció una propuesta para explicar los fantasmas aplásicos, a través del 'sistema espejo' y la enacción. Las aplasias son una condición somática que presentan personas que tuvieron un desarrollo atípico y éste, en algunas ocasiones, se puede observar debido a la ausencia de alguna extremidad o una parte de ella (mano, brazo, pie o pierna). Los fantasmas aplásicos son experiencias de la extremidad ausente, sin importar que nunca haya estado presente durante la historia de experiencia corporal de los sujetos. Estos casos son muy interesantes debido a que nos invitan a plantearnos diversas interrogantes: ¿cuáles son los mecanismos (biológicos y culturales) inmersos para que una persona pueda experimentar una experiencia fantasma aplásica? ¿Cuál es la importancia de la corporización para nuestros procesos cognitivos? Si bien las conclusiones de aquel trabajo pusieron en evidencia los componentes cerebrales vinculados con el reconocimiento de la acción de nuestros congéneres, otra de sus aportaciones fue reconocer la importancia del componente social para explicar el por qué en algunas de las personas aplásicas aparecen estos fantasmas. Según estas investigadoras, el mundo es experimentado por los individuos en términos de las posibilidades de acción que un organismo tiene en su medio ambiente, y estos fantasmas se manifiestan entre el desacoplamiento de su condición somática y la forma en la que los miembros de nuestra especie actúan (Wood y Stuart, 2009). En otras palabras, las autoras apuntaron que, a pesar de tener una condición aplásica, sujetos en tales condiciones aprehenden y aprenden formas de actuar y de ser en el mundo a través de la historia de la corporización con sus congéneres. Por lo tanto, se puede observar que, para los partidarios del enactivismo sensoriomotor, es necesario comprender que, a través de la acción y el movimiento, se genera nuestro hacer sentido y la emergencia de un conocimiento del mundo (Sheets-Johnstone, 2011); es decir, *enactuamos*. Esta organización enactiva se puede plantear —según Di Paolo et al. (2017)— en distintos niveles de emergencia, que van desde un nivel básico que los permite distinguirse como células (Thompson, 2007), hasta niveles de interacción sociocultural (De Jaegher y Di Paolo, 2007).

El biólogo teórico Humberto Maturana, en coautoría con Varela en un trabajo de 1994, ya argumentaban que podemos analizar y dividir sus conocidos 'sistemas autopoiéticos' en tres categorías u 'órdenes': el primero correspondería a las células; el segundo orden señalaría a un organismo, debido a que es un conjunto de agregados celulares, y el tercer orden referiría al conjunto de organismos —por ejemplo, colonias de hormigas, colmenas o incluso un sistema social—. En el caso de los seres humanos, esta idea es relevante porque nos guía a analizar la emergencia de los aspectos sociales y culturales a través del proceso de corporización. Su importancia radica en entender que los organismos tienen un proceso ontogenético que implica un cambio dinámico a lo largo de su vida. Además, estos cambios están inmersos en un tiempo y un espacio que determinarán las formas de ser, percibir e interactuar en el mundo. Lo anterior nos invita a plantearnos la génesis de este ‘saber hacer’, que emerge en conjunto con este bajo nivel de individualidad que le da sentido al mundo debido al acoplamiento y a la mutualidad intrínseca del sistema organismo-ambiente.

Siguiendo la línea de Thompson (2007), podemos advertir que las propuestas de este enactivismo sensoriomotor tienen tres características principales. En primer lugar, para esta perspectiva corporizada con una fuerte orientación al interaccionismo, el sistema nervioso es un sistema dinámico autónomo. Además, no procesa información en el sentido computacionalista, sino que busca y crea significados en la acción. Con el caso de las personas aplásicas se evidenciaron algunos de los principales elementos —por ejemplo, la intersubjetividad— implicados en este ejercicio. En segundo lugar, para esta clase de enactivistas, la cognición es un ‘saber hacer’ que está inmerso en una dimensión situada y corporizada —es decir, los animales estamos acoplados a nuestros ambientes debido a una relación de mutualidad—. En tercer lugar, se postula que el mundo no está ‘dado de antemano’, sino que se enactúa a través de un dominio relacional. En otras palabras, para esta orientación de las ciencias cognitivas contemporáneas, la cognición es la historia de acoplamiento estructural que enactúa un mundo que emerge a través de un conjunto de elementos interconectados (Varela, 1990). Por lo anterior, *es posible evidenciar algunos paralelismos epistémicos importantes que fueron trazados en la sección anterior, donde tratamos la mutualidad organismo-ambiente en la TCN, en tanto perspectiva contemporánea en el evolucionismo*. A su modo y desde las tradiciones investigativas que sustentan su trabajo, los enactivistas indagan en esa interacción y cómo ésta emerge en cada nicho ontogenético.

4. Evolución, cognición y juego

Con las ideas expuestas en las secciones anteriores, hemos enfatizado la importancia del carácter dinámico de los organismos que posibilita modificar los ambientes selectivos y, además, construir y reconstruir formas de ser y estar en el mundo. También hemos visto que reflexionar sobre este punto y su impacto para comprender la evolución y la cognición ha sido una tarea central para las comunidades científicas relevantes. Sin embargo, a pesar de esto, una de las conductas que ha recibido poca atención en este contexto es, precisamente, el juego. En la introducción de este trabajo, expusimos que una de las razones por las que consideramos relevante incorporar este elemento con las herramientas conceptuales aquí desplegadas es que éste puede ser estudiado de manera dual —es decir, como conducta o comportamiento—. En esos términos, queda claro que es posible rastrear el juego en diferentes especies. Finalmente, y a pesar de las múltiples acepciones con las que ha sido definido (Sutton-Smith, 1997), esta conceptualización evolucionista-enactivista renovada permite entrever su importancia para el desarrollo de habilidades motoras, sociales y cognitivas. En lo que sigue desarrollaremos esta cuestión.

4.1 Construyendo un mundo a través del juego

El juego en el reino animal ha sido descrito principalmente a partir de cinco aspectos (Burghardt, 2005): (i) es espontáneo, placentero, gratificante, reforzador o autotélico; (ii) es una conducta que no es seria (p. ej., cuando un organismo simula una pelea); (iii) se realiza repetidamente en una forma similar, pero no rígidamente estereotipada, durante al menos una parte de la ontogenia del animal; (iv) ocurre cuando un animal está adecuadamente alimentado, sano y libre de estrés; y (v) la conducta consiste en acciones que no contribuyen directamente a la supervivencia actual. Sin embargo, Bateson y Martin (2013) sumaron un aspecto que consideraron distintivo para robustecer la compresión de esta conducta: (vi) el *juego juguetón* (*playful play*). Esta categoría se distingue, concretamente, por ir acompañada de un estado motivacional positivo (*playfulness*) que no necesariamente es observable. La importancia de enfatizar este rasgo es debido a que pueden existir manifestaciones aparentemente lúdicas que son generadas por la competencia o la agresión. Por lo tanto, el *juego juguetón* puede ser entendido como un mecanismo subyacente que guía a los organismos a indagar el ambiente de una manera espontánea y flexible.

Estas seis características destacan la importancia del contexto, del ambiente, de las emociones y del cuerpo en el estudio del juego como un elemento cognitivo de los organismos. La dimensión analógica del juego, implícita en su descripción, es esencial cuando pensamos en los organismos que 'atrapamos' el mundo a través de la motricidad y adquirimos este 'saber hacer', como es el caso de los seres humanos y todos los animales que utilizamos la locomoción para navegar en el ambiente. Lo anterior es porque a través de esta capacidad motriz es posible adquirir un conjunto de rasgos particulares de cada especie que están situados en un tiempo y un espacio. Además, incluir el '*juego juguetón*' como un rasgo del juego conlleva a una asociación con el ámbito de las emociones. Lo anterior ha sido considerado sustancial en el estudio del vínculo entre juego, emociones y evolución. Por ejemplo, Maturana y Verden-Zöller (1993) defendieron que el juego entre infantes y cuidadores es vital para el desarrollo de la consciencia social e individual. Específicamente, porque esta práctica es guiada por la emoción que, según los autores, fue el motor que nos permitió convertirnos en primates cooperativos que preservaron un modo de vida y que ha sido abandonada en la visión occidental —a saber, el amor—[4]. Si estas ideas son acertadas, entonces, es imperante indagar sobre cuál es el rol del juego y su importancia durante el proceso de construcción de nicho y la emergencia de la cognición. Como expusimos en las

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[4] La relevancia de incluir el componente emocional ha tenido un lugar central en las discusiones provenientes de las ciencias cognitivas (e.g. Damasio, 1994; Dalgleish, 2004; Parisi y Petrosino, 2010). No obstante, la conexión entre juego-emoción no ha recibido la misma atención por parte de la comunidad de especialistas.

secciones anteriores, los diferentes canales de herencia tienen un rol constitutivo durante la construcción de nicho ontogenético, que repercutirá en la forma en que percibimos, interactuamos y jugamos en el mundo.

