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Conserving functions across generations: heredity in light of biological organization

Matteo Mossio Gaëlle Pontarotti

Abstract

We develop a conceptual framework that connects biological heredity and organization. Heredity designates the cross-generation conservation of functional elements, defined as constraints subject to organizational closure. While hereditary objects are functional constituents of biological systems, any other entity that is stable across generations – and possibly involved in the recurrence of phenotypes – belongs to their environment. The central outcome of the organizational perspective consists in extending the scope of heredity beyond the genetic domain without merging it with the broad category of cross-generation stability. After discussing some implications, we conclude with a reflection on the relationship between stability and variation.

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1 Introduction

In biology, heredity generally designates the recurrence of phenotypes across generations. Heredity plays a fundamental role in evolutionary theory, insofar as evolution takes place when natural selection acts on phenotypic variations that are heritable, or in other words, that are stably passed on to subsequent generations. One of the central themes of this paper is to show that, while it lies at the crossroads between biological stability and variation, heredity is first and foremost a matter of stability.

Heredity has for a long time been conceived from a gene-centred perspective and explained by appealing to the transmission of DNA sequences from ancestors to offspring. However, an increasing number of studies have recently suggested that a wider range of causal factors might be involved in this phenomenon. This broadened scope is usually referred to as ‘extended heredity’ (Bonduriansky and Day [2018]) and is often considered a significant scientific step forward, a move beyond the limitations of the gene-centred conception (Jablonka and Lamb [2005]; Danchin *et al.* [2011]). The problem we address in this paper is that the extension of heredity may entail the risk of over-extending the concept (Merlin [2017]).

In the absence of suitable conceptual boundaries, the extension of heredity may result in the category of hereditary factors being broadened to include a wide variety of elements whose only common features would be their stability across generations and the fact that they contribute in some way to the recurrence of phenotypes. Anything appearing to be a transmitted ‘resource’ would hence count as being hereditary, and ‘heredity’ would merge into the broader concept of ‘cross-generation stability’. The convergence between heredity and stability would call into question a traditional assumption made by the scientific study of heredity which, since the mid-nineteenth century (López-Beltrán [1994]), has viewed it as a specific explanatory concept. Traditionally, heredity has designated a certain kind of biological stability, associated with a certain kind of causality: it refers to the specific role played by specific stable objects (hereditary factors) in the recurrence of traits. If heredity were to merge with cross-generation stability, its extension would take the opposite path, by turning it into a very large and all-encompassing concept. Yet, such a broad characterization runs the risk of overlooking distinctions (in particular between different stable factors and different causal regimes) which may be helpful for disentangling the complex phenomenon of cross-generation biological stability and locating heredity within that broad phenomenon. Thus, an overly comprehensive concept of heredity might lose much of its explanatory power.

For this reason, we submit that an insufficiently ‘bounded’ extension involves the risk of leading to a detrimental over-extension of heredity.

Alternatives do exist, however. In recent years, several accounts have suggested that heredity can be extended beyond the genetic conception while still designating a theoretically distinguishable phenomenon, located within the broader one of biological cross-generation stability. Many central insights have been put forward and discussed. We submit, however, that further conceptual work is required to come to an adequate characterization of biological heredity as a specific kind of cross-generation stability determined by certain factors that are themselves stable for specific reasons. This paper aims to contribute to such a characterization. Our strategy consists in further elaborating on the connection between heredity and organization outlined in previous proposals promoting an organizational perspective of biological heredity (see, for instance, Pontarotti [2015]). By applying organizational principles, we formulate a hypothesis in which biological heredity denotes stability over generations of those elements that are constitutive parts of the organization of a biological system.

In the next section (section 2), we provide an overview of recent scientific and philosophical works that deal with extended heredity, and offer an analysis of the risk of over-extension. We argue that the restrictive association between ‘hereditary’ and ‘genetic’ is being replaced by the permissive equivalence between ‘hereditary’ and ‘stable’ and that, in spite of their virtues, existing conceptual accounts do not succeed in countering this tendency in a fully satisfactory way. This leads us to claim that an alternative proposal is required.

