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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).

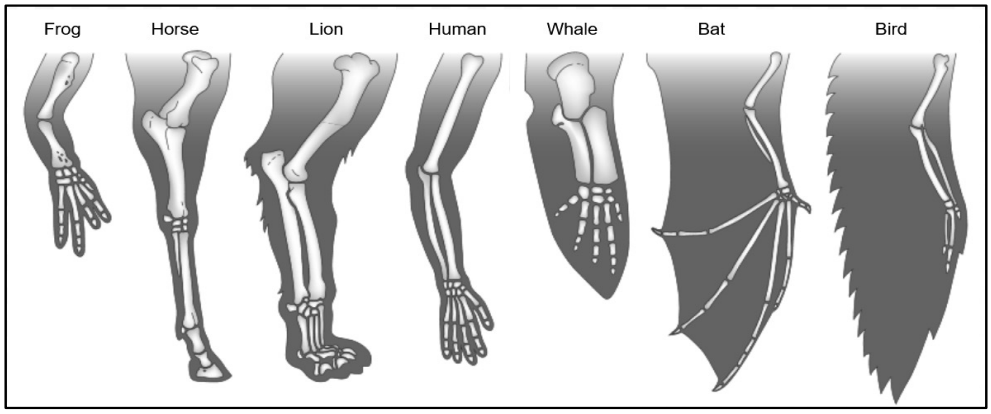

Fig. 1. The tetrapod limb instantiated in various vertebrate species. Modified from: Wagner 2007.

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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