Sin estar involucrados directamente en los debates teóricos evolucionistas presentados aquí, Pellegrini et al. (2007) estudiaron la importancia del juego en la ontogenia y la filogenia. Su investigación estuvo guiada bajo el supuesto de que los organismos inmaduros —en el sentido fisiológico, motor y cognitivo— juegan para explorar su entorno y así desarrollar conductas que podrían llegar a ser adaptativas. En otras palabras, los organismos con largos períodos de inmadurez podrían generar durante la ontogenia, a través del juego, nuevos fenotipos y trayectorias de desarrollo en respuesta a novedades ambientales. Por ejemplo, las personas que juegan fútbol[5] desde una edad temprana tienen cambios importantes en huesos y músculos de las extremidades inferiores. Entonces, siguiendo este razonamiento, en los organismos con largos períodos de inmadurez, el juego ayuda a desarrollar un conjunto de habilidades necesarias que podrían ser eficaces en su ecología, p. ej., para la supervivencia o la reproducción. Esta hipótesis es interesante por diferentes razones. En primer lugar, como expusimos en la introducción de este trabajo, otorga un lugar central al organismo que está indagando, construyendo y transformando el mundo activamente. En segundo lugar, nos invita a vincular el juego con diferentes mecanismos, procesos y factores ontogenéticos, sensoriomotores y filogenéticos para entender la plasticidad del desarrollo en relación con la adaptación del organismo en su entorno, y su posible impacto evolutivo.

Con lo anterior se puede observar que profundizar en la relación entre el juego, la plasticidad fenotípica, las habilidades sensoriomotoras y los diferentes canales de herencia, podría enriquecer cualquier teorización sobre la importancia del componente lúdico en la evolución. Un concepto que resulta vital para comprender el alcance explicativo de esta afirmación fue postulado en la Psicología Ecológica[6] de Gibson (1979) y se refiere a las posibilidades de acción que un

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[5] Algunos trabajos de corte enactivista se han centrado en investigar las aportaciones conceptuales de la visión corporizada para las ciencias del deporte (Avilés et al., 2014; Avilés et al., 2020; Krein y Ilundáin-Agurruza, 2017). Sin embargo, en este ejemplo nos interesan las implicaciones de la práctica lúdica durante los períodos juveniles y no necesariamente su dimensión deportiva. Las diferencias y similitudes entre juego y deporte no son de particular interés para este artículo. Para conocer una aproximación acerca de este debate sugerimos consultar el trabajo de Feezell (2013).

[6] Si bien la Psicología Ecológica está dentro de las posturas corporizadas de la cognición, difiere del enactivismo en varias formas de cómo comprender la relación entre el ambiente y el organismo, aunque en ambas el ambiente es constitutivo de la cognición (véase p. ej., Heras-Escribano, 2019). Para el uso de la noción de *affordance*, Chemero (2009) planteó las *affordances dinámicas (2.0)* que se caracterizan por ser relacionales y compatibles con el enactivismo. Esto es importante porque el concepto *affordance* es controversial y, a partir del planteamiento de Gibson (1979), se ha reformulado con distintos objetivos. Estamos de acuerdo con Chemero (2009) debido a que su propuesta es un camino sólido para fortalecer nuestro entendimiento, al respecto del acoplamiento entre los organismos y sus ambientes.

organismo tiene en el mundo: las *affordances*. Esta propuesta ha tenido una influencia importante que atraviesa una gran diversidad de áreas del conocimiento debido a, por un lado, su carácter antagónico al cognitivismo que lo convirtió en una de las principales banderas que subyacen a la cognición corporizada (Wilson, 2002) y, por otro lado, el énfasis en que la unidad de análisis en el estudio de la percepción es el sistema organismo-ambiente (Gibson, 1979). Sin embargo, ¿cómo podemos estudiar el vínculo entre *affordance*s y el juego?

Una de las discusiones más fructíferas, en el contexto de la filosofía de la biología y vinculada con la problemática trazada en este texto, ha estado enfocada en dilucidar el lugar de las *affordances* en el marco contemporáneo del pensamiento evolutivo. Recientemente, Heras-Escribano (2020) defendió que éstas tienen un carácter dual en la evolución. Su propuesta es, principalmente, que las *affordances* son presiones selectivas y también herencias ecológicas, pero esto dependerá de la etapa temporal del proceso evolutivo que se analice. Por una parte, son presiones selectivas cuando el organismo tiene que extraer información ecológica de su entorno para consumar un objetivo. Pensemos, por ejemplo, en los primeros homínidos que aprendieron a manipular huesos, piedras, madera y una amplia diversidad de objetos. Dominar esta manipulación de artefactos permitió a nuestros antepasados, entre otras cosas, ampliar sus posibilidades de sobrevivencia. En este caso, aprender a manipular esos objetos ilustra el papel de las *affordances,* entendidas como una presión selectiva. Por otra parte, el éxito de estas técnicas de utilización de artefactos dentro un grupo de homínidos fue transmitido de una generación a otra y, precisamente, aquí podemos observar el rol de herencia ecológica de las *affordances*. Aquí es posible analizar cómo estos mecanismos evolutivos —la selección natural y la construcción de nicho— interactúan con los organismos en dos momentos diferentes de la historia evolutiva. En esta misma línea, Bateson y Martin (2013) argumentaron que la importancia del juego es que facilita la creatividad y la innovación, en general para las diferentes especies de animales y, en particular, para las sociedades humanas. En otras palabras, "el juego genera nuevas formas de relacionarse con el ambiente" (Bateson y Martin, 2013, 4). Este ambiente es dinámico y está en un constante cambio, y jugar es el catalizador de nuevos comportamientos que podrían cambiar la visión del mundo dentro de esos grupos humanos al generar inventos novedosos. Muchas de las grandes innovaciones del mundo occidental tienen antecedentes en algún juguete: las máquinas de vapor, los aviones, el cañón o los relojes mecánicos (Brown y Vaughan, 2009) son algunos ejemplos que apoyan esta idea. Estas reflexiones nos guían a hipotetizar sobre el impacto del juego para la generación de nuevos fenotipos que conllevan nuevas habilidades y que son potencialmente adaptativos y heredables: un camino para construir y enactuar el mundo.

¿Qué importancia tiene el juego en los contextos ecológico-evolutivos, enactivo-cognitivos de otras especies de homínidos y primates? Fuentes (2017) relató el caso de un macaco dominante que, debido a un accidente, cambió su rol social y fue sometido a situaciones que no estaban en su repertorio comportamental.

Después del desafortunado suceso fue expulsado del grupo y tuvo que cambiar su conducta dominante por una más adecuada a su nuevo estatus jerárquico; es decir, tuvo que hacerse más simpático. Lo notable de este suceso es que pone en evidencia cómo un cambio de contexto permeó la conducta de este primate, el cual tuvo que adaptarse a nuevos retos. No obstante, una característica sobresaliente de este ejemplo radica en que la experiencia del macaco estuvo enmarcada por un grupo que reguló qué clase de conductas eran permitidas o no. Pareciera que la creatividad permitió que este mono pudiera vivir en el dinamismo social en el que estaba inmerso. Sin embargo, ¿este rasgo creativo fue impulsado por un ejercicio lúdico? Desde hace décadas, autores como Bekoff (1976) han investigado la importancia del juego social durante la ontogenia y han defendido que, a través del juego entre pares, los animales jóvenes aprenden un conjunto de habilidades sociales —por ejemplo, la cooperación— que son esenciales para vivir en esta dinámica.

Parece ser que jugar durante los períodos juveniles está en estrecha relación con la plasticidad fenotípica y el aprendizaje. Es viable suponer que, a través de esta actividad, los organismos pueden experimentar diferentes situaciones hipotéticas que podrían ser útiles en su vida adulta. Los supuestos escenarios creados a través del juego serían esenciales para la generación de nuevas formas de interacción en el ambiente que podrían ser transmitidos a la siguiente generación. A este respecto, Kendal et al. (2005) presentaron un conjunto de tareas de forrajeo, consistentes en abrir diferentes cajas que contenían alimentos regulares o novedosos, ante grupos de primates. En dicho estudio se encontró que los adultos eran más exitosos que los jóvenes al enfrentar nuevos retos. Una de las interpretaciones de este resultado fue que la experiencia, con relación a la manipulación de objetos obtenida a lo largo de su vida, tuvo un lugar central. Los autores no profundizaron en los detalles respecto al rol del juego para la obtención de esa experiencia; no obstante, una posible conjetura es que, a partir de la relación entre la percepción y la acción, estos individuos primates pudieron construir un mundo durante su ontogenia que desembocó en una mejor actuación en esta tarea. Además, si el juego es una conducta característica de esta clase de animales, explorar el ambiente a través de este ejercicio debió ser parte fundamental de sus procesos de construcción de ‘nichos primates’.