Section 3 outlines an organizational account of biological heredity. We rely on recent work that characterizes organization as a specific regime that contributes to maintaining its own conditions of existence (Moreno and Mossio [2015]). In organized systems, the components depend on each other for their maintenance over time and we refer to their mutual dependence as (organizational) closure. In particular, we characterize the relevant components as constraints controlling the thermodynamic flow, and we argue that constraints subject to closure are understood as having a function within the organization. Our main claim is that heredity refers to the ‘conservation through closure of functional patterns across generations of biological systems’. Conservation does not – or does not only – depend on the organization of each successive system, but rather on its insertion into an encompassing cross-generation

organization. In turn, ‘hereditary objects’¹ are functional constraints that are stable due to their being subject to cross-generation closure, be they molecular genes, microorganisms, artefacts, or other kinds of objects.

In section 4, we explore some implications of the account. In particular, we show how an organizational perspective enables heredity to be distinguished from other kinds of cross-generation stability. While hereditary objects are constraints subject to closure, all other entities that are stable across generations – and may play a role in the recurrence of phenotypes – belong to their environment. The distinction between heredity and other kinds of cross-generation stability enables the characterization of different (although related) phenomena, which call for different explanations. As a result, the organizational account of biological heredity contributes in an original way to the aim of extending heredity without merging it with cross-generation stability, by relying on explicit theoretical principles. We further explore other implications such as the possibility of thinking about heredity at various levels of biological organization. We also address potential objections related to the status of non-functional and dysfunctional parts.

In the conclusion, we reflect on the relationship between stability and variation. Although heredity is conceptualized as a kind of stability, we argue that the organizational perspective has no difficulty integrating biological change into its conceptual framework. Beyond the specific issue of biological heredity, this paper aims to show that the organizational framework can make useful contributions to theoretical and philosophical debates, particularly in relation to evolutionary theory.

¹ In this paper, we employ the generic expression ‘hereditary objects’ to refer to both hereditary factors and traits. The reasons for this choice are outlined in section 3.

2 From extended heredity to cross-generation stability

The gene-centric view of heredity has recently been challenged by an abundant literature focusing on the transmission of multifarious causal factors involved in the recurrence of features across generations. In this section, we examine how the extension of the scope of heredity may result in a theoretical conflation of ‘heredity’ and ‘cross-generation stability’, and why this constitutes a challenge for biological theory.

2.1 Extending the scope of heredity: a brief state of the art

The term biological heredity traditionally refers to the ‘like-begets-like phenomenon’ (Darwin [1859]; Jacob [1970]) and designates, more precisely, the recurrence of features across generations.

Established as a genuine biological concept by the middle of the nineteenth century, heredity ‘implies a particular kind of independent causation (mechanism, force)’ (López-Beltrán, [1994], p. 214). At the dawn of the twentieth century, classical genetics explained heredity in terms of the presence of the same ‘genetic’ causal factors in ancestors and offspring (Johannsen [1911]). Molecular biology made further sense of hereditary phenomena by invoking the copying and transmission of DNA strands. In this ‘DNA-centric theory of the inheritance of features’ (Mameli [2005], p. 365), a specific cause, namely the copying and transmission of DNA sequences, underpins a specific range of effects, namely the recurrence of features across generations, as well as the variability of offspring and atavism.

During recent years, the DNA-centric perspective has been seriously challenged by many studies detailing different kinds of non-genetic heredity. ‘Epigenetic heredity’ refers to the transmission of epigenetic molecular marks that control gene expression and are correlated with phenotypic effects (Richards [2006]; Jablonka and Raz [2009]). For example, the maintenance of epigenetic marks is involved in the cross-generation recurrence of colour in tomatoes (Manning *et al.* [2006]) and of plants’ defence against predators and pathogens (Holeski *et al.* [2012]). Another case of non-genetic heredity is ‘behavioural heredity’, namely the socially-mediated transmission of behaviours (Galef and Laland [2005]; Danchin *et al.* [2004]). Socially-learned feeding behaviours are classic examples in this domain (Slagsvold and Wiebe [2007]). For its part, ‘ecological heredity’ refers to the cross-generation stability of environmental elements – such as bird nests and beaver dams – which are actively maintained or modified by organisms (Odling-Smee *et al.* [2003]; Odling-Smee [2010]).

Ecological legacies also include shells stably recruited from the environment by hermit crabs (Griffiths and Gray [1997]) and plants stably chosen by insects to lay their eggs² (Laland, *et al.* [2001], p. 120). Finally, ‘symbiotic transmission’ concerns the reconstruction of symbiotic associations across generations of hosts (Gilbert *et al.* [2012], p. 325)³. For example, the bacterium *Buchnera aphidicola* can be said to be inherited by pea aphids (Hansen and Moran [2011]). Other elements such as nest sites are sometimes considered parts of extended inherited legacies (Griffiths and Stotz [2013], p. 136). Even the persistence of microgravity has been invoked in the explanation of the recurrence of phenotypes, insofar as it plays a role in the musculoskeletal features of vertebrates (Mameli [2005], p. 389).

To deal with these data, several accounts have been developed to capture extended heredity as a general phenomenon. A variety of strategies can be identified. Some accounts propose understanding heredity as the transmission of both genetic and non-genetic ‘information’ (Jablonka [2002]; Shea [2007]; Danchin *et al.* [2011]; Mesoudi *et al.* [2013]; Bonduriansky and Day [2018]). Others suggest that heredity can be defined as the cross-generation availability of genetic and non-genetic developmental ‘resources’ (Griffiths and Gray, [2004]; Oyama *et al.* [2001]; Griffiths and Stotz [2013]). In this view, biological systems inherit a ‘developmental niche’ (Griffiths and Stotz [2013], p. 134; Stotz [2010]; Stotz [2017]), described as ‘the set of epigenetic, social, ecological, epistemic and symbolic legacies inherited by the organism as necessary developmental resources’ (Stotz [2010], p. 483). Another perspective focuses on material continuity within lineages, understanding inheritance in terms of reproduction, specifically as ‘reproduction with material overlap of evolved mechanisms of development’ (Griesemer [2000], p. S362). Finally, some accounts offer no specific conceptual characterization of extended heredity, but rather evoke, more generally, multifarious ‘factors’ which influence offspring phenotypes (Bonduriansky and Day [2009]; Bonduriansky [2012]; Mameli [2004]; Mameli [2005]).

Overall, the contemporary scientific literature on extended heredity has put the gene-centred account under heavy pressure and calls for a rethink of the very concept of biological heredity (Bonduriansky [2012]; Pontarotti [2015]).

² These plants constitute food resources for insects’ offspring. Imprinting mechanisms are responsible for plant availability across generations.

³ The concept of ‘holobiont’ was proposed to describe a biological system composed of a host and its symbionts (Margulis [1991]; Gilbert *et al.* [2012]).

2.2 Rethinking heredity: conceptual challenges

Upon closer examination, the general accounts outlined above prompt a reassessment of the scope of biological heredity in accordance with two main dimensions. First, they encourage a rethinking of the range of factors and mechanisms underpinning the cross-generation recurrence of features (heredity as a cause), since the maintenance of epigenetic marks and the transmission of nutritional resources do indeed count as additional causes of the reoccurrence of features. Second, they also prompt a rethinking of the range of hereditary features which reoccur across generations (heredity as an effect)⁴. Indeed, it has sometimes been suggested that stable environmental elements should be considered inherited traits. For example, Mameli ([2004], p. 52) describes the hatching plant of certain insects as an environmental hereditary trait. In a similar vein, and in the wake of the idea that ‘the developmental system goes far beyond the traditional phenotype’ (Griffiths and Gray [1994], p. 278), Stotz ([2010], p. 492) argues that the ontogenetic niche – which notably comprises the ecological and social circumstances inherited by the organism – is also part of developmental systems.

The two dimensions of the extension – inherited factors and inherited features – map onto the traditional distinction between what is transmitted and what is observed across generations. Expressed in terms of the genotype/phenotype dichotomy in classical genetics (Johannsen [1911]), this distinction has been a fundamental one since the nineteenth century (Galton [1876]; Weismann [1883]). Even though its relevance will be questioned throughout the rest of this paper, the distinction serves to highlight the fact that the literature on non-genetic heredity suggests that a wide variety of non-genetic elements should be qualified as ‘hereditary’ insofar as they are stable, related to cross-generation similarity and dependent on the activity of previous generations. As a result, while the adjective ‘hereditary’ was synonymous with ‘genetic’ during the twentieth century, it is now closer to ‘stable across generations’. Accordingly, heredity tends to conflate with cross-generation stability.