Considerar el amplio espectro de consecuencias que tiene el juego —para los animales que manifestamos este comportamiento— tiene implicaciones importantes para la comprensión que tenemos de la ontogenia y su impacto en la filogenia, en línea con las problematizaciones evolucionistas revisadas en la primera parte de este trabajo, y los temas enactivos desplegados en la segunda. Los organismos que pertenecemos a numerosas especies de primates (humanos y no-humanos) inspeccionamos, exploramos y adquirimos diferentes capacidades y habilidades que están fuertemente ligadas como nuestra forma de concebir el mundo, que va desde un nivel individual hasta un nivel compartido por miembros de la misma especie, y que da lugar a distintos niveles de emergencia.

Una investigación más que ilustra el vínculo entre el juego y el proceso de construcción de nicho cultural, lo podemos encontrar en el trabajo de Boyette (2018). Ahí, el autor esclareció la importancia que tiene el juego en infantes de sociedades contemporáneas de cazadores-recolectores. Según este autor, el estudio del juego puede ayudarnos a comprender la emergencia de esquemas culturales propios de estos grupos que han sido transmitidos inter- y transgeneracionalmente —a saber, la autonomía, el compartir y el igualitarismo—. Esto se debe a que, a través de este comportamiento lúdico, los jóvenes pueden adquirir y aprender estas pautas. Una característica importante de los juegos en estos grupos es su carácter no competitivo, que ha sido asociado con el reforzamiento de las tres particularidades mencionadas. Lo anterior se hace más evidente si reflexionamos al respecto de la competencia y sus implicaciones en el mundo occidental. Además, según Boyette (2016) existe una evidencia razonable para sustentar que los juegos que practican los individuos no adultos tienen cualidades adaptativas. Un caso relevante proviene de su trabajo etnográfico con el grupo cultural de forrajeadores Aka. Boyette (2016) observó que los niños juegan a recolectar miel; esto implica entrenar el dominio y manipulación de distintas herramientas provenientes de su cultura. Sin embargo, también notó que los niños agricultores Ngandu no practicaban esta clase de juego, a pesar de estar geográficamente situados en el mismo ambiente. ¿Por qué ocurre esto? La respuesta podría atribuirse a que el juego está “motivado, organizado e imbuido en un grupo cultural particular” (Boyette, 2016, 160). Si bien esa interpretación parece demasiado abierta, el resultado en sí mismo sugiere que podemos entender el juego como un andamio ontogenético con propiedades de eficacia causal. En la Figura 3 mostramos nuestra propuesta concerniente al lugar del juego, y los procesos en los que está presente, en distintas temporalidades de un grupo humano, empleando una modificación de la conocida representación gráfica de la TCN.[7]

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[7] En autores como Arthur (2011) es posible estudiar otra aproximación visual a la importancia del eje ontogenético dentro del pensamiento evolutivo contemporáneo.

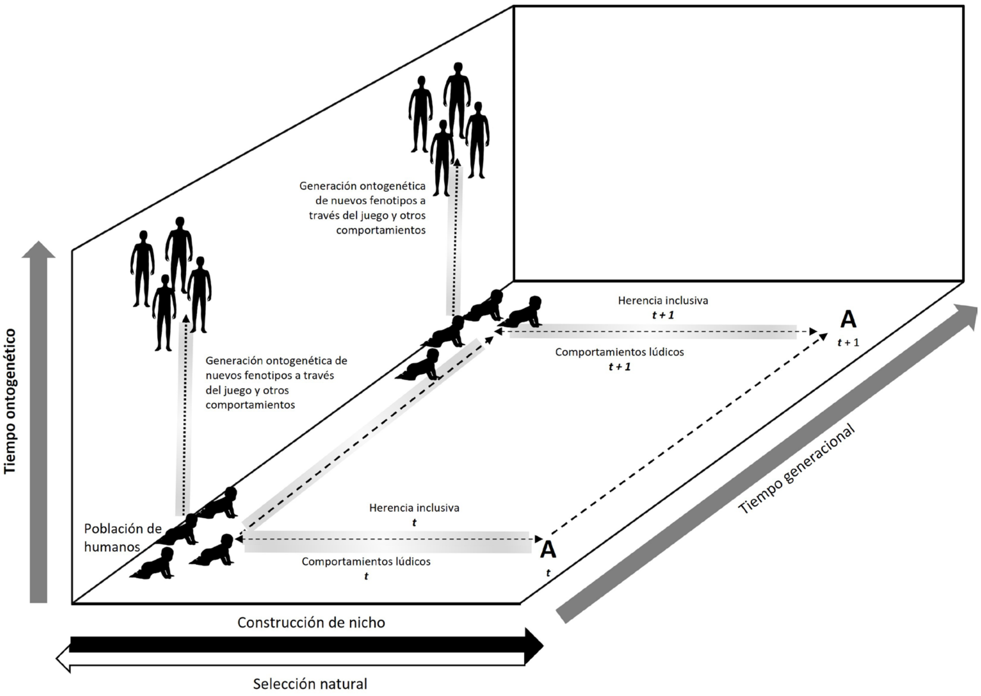

Figura 3. El juego en la ontogenia y filogenia de los seres humanos y su implicación causal en diversos procesos individuales y colectivos. En la imagen se puede estudiar la interacción de las principales nociones teóricas expuestas en este trabajo y la integración del juego. Las dos líneas horizontales indican la causalidad recíproca entre los organismos y el ambiente, tal y como lo prescribe la TCN y su diagramación gráfica canónica (Laland y Sterelny, 2006; Laland y O'Brien, 2011). Adicionalmente, nosotros dibujamos un eje vertical, el cual señala la dimensión ontogenética en la vida de los organismos —en este caso, homínidos del pasado o bien representantes actuales de *Homo sapiens*—. En relación con los otros elementos gráficos presentados en esta figura, este eje adicional insinúa que, a través del estudio del nicho ontogenético, se podría esclarecer "el origen de la variación fenotípica potencialmente adaptativa y heredable" (Stotz, 2017, 2). Las siluetas de color negro representan una población de humanos en su fase infantil y adulta, y el tiempo que transcurre entre una generación y otra es representado por una línea inclinada. Como es costumbre en los diagramas de la TCN, el ambiente es ilustrado por una letra **A**. Las flechas punteadas de color negro muestran las diferentes clases de herencia—genética, ecológica, genética, comportamental y simbólica— implicadas, entre una generación y otra, en la construcción de esta clase de nicho (Jablonka y Lamb, 2007; Odling-Smee y Laland, 2011; Fuentes, 2016, 2017; Bonduriansky y Day, 2018; Laland y Uller, 2021). Finalmente, una línea gris sombreada señala la importancia del juego y su posible impacto en el modelo evolutivo.

4. Conclusiones

El juego es un componente central en el proceso de construcción de nicho y la emergencia de la cognición. Si se nos permite una expresión metafórica, jugar es un sendero para explorar, descubrir, construir y cimentar nuevas formas de ser y estar en el mundo. A través del rol activo del organismo en su ambiente ontogenético, es posible adquirir y desarrollar diferentes habilidades motoras, sociales y cognitivas que son potencialmente adaptativas. Para sustentar esta afirmación, en este trabajo revisamos inicialmente dos marcos teóricos que son esenciales para comprender el carácter dinámico de los organismos. Por una parte, la Teoría de Construcción de Nicho (TCN) y dos de sus componentes conceptuales: el *nicho cultural* y el *nicho ontogenético*. Ahí enfatizamos el dinamismo de la relación entre selección natural y construcción de nicho, así como los diferentes canales de herencia en los que está inmerso un organismo, más allá de la dimensión estrictamente genética. En segundo lugar, retomamos los principales supuestos del enactivismo y una de sus aproximaciones: el *enactivismo sensoriomotor*. Ahí mostramos cómo a través de la interacción entre el cuerpo y el ambiente, los organismos adquirimos este 'saber hacer' que posibilita que naveguemos en el mundo. A la luz de las aportaciones de estos programas de investigación, introdujimos el caso del *juego* para enfatizar su importancia durante el proceso de construcción de nicho y la emergencia de la cognición. Como se pudo observar, esta actividad organísmica polifacética y multifactorial es un camino que necesita ser analizado para robustecer la comprensión de las particularidades inmersas en la interacción y desarrollo de muchos organismos animales, particularmente en especies de primates. Como señaló Maturana (1993), es imperante dejar cierta 'ceguera cultural' y no descuidar más la investigación del juego y las emociones, ya que estos elementos podrían esclarecer aspectos de la evolución que no han sido estudiados a profundidad.

De lo anterior se sigue que algunas de las implicaciones que podría tener la exploración del juego son principalmente dos. Por un lado, en el plano académico es viable investigar para aportar elementos que nos guíen a una ruptura con la dicotomía entre juego y trabajo (o entre una actividad seria y una que no lo es), y replantear el estatus epistémico y ontológico de esta conducta. Además, al conjugar elementos conceptuales provenientes de distintas disciplinas, un trabajo investigativo de esta clase permitiría avanzar en problemáticas particulares del pensamiento evolutivo contemporáneo y de las ciencias cognitivas corporizadas. Por otro lado, en el campo de la educación, un enfoque que coloque al juego en una dimensión evolutiva y enactiva podría repercutir en programas educativos más robustos, que nos enseñen a relacionarnos de diferentes maneras en el ambiente. Esto implicaría pensar en el sistema organismo-ambiente desde que somos infantes, o bien fomentar la enseñanza de juegos que lleven implícita una práctica inmersa en la cooperación y la igualdad en lugar de la competencia y la agresividad, como es el caso de muchos juegos occidentales. Al respecto de este último enunciado, el trabajo de Boyette (2016; 2018), y otras investigaciones de ese corte, invitan a la comunidad de especialistas a reflexionar sobre *la importancia de comprender la forma en que juegan las diferentes sociedades*. Al fin y al cabo, los juegos son parte del dinamismo que caracteriza los nichos construidos en los que los seres humanos desarrollamos, eco-evolutivamente, nuestras habilidades de enactividad sensoriomotora y cognitiva.

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Organisms, Life Relations, and Evolution: Inter-Dependencies after Kropotkin's *Mutual Aid*

Organismos, relaciones de vida y evolución: inter-dependencias a partir del Apoyo Mutuo *de Kropotkin*

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Abstract

We examine some implications of Kropotkin's seminal work on mutual aid as a factor of evolution to analyze how non-competitive life relations are understood in current biological theories. We distinguish two research lines deriving from his work:; one of them studies intraspecific relations of altruism and selfishness, and the other one is focused on interspecific symbiotic relations. Furthermore, we use the example of pregnancy and viviparity is used to extend the analysis to the evolution of novel inter-organismic characters. We conclude with a conceptual review of how collaborations and inter-dependencies among organisms shape individual autonomy and sociability in organismal evolutionary biology.

Keywords: altruism; symbiosis; ontologies; sociability; individuality; viviparity; reproduction; autonomy.

Resumen

En este trabajo examinamos ciertas implicaciones de la obra seminal de Kropotkin sobre el apoyo mutuo como factor evolutivo para analizar cómo se entienden las relaciones de vida no competitivas en las teorías biológicas actuales. Distinguimos dos líneas de investigación que pueden derivarse de su obra: una sobre las relaciones intraespecíficas de altruismo y egoísmo, y otra centrada en las relaciones simbióticas interespecíficas. Además, recurrimos a ejemplos de embarazo y viviparidad para extender el análisis hacia la evolución de nuevos caracteres inter-organísmicos. Concluimos con una revisión conceptual de cómo las colaboraciones e inter-dependencias entre organismos conforman la autonomía individual y la sociabilidad desde la biología evolutiva organismal.

Palabras clave: altruismo; simbiosis; ontologías; sociabilidad; individualidad; viviparidad; reproducción; autonomía.

1. Introduction

The organism-based account of evolution develops a different perspective from the one focused at the level of genes or populations, where the organism is established as a salient level of explanation for biological phenomena (Baedke & Fábregas-Tejeda, 2023; Cortés-García & Etxeberria, 2023; Etxeberria & Umerez, 2006; Nicholson, 2014). Since organisms are organized entities, many decisive biological features are grounded on the individual organization of constitutive parts interacting with the environment, and will only appear and stand out at that level.

Moreover, in addition to being constituted in relation to their environments, organisms act on them, they are agents and as a result of that, milieus are also shaped by organic activities. The understanding of organisms as inseparable from their environments, and constituted by the relationship they establish with them, is becoming widespread in the philosophy of biology, but we believe that this environment is often conceived of as inanimate, and more attention should be paid to organism-organism relationships and their bearing in evolution.

In the standard evolutionary theory of the Modern Synthesis, many of the traits that characterize the fitness of organisms, including both their abilities to survive and to reproduce, are already context-dependent and relational (Millstein, 2014, Okasha, 2002). Relationships involved in predator-prey interactions, mating behavior, parental care, etc. shape the individual properties of organisms and characterize the way in which they are constituted, and thus, their survival and reproductive capacities. Many of those relations have been studied within a competitive understanding of Charles Darwin's "struggle for existence", an expression he used under the influence of reading Thomas Malthus and which underlies the idea of natural selection. However, there has always been a debate as to whether it should be understood as a direct competition between organisms and how much scope it allows for cooperation between them.

It is for this reason that we turn to the work of Pyotr Kropotkin, as an author who in the beginning of the twentieth century forthrightly denounced the sheer competitive reading of Darwinian theory and encouraged the development of biological studies that included relations of life that were not necessarily competitive to explain the nature of social bonds and interspecies relations in humans and other species.

Therefore, this paper explores some views on the role of non-competitive relationships between organisms in evolution starting from some aspects implied by Kropotkin's work in his book *Mutual Aid* (1902/2018).

Our analysis combines historical research with philosophical aspects that we believe are relevant to advance organismal biology. The argument proceeds as follows: firstly, we review some of Kropotkin's fundamental ideas on mutual aid as an evolutionary factor in order to emphasize that important aspects of the ontology of relationships in evolution already appear in this book (section 2). Then, we present two major research lines or traditions of which Kropotkin's work can be considered a relevant precedent: one of them centered on intraspecific relations and the possibility of altruism, and the other one addressing strong collaborative interspecies relations articulated in terms of symbiosis and material imbrication (section 3). Next, the example of viviparous reproduction in eutherian mammals is invoked to compare conflict and entanglement models of pregnancy (section 4). Finally, we examine central notions of organismal evolutionary biology, such as individual autonomy and sociability, from the perspective elaborated in the preceding sections.

2. Kropotkin's "*mutual aid*" as an evolutionary factor

2.1 Struggle for existence

The notion of struggle for existence is an expression Darwin (and other contemporaries such as Alfred Russel Wallace) borrowed from Malthus, according to whom the growth of population is an exponential phenomenon, a lot faster than food supplies, therefore when natural populations are constant in size this means that many individuals die (Gayon, 1998). Often this framework is associated with the idea that a competitiveness underlies all relationships among living beings. However, this requirement is controversial and has been debated by scholars. The insight entails that all organisms compete to survive and reproduce "whether with other members of its species, other species, or even its environmental conditions (of drought or temperature, for instance)" (Pence, 2022). Thus, Darwinian interpretations of life and of natural relationships sometimes hold that direct competition between organisms is required for natural selection, although other authors contend that the struggle for existence is broader and encompasses more than competitions (Lennox & Wilson, 1994). In the *Origin of Species,* Darwin himself states: "I use the term Struggle for Existence in a large and metaphorical sense, *including dependence of one being on another*" (1859, 62; emphasis added).

It is precisely to this last sentence by Darwin that Kropotkin seizes upon at the beginning of his book *Mutual Aid: A Factor in Evolution* (Kropotkin, 1902/2018). In this volume, he criticized the interpretation of evolution as a direct competition between organisms and emphasized the role of non-competitive relations among organisms in evolution. His contribution came immersed in what has been considered to be a tradition of Russian naturalists and biologists, who sympathized with Darwin's work and considered themselves Darwinists, yet questioned whether relations in nature can be reduced primarily to competition. In their view, no characterization of life and nature would be complete without addressing that many evolutionary phenomena are only possible as a consequence of collaborative relationships between individuals.

As Daniel Todes elaborates in his highly influential study, the term "struggle for existence" is ambiguous and has multiple potential meanings: "[Russian biologists] were especially careful to make three sets of distinctions: between indirect competition and direct struggle [...]; between intraspecific and interspecific relations; and between an organism's relations with other life forms and those with the physical environment." (Todes, 1987, 543). We consider this threefold distinction to be highly commendable and should be borne in mind when dealing with inter-organismic relations.