The merging of heredity and cross-generation stability is more closely linked to some of the specific approaches mentioned in the previous sub-section than others. Firstly, it is induced by the return of metaphor-like conceptions: by appealing to concepts like ‘information’ and ‘resources’ without conceptualizing them in the biological context, some accounts implicitly

⁴ Some authors make a distinction between ‘heredity’ and ‘inheritance’. Bonduriansky ([2012]), for instance, argues that the former refers to the phenomenon of trans-generation recurrence of phenotypes, while the latter designates the underlying mechanisms. Griesemer ([2000], p. S356) also distinguishes heredity – as the degree of parent-offering relation measured by their correlation – from inheritance – the process through which heredity is instantiated.

rely on the model of the transmission of goods from one generation to the next⁵, and thereby qualify both stable parts of biological systems and stable parts of their environment as hereditary. Secondly, the conflation concerns those accounts which, by extending heredity without offering a specific conceptual characterization, pave the way to interpreting stable environmental features as being hereditary. Overall, these views exclude very few cross-generation stable elements from the field of heredity. For example, for some authors, habitats count as inherited resources (Griffiths and Stotz [2013], p. 136), or as inherited information (Danchin *et al.* [2011], p. 480). Similarly, extra-organismal ambient conditions are also referred to as being inherited (Bonduriansky and Day [2009], p. 106).

One could reply that such an inclusive understanding of heredity poses a fundamental difficulty in terms of drawing a clear-cut boundary between the biological systems involved in hereditary processes and their environment. We will, however, argue that such a distinction can be made on theoretical grounds, which implies that the adjective ‘hereditary’ cannot consistently apply to both parts of biological systems and environmental elements without losing much of its accuracy. This does not mean that elements traditionally qualified as environmental cannot be reconceptualized as hereditary parts of biological systems by virtue of an explicit theoretical criterion (or indeed that the environment does not play a role in the recurrence of features). However, a clear distinction should be made between this strategy and the fact of qualifying as hereditary any biologically-relevant element that is stable across generations, which would obscure the fact that heredity can be construed as a specific kind of biological stability associated with a specific kind of causality (which may be realized by genetic or non-genetic mechanisms).

As a matter of fact, some accounts, in particular Griesemer’s ([2000]) and Jablonka’s ([2002]), have proposed more restrictive characterizations of heredity. Although they rely on very different conceptual frameworks, we view their motivations and implications as substantially similar to those of the organizational account advocated here. Nevertheless, we believe that the latter makes a useful contribution by expressing in more explicit and

⁵ In section 4 we provide a characterization of the term ‘resource’ which is narrower than that employed in the recent literature.

principled terms some central ideas that are implicit or ambiguous in both previous accounts, specifically in relation to the delimitation of what counts as a hereditary element⁶.

The insufficiently bounded extension of heredity is what we call its over-extension. The problematic implication for biological research is that this over-extension tends to overlook distinctions that could help us reach a more precise understanding of the complex phenomenon of cross-generation biological stability. For this reason, an overly broad concept of heredity might turn out to be explanatorily impoverished, which would in turn weaken the advantages gained by its extension beyond genes⁷. In line with previous proposals, we submit that heredity can be extended while still remaining an accurate scientific concept, by which we mean that it can still designate a specific kind of causal regime involved in the broader phenomenon of biological cross-generation stability⁸. We argue, in particular, that the organizational framework provides precise theoretical tools to better capture the specificity of heredity even in its extended conception and, hence, to draw a well-grounded boundary between hereditary and non-hereditary stability, under the assumption that different kinds of stability require different kinds of explanation.

3 Biological heredity in light of organization

The main contribution made by this paper consists in establishing a conceptual connection between heredity and organization. Firstly, we rely on the general background hypothesis that biological systems are organized systems and that their organization plays a central role in explaining their maintenance and stability over time (Mossio *et al.* [2016]). And secondly, we submit that heredity refers to the cross-generation recurrence of biological features, and is therefore a form of stability.

Hence, we claim that heredity can be understood by elaborating an account derived from general organizational principles. The argument developed in this paper therefore appeals to

⁶ Some specific points of comparison are outlined in the following sections. We will not discuss the relevance of the notion of information, whose use in biology is highly controversial *per se* (see Longo *et al.* [2012], for a point of view that we share).

⁷ One might even wonder why biological science should bother to continue using a concept (heredity) at all, if it were merged with another one (cross-generation stability).

⁸ When criticizing over-extension, we are assuming that if an account is able to make more precise distinctions than others that have the same agenda (in this case, explaining heredity as a specific kind of biological cross-generation stability without reviving the gene-centred perspective), then it potentially possesses a greater explanatory power and is worth exploring.

several concepts that have recently been explored within the organizational framework for biology. However, their application to heredity requires a broadening of their scope in both space and time.

3.1 Biological organization within organisms and beyond

Organization refers to a certain kind of complexity, distinctively realized by biological systems as opposed to other kinds of natural systems or artefacts. Organized systems are constituted by parts that display both differentiation and integration and that, moreover, maintain each other through their reciprocal interactions. The existence of organized systems as whole entities depends on the overall activity of their parts: accordingly, these systems self-maintain (in a given environment).

The first conceptual move of this paper consists in claiming that the biological systems involved in biological heredity – and more specifically, in extended heredity – can be pertinently described as organized systems. Organized systems are thermodynamically open systems, continuously traversed by a flow of energy and matter that involves the alteration, consumption or production of entities (Bertalanffy [1952]). Organized systems control these transformations through the coordinated action of their parts, which are theoretically characterized as structures exerting *constraints* (Montévil and Mossio [2015]; Pocheville [2010] develops the similar concept of ‘dynamical invariant’)⁹. While acting on these transformations, constraints can be said to be conserved with respect to them, at the relevant time scale. Two canonical examples of biological constraints have been discussed in recent studies (see Montévil and Mossio [2015] for details). The vascular system of animals exerts a constraint on the blood flow without being altered by it; and at a much lower level of description, enzymes change the kinetics of a chemical reaction without being consumed.

At the relevant time scale, constraints exhibit conservation with respect to the transformation on which they act. Yet, constraints are structures which, due to their material arrangement, are subject to degradation at longer time scales, and must therefore be replaced or repaired. For instance, the cells that constitute the vascular system must be nourished, and enzymes

⁹ In the organizational framework, constraints are objects defined in relation to the effects they produce on target processes, due to the specific conserved properties that they possess (see Montévil and Mossio [2015] for a technical treatment). Strictly speaking, therefore, a constraint is a part ‘that produces a given effect’. In what follows, we will use the term to refer to both the part and the effect, unless otherwise specified.

undergo degradation over time and must be replaced. That is where organization steps in. In the natural world, there are situations in which the existence of a set of constraints depends on the effects that they collectively produce on the thermodynamic flow that traverses them. When this occurs, the set of mutually dependent constraints can be said to realize ‘closure’ and, therefore, to be organized: natural systems are biological whenever they are organized in this theoretically precise sense.

There are several implications that are relevant here. First, it has been argued that constraints subject to closure define biological functions (Mossio *et al.* [2009]). All kinds of biological structures and traits to which functions are usually ascribed satisfy the definition of organized constraint, at various different temporal and spatial scales. Organized constraints are defined functionally, not materially, although they are realized in specific material structures. Second, organizational closure plays a central role in explaining the stability of biological phenomena. The maintenance of functional constraints in the long run requires that their conditions of existence be (at least partly) mutually determined by the control they collectively exert on the thermodynamic flow. Third, organization refers to a regime that is typically, but not exclusively, realized by organisms. Although most philosophical and theoretical literature dealing with the notion of biological organization has focused on organisms, there seems to be no principled reason for such a restricted use. Rather, it seems reasonable and scientifically fecund to apply the notion of organization (understood as closure of constraints) to systems described at spatial and temporal scales beyond those of organisms (colonies, symbioses or ecosystems, see for instance Nunes Neto *et al.* [2013]). In particular, we submit that various objects usually included in extended heredity can be understood as functional constraints subject to closure, be it at the scale of organisms or within an encompassing organized system which includes said organisms (the precise determination of the boundaries of organisms being left open here).