2.2 Nature and morality

In his book *The Descent of Man*, first published in 1871, Charles Darwin expanded on the topic of competition and distanced himself even further from a purely competitive interpretation. There, he defended the importance of cooperation in nature, arguing that social instincts, which are common in animals, endow them with "a moral sense or conscience" that lead them to feel sympathy for their fellows and to aid one another in a form of many mutual services (Darwin, 1877, 98, 101). He also had acknowledged that it is not uncommon that animals belonging to different species live together and that this impulse to aid one another is impelled by the satisfaction the individual who performs the service receives for their action (100, 104). Darwin hypothesized that these sensations of sympathy that prompt animals to live together were developed in order to induce those animals that would benefit from living in society to gather in groups (105). Moreover, Darwin importantly distinguished the emotion of sympathy from that of love. Unlike social Darwinism, which considered that competitiveness prevailed in nature and in society, Darwin makes some place for cooperative instincts, favored in particular at the level of the group.

Thomas H. Huxley also elaborated on the topic of nature and morality in his book *The Struggle for Existence in Human Society* (1888). There, he criticized the social Darwinist thesis that nature is ruled by fierce competition and has a normative value, so that struggle is the only way to reach progress in society. In contrast, he proposes a more radical separation between nature and morality: while in nature the struggle for survival prevails, human societies come about because there are principles of cooperation. Human civilized society is then a social construction in which principles different from those that dominate in nature prevail. Therefore, cooperation is only possible when the struggle for life that corresponds to nature is reduced to a minimum in society due to "unnatural" cooperative moral principles (Dugatkin, 2006; Huxley, 1888).

Kropotkin's work on *mutual aid* generally falls broadly within this network of discussions outlined above, but the elaboration of his proposal was triggered in response to Huxley's argument. He disagrees that the animal world is all about fighting, "at the same level as a gladiators' show," in Huxley's words (Huxley, 1894, 200). In response to Huxley, Kropotkin argues that nature is itself cooperative, and he appeals to science to offer a "naturalized" alternative to explaining cooperation among both humans and other animals. Although Kropotkin has been considered more of a political thinker than a scientist, some scholars contend that he was a high esteemed scientist for his contributions to Geography and Earth Sciences, whereas his theory of mutual aid was "mostly rejected or ignored" and suggest that there was an "a priori rejection" of his thesis by the scientific community (Johnson, 2019, 5). The influence of his thinking for scientific reasoning has been overall underappreciated.

2.3 A Russian tradition

The emphasis on the role of cooperation in evolution has been judged to be a main point of disagreement between the British (and, generally the Western) evolutionary tradition and others (Oldroyd, 1986), including the Russian one (Todes, 1989). Kropotkin states that he was inspired by the Russian biologist Karl Kessler, who proposed the notion of mutual aid and defended its relevance for the evolution of species in a speech delivered in December 1879 at the St. Petersburg Society of Naturalists, under the title *On the Law of Mutual Aid*. The ideas put forward in his speech were received with enthusiasm within Russian academia and, although Kessler died before he could develop his theory, the idea of the relevance of mutual aid in nature became a common component of Russian evolutionary thought (Todes, 1989), and served as a starting point for the development of later lines of research on the collaborative nature of relationships between animals. Particularly, the Russian tradition claimed that rather than struggle between individuals belonging to the same species, it is the direct action of the environment, combined with geographic isolation, that produces new species, while mutual aid between individuals increases the likelihood that these new variants will survive and develop (Todes, 1989).

In contrast to Kessler's ideas, Kropotkin's theory is built in terms of instincts of sympathy between individuals, which would have evolved as a response to the need to adapt to the harsh conditions of living. A central idea in Kropotkin's work is that organisms fight other organisms when resources are limited, as anticipated by Malthus, but cooperate when they face adverse environmental conditions or threats posed by members of other species (e.g., predators). Subsequently, this hypothesis on the natural evolution of mutual aid served him to naturalize his political and moral theory regarding human societies.

Kropotkin's views were also motivated by his observations, during his expeditions through Siberia and the Manchurian peninsula, that competition between individuals of the same species for resources was not the norm, but the exception. Kropotkin argues that the struggle for existence occurs primarily in the face of adverse environmental conditions, not as competition between individuals of the same species for the access to scarce resources:

> [...] even in those few spots where animal life teemed in abundance, I failed to find –although I was eagerly looking for it– that bitter struggle for

> the means of existence, AMONG ANIMALS BELONGING TO THE SAME SPECIES, which was considered by most Darwinists (though not always by Darwin himself) as the dominant characteristic of struggle for life, and the main factor of evolution. (Kropotkin, 1902/2018, 1; emphasis is original)

The harshness of living conditions is the main obstacle to the survival of individuals and the maintenance of species, so that mutual aid between individuals can be expected to be a valuable resource (Dugatkin, 2006; Kropotkin, 1902/2018). Kropotkin argues that mutual aid is far more frequent than competition between individuals of the same species and refers to several examples of cooperative sociability in the animal kingdom. In building his argument, he relies both on his own observations of migrations of large ruminants in the Siberian steppe and large flocks of birds for mutual protection, as on examples of cooperation and mutual aid in (almost) all major animal groups, both vertebrate and invertebrate, drawing on a copious literature in zoology and ethology.

Hence, in order to understand life and nature, we must attend to cooperation between individuals as much or more than to competition: "Kropotkin has therefore created a dichotomy within the general notion of struggle – two forms with opposite import: (1) organism against organism of the same species for limited resources, which leads to competition; and (2) organism against environment, which leads to cooperation." (Gould, 1988). In this sense, as Gould (1988,18) remarks, Kropotkin should not be read as an isolated thinker, but as representative of a "standard, well-developed Russian critique of Darwin, based on interesting reasons and coherent national traditions."

Kropotkin did not view cooperation and mutual aid as being based on reciprocity, at least not in the sense of tit-for-tat exchanges. Following Darwin, he considered mutual aid a natural instinct in humans and animals, a means of fulfilling a natural desire for social connection and community, a capacity not limited to within-species cooperation, but occurring also between different species, as observed in symbiotic relationships. He conceived of mutual aid as a fundamental principle of evolution, not based on an individualistic, self-interested calculation of benefits and costs, but on a holistic view of relationships and inter-dependencies (Azurmendi, 2016).

2.4 Life relations

A main theoretical contribution of Kessler's work that we want to underline is the introduction of the concept of "life relations" between different organisms, which operate as an evolutionary factor in nature (Todes, 1989). Kessler referred to these "life relations" as inter-organismic dependencies occurring in relation to two types of drives: the need for food and the impulse to reproduce. Of the two, reproduction is presented as the activity in which collaborative relationships are more likely to be established:

> The 'life relations' among fish, however, were fluid and subject to two distinct influences: while the drive for food generated a harsh, individualistic struggle, the drive to reproduce often led fish to live peacefully together. (Todes, 1989, 110)

According to Kessler's observations in fish, fighting and competition are more often associated with foraging, while cooperation and sociability are connected to reproduction. We are particularly interested in the concept of "life relations" because of its positive aspects with respect to the role that cooperation plays in evolution. However, this distinction did not hold in the subsequent literature on cooperation within the mutual aid tradition (for instance, Kropotkin does not attribute cooperation to certain life functions or drives), but it does provide a basis for exploring the importance of reproductive life relations when examining biological ontologies.

In the next sections, we suggest that Kropotkin's ideas resonate with much of the later literature on social collaboration between individuals and constitute a good starting point for a conception of life which stresses mutual relations for, after all, "[s]ocial life —that is, *we*, not *I*— is the normal form of life. *It is life itself*" (Kropotkin, 1922/2009, 44-45; emphasis in the original).

From these nineteenth-century discussions, two ways of understanding and studying the relationships between organisms and their role in evolution can be distinguished in the history and philosophy of biology. They are associated with two important scientific problems of a great philosophical interest: the relative role of collaboration in evolution and the genesis of new types of individualities in the evolution of the living world. Both have been quite controversial for different reasons as we will show in the following section.

3. Collaborative relationships: two research lines

Throughout the twentieth century, two very important research lines were developed in evolutionary biology addressing the role of collaborations, and not just competition, in evolution. They both share at least a derived connection with the work of Kropotkin, or with the idea that it is important to study how collaborations evolve and influence evolution.

The first research line focuses on whether there can be altruist behavior between individuals of the same species on the basis of evolutionary dynamics (Etxeberria & Pérez Iglesias, 2020). Relationships between individuals are modeled in game theory terms, where individuals must always maximize their benefits. This way of conceiving relationships in nature is based on an idealized notion of individuality, according to which the individual organism (and sometimes the individual gene), clearly delimited and individualized in its environment, is the relevant unit in ecological interactions and hence, in evolution.