One example would be epigenetic marks. Recent studies show that a hereditary trait such as resistance against pathogens in plants may correlate with the maintenance across generations of epigenetic marks, and more precisely DNA methylation, histone modifications and small RNA (Holeski *et al.*, [2012]). Epigenetic marks contribute to maintaining the system by affecting metabolic processes and resistance to pathogens while being stable with respect to the specific processes of gene transcription on which they exert a constraint. At longer time scales, they are maintained by the organism through several enzymatic effects, which makes them relevant candidates for being considered constraints subject to closure.

Another typical example is symbiotic microorganisms. Many insects, for instance, rely on symbiotic associates to perform biosynthesis and nutrient degradation (Douglas [2009]). Among these, pea aphids rely on the bacterium *Buchnera aphidicola* to synthesize essential amino acids (Hansen and Moran [2011]). In this case, bacterial symbionts live in specific cells (bacteriocytes) and are transmitted through internal channels; by enabling accessibility to food, they exert a functional constraint that contributes to maintaining the whole host-symbionts system. In turn, this system contributes to their maintenance, by making the nutrients consumed by the microorganisms available. As a result, the system constituted by host and symbionts can be described as realizing an organization, beyond the boundaries of typical organisms, in which symbiotic microorganisms exert a functional constraint.

Bird nests, which are classic examples of ecological legacies, can also be considered constraints subject to spatially-extended closure. Indeed, just as birds' parts, nests contribute to birds' maintenance by determining the way matter and energy are used, channelled and transformed. While they are conserved at the relevant scale at which they exert their role, they are also maintained by birds at longer time scales. Therefore, a nest could be described as a functional constraint subject to closure in the birds-nest system.

As functional constraints, the stability over time of these objects depends on the mutual interactions at work in the organization to which they belong. Of course, the maintenance of entities as different as epigenetic marks, symbionts or bird nests calls for different specific explanations; yet all of them are stable in the long run because they make a contribution to maintaining a closed organization that, in turn, contributes to maintaining their conditions of existence.

3.2 Extending organization in time

The second conceptual move of this paper consists in extending biological organization beyond the temporal boundaries that delimit each generation of biological system (referred to here as 'intra-generation systems').

In most cases, the existence of intra-generation systems depends on conditions that are (at least partially) established by previous intra-generation systems (belonging to the same lineage). In our theoretical framework, this means that each intra-generation system exists because of certain constraints exerted by previous intra-generation systems, in such a way that their temporal succession can be described as a continuous chain of organized systems

connected through constraint dependencies. We label such a situation ‘organizational continuity’. In the natural world, successive biological systems connected through organizational continuity tend to exhibit a high degree of functional similarity, although this does not necessarily imply invariance. Indeed, biological systems undergo variation over time, thereby preventing the recurrence of identical organized systems (Montévil *et al.* [2016]). Relying on an argument put forward by Saborido, Mossio and Moreno (Saborido *et al.* [2011], Mossio and Saborido [2016]), we maintain that, when similar functional patterns recur in successive systems, organizational continuity can be understood as the self-maintenance of a particular cross-generation organization.

In general, the description of organizational closure requires considering a time interval during which constraints are exerted and their dependencies occur. If constraints are stable enough during that interval, the chain of dependencies eventually folds up, and closure is realized. Once closure is realized, its theoretical description makes abstraction from the unfolding of the dependencies during the time interval, and refers instead to an ‘atemporal’ (or ‘relational’) network of mutual relations between constraints (what we call an organization). The reason for abstracting time is that closure is not realized by the system at a given point in time, but is rather ‘a set of processes taking place at different time scales [...]’. Thus, the whole network of dependencies should be considered as one “block” extended over multiple time scales’ (Montévil and Mossio [2015], p. 187). The description of closure by the observer must represent at a glance what the system realizes in time¹⁰.