The second research line examines how relations between organisms transcend individualistic ontology: it postulates the emergence of new types of entities based on processes of symbiosis and interweaving between individuals. In this second tradition, through the development of *naturalized ontological models*, the evolutionary role of heterogeneous individuals, such as chimeras or holobionts, is considered.[1]

3.1 Intraspecific relations

The first perspective views evolution through the lens of fitness, and assumes that the traits of biological individuals reflect their individual interests; therefore, the goal of evolution is to increase the fitness of individuals. Mathematical models attempt to assess the degree to which relationships between individuals may be advantageous or disadvantageous in maximizing the organism's fitness. From this perspective, natural selection would not favor acts of biological altruism resulting in improving the fitness of other individuals while decreasing the fitness value of the individual performing the altruist behavior (Lewens, 2015). Hence, in evolutionary biology altruism seems not to be possible in view of certain theoretical assumptions.

This paradox has been addressed by mainstream evolutionary biology during the twentieth century by either denying the existence of altruism in nature or finding alternative ways of explaining the evolution of altruism. Both strategies have been explored by the elaboration of game theoretical mathematical models in terms of conflict of interests. It is within this research line that the group selection controversy takes place, which debates the feasibility and strength of natural

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[1] An anonymous reviewer sensibly noted that these two traditions that we describe here are the ones that gave rise to the 'evolutionary change' and 'adaptationist' traditions, respectively, as distinguished in (Goodnight, 2015). The former, which corresponds to kin selection theory, tries to explain social traits such as altruism by identifying the adaptive forces that lead to it; in contrast, the latter tradition, which is identified with the theory of multilevel selection, focuses on measuring ongoing selective processes. This points to the relevance of our historical work for current biological practice .

selection at the level of the group, in contrast to the level of the individual. Group selection, in contrast to individual selection, could explain the evolution of collaborative behaviors. As mentioned before, Darwin had already tried to explain these phenomena by making use of group selection thinking. In *The Descent of Man* (1877, 132, 610), he discusses the idea that natural selection could act at different levels of organization, including the level of the group. Darwin argues that the advance of morality would give an evolutionary advantage to cooperative tribes over those formed by selfish individuals. This idea was also defended by Alfred Russel Wallace, who firmly believed that competition between groups could lead to the evolution of cooperative behaviors. He also proposed that group selection could help to explain the evolution of moral behavior in humans, and that the development of such instincts could help groups to compete more effectively against other groups (Durant, 1979).

This idea, however, became highly controversial during the development of evolutionary thought during the twentieth century. The precursors of the Modern Synthesis, who developed the first evolutionary mathematical models during the 1920s and 1930s (Ronald Fisher, J. B. S. Haldane and Sewall Wright) understood that group selection may allow the evolution of altruism, but they "doubted the importance of this evolutionary mechanism" (Okasha, 2020). However, Sewall Wright developed his *shifting balance theory* in 1932, where he considered inter-group selection in the evolution of natural populations (Wade & Goodnight, 1998). Later on, during the mid-twentieth century, different biologists, most notably Konrad Lorenz, began to study cooperation in animals by making use of group-based thinking, but these studies did not prosper much further, as several mathematical models discredited the idea of group selection at the time, and the hypothesis lost its prestige within the scientific community (Okasha, 2020). In the 1960s, George C. Williams and John Maynard Smith also opposed to group selection theory by questioning (mathematically) the possibility of it evolving, since, they argued, group selection was a very weak evolutionary force. Hence, it would eventually lead to altruistic strategies being exploited for the benefit of selfish individuals, and therefore, they would eventually disappear. However, by this time Michael Wade was doing both theoretical and empirical work proving the role of group selection in the evolution of social behaviors such as cooperation (Wade, 2016).

Later models tried to understand behaviors of apparent altruism among genetically related individuals, while maintaining the selfish premise. *Kin selection*, initially proposed by William Hamilton, explains altruism on the basis of *inclusive fitness*, which allows to calculate whether it is worthwhile for an individual to help relatives carrying the same genes. These are strategies to preserve certain genes regardless of who their carriers are in the form of apparently altruist behaviors that would mask an ultimately selfish reality, as Richard Dawkins (1976) concluded.

An alternative to kin selection was offered by Robert L. Trivers (1971), who developed the theory of *reciprocal altruism* in order to explain support between individuals that do not belong to the same family, population or species. Here, the basis for explaining altruism is not shared genes but reciprocity. Altruism depends on the probability that the favor performed will be returned in the future. Hence, altruism will only evolve if this probability is high. According to this model, the disadvantages for altruistic individuals are compensated by the help that the current helper will receive in the future. This would be the basis on which cooperative behavior would evolve.

Later, by relying on the work of Wade and others who had been elaborating on the idea of group selection, Elliott Sober and David Sloan Wilson (1998) would defend the feasibility of group selection; they developed a model that demonstrated the advantage of groups where altruist individuals abound, with respect to groups where altruists are more scarce, even when selfish individuals do better than altruists within the group.

The strand of this research line that rejects group selection has been built on the premise that individuals are largely self-sufficient, and that their investments are best for themselves and not for other individuals. Hence, they conclude that altruism ought to be rare or insignificant in nature, and apparently non-existent in the most primitive organisms, so that it cannot build up evolutionarily until humans.

In sum, within this research line, questions of cooperation and competition are discussed in the framework of an understanding of evolution in which organisms must maximize their fitness. In general, with the exception of Trivers, models are restricted to cases of intraspecific relationships. Kinship, reciprocity, or group cohesion are the features that make it possible to transcend selfishness in certain special cases. When relations between organisms are considered beyond a strict individualistic framework, evolution can be compatible with altruistic manifestations, even in the framework of population genetics. This is precisely the aim of group selection scientists and the motivation of multi-level selection theories.

With respect to the theses defended by kin selection advocates, we can note that Kropotkin already criticized in his writings the fact that cooperation is conceived at the level of the family, since he considers that family relationships between individuals were formed later in evolution than those occurring in the wider group or tribe. Therefore, relatedness cannot be the foundation of social organization. Kropotkin is convinced that cooperation is the norm rather than the exception in nature, and present in all forms of life, microbes included. Consequently, he argued that altruistic principles of cooperation constitute an instinct, a basic drive of life, instead of a social construct as Huxley proposed. The contribution of Kropotkin and the proponents of mutual aid to the research agenda of the group selection theory is the realization that fitness can also be increased by cooperation. For instance, Mark Borrello (2004) finds a parallelism between group selection and Kropotkin's mutual aid, in contrast to the view of nature where struggle of each against all prevails, such as Huxley's.

3.2 Interspecific relations

The second biological research line for which Kropotkin's cooperative thinking is relevant is the one centered on symbiosis and, more importantly, the theory of endosymbiosis, which gave rise to the notion of the holobiont. Kropotkin makes a brief mention of the possibility of cooperation even among microbes, when he states that "Mutual aid is met with even amidst the lowest animals, and we must be prepared to learn some day, from the students of microscopical pond-life, facts of unconscious mutual support, even from the life of micro-organisms" (Kropotkin, 1902/2018, 13–14). Indeed, Kropotkin appears as a precedent for work on evolution by association of individuals (Sapp, 1994), holobionts (Baedke et al., 2020) and symbiosis (Toepfer, 2011, Carrapiço, 2015, Suárez, 2018).

On her part, Lynn Margulis often acknowledged debts in her ideas of evolution by symbiosis or association of individuals to her Russian precedents (such as Brandt), who originated in the same research line stemming from Kessler's seminal speech (Lazcano & Peretó, 2021). Also, Margulis noted that Kropotkin's work on mutual aid had "inextricably permeated discussions regarding the participants in symbiosis" (Margulis, 1997, 298). Margulis developed a collaborative view of life, according to which evolution occurs on the basis of the relationships established between organisms. This was called the theory of symbiogenesis, a phenomenon that constitutes a major factor in evolution (Sagan, 1967). In general terms, within this research line, collaborations between individuals of different species in the co-constitution of individuals is studied. Also, the importance of microbes on Earth is stressed, something that until a few decades before was not so evident, since studies of both life and evolution were mostly limited on animals and plants. Margulis, in contrast, focused on the microcosm of the smallest organisms on the planet and was interested in how they relate to each other. In particular, she elaborated the endosymbiotic theory of the origin of eukaryotic cells, which emphasizes the origin of eukaryotic cells as the most remarkable discontinuity in the evolution of life on Earth, an evolutionary transition that is not due to the slow and progressive accumulation of mutations under the scrutiny of natural selection, but by the *collaboration* between two prokaryotic cells that previously had independent lives and that, after the association, give rise to a new kind of individual: the eukaryotic cell.