Within closure, the mutual dependencies between constraints explain their stability during the time interval under scrutiny (say: a few hours for a unicellular organism, and days or weeks for a multicellular one). Let us now consider a time interval wide enough to include a succession of organized systems connected through organizational continuity and exhibiting functional similarity. Because of organizational continuity, the succession of organized systems can be understood as a continuous chain of constraint dependencies unfolding in time, across generations. Given that a set of functional constraints are stable beyond the temporal boundaries of each generation, closure can also be extended beyond these

¹⁰ In addition to the theoretical dimension, the fact of describing closure by abstracting it from time also has a philosophical implication (see Mossio and Bich [2017], p. 1102). Insofar as it consists of a circular relationship between causes and effects – between existence and activity – closure may be criticized for implying an inversion of the arrow of time and, therefore, not being a legitimate scientific concept. This is why it is important, in the context of a strategy for naturalization, to specify the exact nature of the relationship between closure and time.

boundaries, enabling the entire situation to be described as the self-maintenance of a particular cross-generation organization within that wider interval (Pocheville [2010], [2018] suggests an analogous ‘rescaling’ across biological generations in an evolutionary framework).

The idea of cross-generation organization requires three clarifications.

First, while the stability of functional constraints within an organism usually takes the form of a continuous persistence, their stability within a cross-generation organization may imply their recurrence and, possibly, the temporal coexistence of several instances (when parents and offspring co-exist). We claim that the recurrence of a similar network of constraints connected through organizational continuity can be legitimately interpreted as the stability of the same particular functional organization. Even though it is not continuously persistent, a cross-generation organization continuously sets the conditions enabling its own reestablishment. Because of the enduring influence on its own conditions of existence, it is legitimate to claim – we submit – that a particular biological organization never ceases to exist. We therefore take the conservation of functions through organizational continuity as a sufficient criterion for interpreting cross-generation organization as a particular object (see also Saborido *et al.* [2011], for a converging argument). In turn, the successive intra-generation systems constitute in this respect instances of the same particular cross-generation organization. In particular, insofar as they are parts of the same cross-generation organization, the recurring constraints can also be understood as temporal instances of the same functional object¹¹.

Second, the reproduction of an organized system may sometimes be a specific phase within a complex life cycle, during which biological organization undergoes massive functional variations. In this case, the recurrence of functional constraints can be observed only by

¹¹A possible objection to considering successive intra-generation systems as realizing a particular cross-generation organization comes from sexual reproduction: if offspring and parents are instances of the same organization, then it follows that both parents are also instances of that same organization, in virtue of the idea of transitivity that goes together with identity. The organizational account therefore seems to be committed to the multiple instantiation of particulars. Although we do not offer a full-fledged reply to this objection here, we would like to make a twofold comment. Firstly, the account is indeed consistent with the possibility that cross-generation organization can be realized by several co-existing instances since, as explained in the text, this is an implication of the conceptual framework. We believe that the coherence and fecundity of the account support the acceptance of this implication, in spite of its somewhat ‘strange’ metaphysical connotation. Secondly, it is important to highlight that the implication holds only in relation to the concept of cross-generation organization and its role in understanding biological heredity. Beyond this specific context, there are good reasons for considering intra-generation systems as distinct particulars and, moreover, for forbidding the multiple instantiation of their organization.

considering the relevant time scale, for instance, that at which similar phases of the life cycle can be compared. Considering a specific time scale for describing constraint stability and, therefore, cross-generation closure, means ignoring the organizational changes that occur during the cycles at shorter and longer time scales. Functional constraints are stable because they (stably) recur through organizational continuity. In other words, they exhibit conservation at the relevant time scale, just as they do within intra-generation organizations.

Third, and crucially, the fact that several intra-generation systems can be merged into a particular cross-generation organization does not mean that generations disappear; quite the contrary, in fact: the organizational account of biological heredity envisages the possibility of distinguishing between generations belonging to the same lineage, while maintaining that these successive generations can also be seen as a single particular organization. What justifies distinguishing between generations from an organizational perspective? Whereas cross-generation closure relies on the underlying organizational continuity, intra-generation systems are identified and separated by specific organizational discontinuities. In particular, organizational discontinuities map onto the idea of reproduction, typically invoked as a relevant criterion for separating generations belonging to the same lineage. Although we cannot provide here a full-fledged organizational account of reproduction, let us discuss the issue in a preliminary way¹².