The collaboration envisaged in the theory of symbiogenesis is substantially different from other accounts which also consider that there can be cases of interspecific cooperation in the form of mutual aid (such as Trivers' proposal of section 3.1.), as it suggests a tighter form of collaboration involving the generation of new ontologies in the living world.

The fundamental difference between symbiogenesis and the use of the term symbiosis in ecology is that while the latter is a relation between separate individuals, often understood in game theoretical terms, in the former a partnership is established at the organizational level, which alters both the topological configuration and the functional dimension of the new system, from which arises an entangled inter-being between the two parties that are associated. The distinction between the strongest cases (i.e., endosymbiosis) and the weakest (i.e., temporal association) is not sharp, as nicely shown by Javier Suárez and Vanesa Triviño, who argue that cases of symbiosis apart from endosymbiosis, such as holobionts, also entail a fundamental reorganization of the interacting individuals to the point of altering their individuality and identity (Suárez & Triviño, 2020).

The two main avenues or research lines that since Kropotkin have explored collaborations as relations between organisms propose very different ways of approaching the nature of such relations. More importantly than whether they focus on intra- or interspecific relations, we have stressed some of the most remarkable differences in the models that are proposed: while the first approach elaborates game theoretical models that try to reflect the evolution of natural populations in terms of fitness values and differing interests, the second research line focuses on the material dimension of the relations between organisms and the entanglements that give rise to new systems and individualities.[2]

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[2] The second research line has recently extended towards different kinds of models for the evolution of holobionts. Notably Huitzil et al. (2018) model the host and the microbiota as Boolean networks, Roughgarden (2020) compares vertical and horizontal transmission of microbiota within a multilevel selection framework and Lloyd & Wade (2019) discuss holobionts using community genetics and population genetics models.

4. “Life relations” in viviparous reproduction

In the process of reproduction, various forms of relationships can occur between organisms, including those that reproduce sexually and those that reproduce asexually. However, in sexual reproductive relations we observe a greater diversity of inter-organismic relational dependencies: between sexual partners during mating and/or fertilization, between the gestating individual and the developing embryos for incubation and food provision, between parents and their offspring during parental care, and even care relationships between individuals without direct kinship (alloparenting).

In this section, we illustrate the female-fetus inter-dependence in viviparous reproduction to compare the contrasting interpretations of pregnancy from the two research lines in the previous section. The former suggests a conflict between the mother and embryo that needs resolution, while the latter proposes collaborative mechanisms that sustain gestation duration.

4.1 Modeling eutherian pregnancy as a conflict

Mother-offspring relations have been modeled in standard biology during the twentieth century as conflict between the interests of the gestating organism *versus* those of the conceptus, or embryo, both conceived as discrete individuals according to the first research line of section 3. The way in which individuality and evolution are conceptualized within the standard framework of the Modern Synthesis has led to this depiction of the mother-offspring relationship. Individuals are considered to be distinct, cohesive entities with traits that can exhibit some degree of heritable variation. Such variation can influence the likelihood of successful reproduction and may, therefore, be subject to natural selection. Then, ecological interactions between individuals, including those that occur during reproduction, are typically analyzed in terms of their impact on the fitness of the parties involved. As a result, the prevailing narrative often portrays these interactions as a struggle between individuals with competing interests. This perspective is also applied to reproductive relationships during gestation in viviparous species.

The conflict hypothesis of mammalian pregnancy can be traced back to the work of Peter Medawar, who in 1953 defined the immunological paradox of pregnancy: “how does the pregnant mother manage to nourish within herself, for many weeks or months, a fetus which, antigenetically, is a foreign body?” (Medawar, 1953, quoted in Schjenken et al., 2012, 212). Medawar arrived at this paradoxical situation by drawing a comparison between the immunological circumstances of the embryo during gestation and a semi-allogenic graft.

The latter refers to a foreign organ or tissue that possesses allogenic antibodies, which should typically trigger the immune system to recognize it as non-self and prompt rejection by the organism.

However, this analogy is inappropriate because, in contrast to what occurs in the case of a transplant, during pregnancy the circulatory systems of mother and embryo do not mix, as the placenta acts as an anatomical and immunological barrier (Male, 2021). Victoria Male argues that the immune situation of pregnancy is more akin to that of the gut in presence of the microbiome, which enjoys an *immune privilege*. This situation allows the uterus to establish and maintain some lack of response to external elements at the mother-embryo interface, which includes the placenta and the uterine wall (Male, 2021). This form of immunological tolerance should be understood as an active and collaborative immunoregulation carried out by the systems of the mother and the embryo, not as a phenomenon of immunosuppression or a "sabotage" of the passive mother's immunology by the developing embryo[3]. Hence, this shows how studies on reproductive immunology are flawed insofar as they are based on a false assumption that misleads a proper understanding of reproductive ontology. This conflict-oriented mode of reasoning, which is built upon a bias in scientific practice, has shaped a whole research line that tries to identify immune regulatory mechanisms to aid embryo tolerance (see Schjenken et al., 2012 for a review).

This conception of reproductive immunology as a conflict between mother and embryo has been very influential in the evolutionary conceptualization of pregnancy, leading to the formulation of the so-called "mother-offspring conflict hypothesis" (Haig, 1993, 1996). In his work, David Haig argues that, because mother and fetus possess an unequal genetic makeup, they may have misaligned "interests" in nutrient supply. From an evolutionary point of view, fetal genes would have been selected to increase investment, while maternal genes would be selected to limit nutrient transfer. Thus, because half of the fetal genome is of paternal origin, the optimal amount of investment for the fetus is always higher than that of the mother, so that mother and fetus are predetermined to compete for resources. This model, formulated in economic terms of investment, competition for available resources and conflict of interests, clearly reflects the mode of reasoning characteristic of the standard framework of the Modern Synthesis and to the theory of kin selection explained in section 3. This account, in which warlike terminology abounds, seems but an extension of the interpretation of nature as fierce competition for survival, conceptualizing the mother-fetus interface as

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[3] This form of collaborative immunoregulation is clearly illustrated by the fact that components of both maternal and embryonic origin participate in the immunoregulation that allows implantation and maintenance of the embryo in the maternal uterus in pregnancies with invasive implantation, as in the case of primates and rodents (Male, 2021).

a "battlefield" (Haig, 2003, 500), where the mother tries to contain the "fetal invasion" (Haig, 2003, 502). However, this interpretation of the relationships established during gestation, which supports the pregnancy conflict hypothesis, is not the only possible one: models of maternal-fetal coadaptation have been formulated, which predict the evolution of genetic factors that favor the integration of maternal and fetal traits (Wolf & Hager, 2006, 2009). Furthermore, the prevalence of matrigenetic control (i.e., dependent on maternally derived genes) in placental development and embryo selection at implantation indicates that the depiction of the embryo manipulating maternal physiology toward increased investment is flawed.

The mother-offspring conflict hypothesis is in agreement with a conception of pregnancy that regards the mother's body as a mere container of the developing embryo: the so-called *container model* of pregnancy, according to which the female uterus is nothing but a vessel that contains the embryo who, purportedly, has by itself all the necessary tools for developing. This model is as well aligned with the way in which individuality and evolution are understood within the standard framework of the Modern Synthesis, which neglects the causal importance of developmental processes and material entanglements, and, correspondingly, does not pay attention to the relationships between mother and embryo in the generation of the progeny. The container model of pregnancy has been recently criticized from many different perspectives (Gilbert, 2022; Kingma, 2018, 2019; Nuño de la Rosa et al., 2021).

The issue is that the pregnant female-embryo relationship is often modeled in the same terms as inter-organismic relationships in kin selection models, which assume that individuals must maximize their own fitness to evolve. This is problematic for reproductive relationships where both parties aim to achieve a shared goal and perform functions that are not solely individualistic.

4.2 Modeling eutherian pregnancy as an emerging symbiotic unit

Alternative models to the conflict account of pregnancy appear to be closer in inspiration to interspecific models of entanglement and symbiosis (than to the intraspecific ones). For example, a recent proposal consists in overcoming the mother-embryo conflict view to embrace a cooperative perspective of the relations that are established during pregnancy in eutherian mammals. In Nuño de la Rosa et al. (2021) an ontological view of relations of inter-dependency in eutherian pregnancy involves the emergence of a new form of joint individuality based on the physiological entanglement constituted by the gestating mother and the developing embryo.

While emphasizing the historical dimension of the evolution of pregnancy, in this model viviparous gestation implies the emergence of a new type of biological individual: the pregnant female as a *historical individual* (Nuño de la Rosa et al., 2021). This gestating individual, composed of the integrated physiology of female and embryo, has a transitory character, this being one of the fundamental aspects of its ontology. Eutherian pregnancy, as well as the historical individual of the pregnant female, is a stationary stage, which is temporally delimited by two inflammatory events: the implantation of the embryo and the delivery. Hence, this model offers a strikingly different view of the role of the immune system in pregnancy from that proposed in the conflict model. Here, the immune system is not a limiter of mother-embryo interaction or an element of conflict, but a facilitator of the incubation relationship and the exchange of substances. The evolution of eutherian viviparity involves the evolution of a new cell type that is fundamental for the establishment and maintenance of mother-embryo relations during gestation: the decidual cells. This new cell type, involved in the exchange of nutrients and waste substances between mother and embryo, arises as a consequence of the recruitment of the inflammatory mechanisms of the innate immune system, which allow the implantation of the embryo in the endometrium (Erkenbrack et al., 2018; Stadtmauer & Wagner, 2020; Wagner et al., 2014).

According to this model, the development of the embryo occurs from a stage of quasi-non-differentiation in this emergent and transient individual that constitutes the *pregnant* gestating female, to a stage of birth, after which the individual constituted by the gestating female would cease to exist and gives way to female and offspring as separate beings; although the connection remains close after birth, the interacting entities no longer consist of a single individual (Nuño de la Rosa et al., 2021). Therefore, according to this model, the mother-embryo relationship is the result of a form of *collaboration* in evolution, where the mother's physiological systems are reorganized and accommodated to incorporate the developing embryo; therefore, both mother and embryo collaborate in reproduction through the establishment of the transient individual of the pregnant female.

Thus, as illustrated throughout this section, the ideas initially proposed by Kessler in the context of Russian biology, and importantly developed by Kropotkin, are of great relevance when discussing ontological problems about life relations in reproduction. The notion of mutual aid, extended to genetic and physiological collaboration between individuals for reproduction, offers a compelling alternative to accounts restricted to competition and conflict in biology.

5. On collaborations and inter-dependencies

The inter-organismic dependencies which we discussed in the previous sections can be seen as a special class of life relations in that they exert a form of top-down influence in the *relata*, which is a fundamental and unavoidable feature of life as an Earthly phenomenon. The concept of *inter-dependence*, which involves a form of top-down causation, refers to the collaborative relationships that have been stabilized through evolution between (two or more) organisms of the same or different species. These relationships can have an impact on the development and evolution of the involved organisms. These supra-organismal phenomena can occur at the social level within an organism's ecological environment, and they have the potential to modify the interactions in which individuals participate, thereby influencing their adaptability.

The form of collaborative relationality as dependence on the others that we propose in this paper endows significant consequences for organismal autonomy. Autonomy is often associated with views in which autonomous individuals appear to be self-contained to a large extent (in the sense that their identity depends only on internal conditions), and whose goals are related to self-development and self-maintenance (Moreno et al., 2008; Moreno & Mossio, 2015). Such internal organization secures the system from being altered by the external environment by maintaining their internal stability (Bich et al, 2016; Rosslenbroich, 2014). This conception of autonomy, which overemphasizes individuality, has been the target of many criticisms, especially in domains related to care, such as healthcare, or political and economic scenarios defending collectively regulated settings (Armstrong et al., 2019; Mackenzie & Stoljar, 2000). In this paper, we have shown a perspective that opposes to this conception within the biological domain: in Pyotr Kropotkin's "mutual aid" scenario not only cooperation is enhanced instead of competition, but also it is based on a different notion of individuality, which is stronger in the sense of being more comprehensive and richer because it conceives of multiple biological inter-dependencies. Hence we can identify two different understandings of autonomy in biology: one of them relates to isolation in the sense of independence from the effects the environment and focuses on the inner workings and processes of the organisms, and the other one has to do with the interactions of a system with the environment and others and how those relationships shape the identity and individuality of the organism.

This theory about the evolutionary relevance of mutual aid in nature certainly makes sense in the framework of an agential theory of evolution, which understands evolutionary change as the product of interactions between the agent organism with its environment, including other agents.

It is generally understood that the agential behavior of organisms emerges from the individual's struggle for existence in their environment (Jaeger, 2021). From the lens of our reading of Kropotkin, this "struggle for existence" can be viewed in a wider way which includes organisms collaborating for survival in a co-dependent way. Hence, life relations (both inter- and intraspecific) would have an enormous evolutionary value, because, through agential evolution, they would importantly construct and shape the environment in which organism-agents dwell, which have important effects on the evolution of new characteristics, be they social or morphological. For example, the complex intraspecific relations observed in some social insects can be interpreted as an emergent organizational level facilitated by cooperative sociability in a framework of reciprocal causality between the organismic level and the colony, including top-down influences of the social relations between organisms in the wider framework of the colony upon the individual insects (cf. Canciani et al., 2019). Correspondingly, interspecific cooperation undoubtedly plays a fundamental role in the evolution of many species.

Some of the most important discussions about the evolution of sociability have revolved around kinship (*does it facilitate prosocial and cooperative behavior?)* and reciprocity (*does the evolution of prosocial behavior require a basis for reciprocity?).* A recent collection on the topic (Swain et al., 2021) criticizes the idea of associating solidarity with reciprocity as this scheme does not ensure the advance of a collaborative social organization.

One issue where Kropotkin's position seems to challenge some intuitions about the evolution of sociability is the need for helping others to be compensated by reciprocity. Although throughout his book Kropotkin seems to compel the idea that reciprocity at a social level is what sustains mutual aid, it does not occur necessarily in one-to-one instances of cooperation. Thus, not every single case of mutual aid between any two individuals needs to be reciprocal in the sense of rendering a net positive balance for each of the participants in any particular relation. It is in the wider frame of social inter-dependence in which mutual aid is sustained and the top-down influence of life relations upon organisms is exerted.

Therefore, when it comes to the evolution of prosocial behavior, the greater difficulty is to account for the dynamics of commitment between collaborative sociability and autonomy. In doing so, we would have to explore what types of behaviors and inter-dependencies favor the evolution of a form of sociability that guarantees autonomy, while being based on dependencies and relationships between individuals.

Among the cooperative relations discussed in section 3, reciprocal altruism has received a great deal of attention. An important contribution of Trivers' model of reciprocal altruism (reviewed in section 3) is that it can explain altruistic behavior between individuals belonging to different species. Trivers presents the examples of cleaning symbioses between fish of different species and warning calls between birds belonging to the same species. The basic thesis is that natural selection may favor altruistic behaviors of this type because they are beneficial to the altruistic organism in the medium/long term, as well as to the organism receiving the help in the short term.

Since it does not benefit the fitness of the altruistic individual even in the medium/long term, non-reciprocal altruism is difficult to integrate into evolutionary theory. And yet, it seems clear that, at least in the case of human beings, some individuals behave in non-reciprocal altruistic ways toward strangers that are difficult to be explained by kin selection and reciprocal altruism (Singer, 2011).

Michael Tomasello (2016) relates altruism, reciprocal or not, to inter-dependence: individuals of socially complex species depend on each other in many ways and, if an organism's fitness depends on the group (as, for example, to defend against predators, to make alarm calls, as coalition partners, etc.), then it is in the organism's interest that group mates do well. In these cases, cooperating or helping is not a sacrifice, but an investment at the group level. Altruism, then, would be an essential part of the social lives of organisms living in inter-dependent relationships with other organisms.

One of the aims of this paper has been to examine the role of collaborative relations within an organismal framework concerned with the notion of autonomy in biological explanations. The notion of autonomy as individuality has to be questioned to emphasize inter-organismic relations in charge of many of the features of organisms. Accordingly, the challenge in biology is how to understand autonomy in a way that it does not restrict the identity of an individual to its internal organization and addresses the relevance of interactions with the environment (including other living beings), while it allows us to understand individuality as a true self-determination that emerges from a set of inter-dependencies.

6. Conclusions

The goal of this paper was to explore the evolutionary significance of collaborative relationships among organisms, whether they belong to the same species or different ones. We accomplished this by drawing on Kropotkin's ideas as well as various biological research lines that have been inspired by them: the first debate concerning altruism and the second concerning symbiotic ontology. The former has led to several research projects on pro-social behavior from various biological disciplines such as ethology and behavioral ecology. These projects fall under the paradigm of evolutionary biology, which views organism-environment fit as optimizing adaptations. The second topic under consideration pertains to the way in which individualities are merged or interwoven during evolution, whether the individuals belong to the same species or different ones. Apart from symbiosis, we also examined the development of transient individualities during eutherian viviparous reproduction. In this scenario, collaborating individuals not only assist each other, but also become integrated or fused with each other, resulting in the emergence of novel ontologies that vary in terms of their stability. This provides the basis for our investigation of inter-dependence as an evolutionary factor in organism-centered evolutionary biology. By taking inter-dependence into account, our perspective on individuality, agency, and sociability is transformed.

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