By organizational discontinuity, we generally mean a functional change (an alteration, disappearance or appearance of one or more functional constraints) occurring in the temporal unfolding of constraint dependencies. In some circumstances, organizational discontinuities lead – through a fission event – to the appearance of two or more organized systems, all of which are organizationally continuous with the preceding single one, and yet reciprocally independent in functional terms. Fission can be described as a situation in which a set of functional constraints initially subject to a single closure undergo a reorganization leading to their partition into at least two distinguishable, non pre-existing, organized systems. To use Griesemer's ([2000]) words, biological fission implies 'material overlap', which is the fact that, during the multiplication of systems, 'organized physical parts of the parents at one time become organized physical parts of offspring at other times' (p. S359). When fission occurs, the resulting functional separation between the systems (which usually goes with a spatial

¹² DiFrisco and Mossio (forthcoming) explore organizational requirements for drawing the boundaries between generations and, thereby, distinguishing reproduction from development. In the following paragraphs, we substantially rely on their account.

separation) enables a temporal boundary to be drawn between different generations of organized systems, while including them in the same lineage. In a first approximation, the single preceding system is the producer, the parent, and belongs to the previous generation, while the new systems are the produced ones, the offspring, and constitute the new generation. Note that the organized systems that constitute the new generation, while exhibiting functional/spatial separation, are all organizationally continuous with the preceding one. The coexistence of organizational continuity and discontinuity is a central hallmark of our account of heredity.

Furthermore, from the background hypothesis that holds that the successive intra-generation systems also realize a single cross-generation organization, it follows that the relationship between the two generations can be understood as reproduction. This is because, as discussed, cross-generation closure implies that a certain degree of functional similarity must exist between the various generations of systems, as a consequence of the conservation of functional constraints across generations. If there were no cross-generation similarities, the discontinuity between the successive generations would be interpreted as the production of new (completely different) organized systems, rather than as reproduction.

In the situation described above, parents cease to exist when reproduction occurs, while new systems – the offspring – come into existence. This is typically what happens in cell division. Yet, the organizational account also applies to another situation, in which a parent persists after reproduction. The two situations are distinguished by the idea of ‘transitory asymmetrical dependence relationships’, which means that before being reciprocally independent, one of the two resulting systems depended on the other, but not vice-versa, during a transitory time. When asymmetry occurs, the dependent system can be understood as the offspring, whereas the non-dependent system can be interpreted as the parent (see DiFrisco and Mossio, forthcoming, for details). Examples of reproduction with asymmetrical dependence are budding or, at the multicellular level, sexual reproduction¹³.

¹³ Sexual reproduction can be described as a complex process during which a zygote maintains a transitory asymmetrical dependence relationship with the mother before becoming a functionally separate organized system later on, typically at birth. In turn, the zygote is the result of the fusion of gametes, which are previously generated through the fission of the cells constituting each parent (at some point in their ontogenesis), and which also maintain an asymmetrical dependence relationship with the parents. In sexual reproduction, fission occurs at the unicellular level, while the asymmetrical dependence holds (at least initially, before the zygote develops) between multicellular organisms and individual cells (gametes or zygotes).

The notion of cross-generation closure originally aimed to provide an organizational account of functions capable of including both intra- and cross-generation functions (Saborido *et al.* [2011]). We usually ascribe functions to reproductive traits even though they are not subject to closure within intra-generation systems. The reason, we argue, is that reproductive traits are subject to cross-generation closure: they are produced by a closed organization at some point in the parents' life cycle, and they contribute to re-establishing that very organization in offspring. More generally, cross-generation closure provides an explanation, within an organizational framework, of the stability of all those traits that are not functional within the boundaries of intra-generation organized systems¹⁴.

The central implication stemming from the extension of organizational closure in time is that most constraints, which are subject to intra-generation closure, are also subject to cross-generation closure. Conceptually, this means that their existence in each generation depends not only on the organization of the intra-generation system, but also on the constraints exerted by previous instances of the organization endowed with the same functional constraints.

3.3 What is biological heredity?

Having analysed the conceptual extensions of biological organization in space and time, let us now turn to heredity. In those circumstances in which a discontinuity - and, therefore, a boundary between at least two generations - can be drawn within organizational continuity, heredity is the conservation of functional constraints across generations. Accordingly, heredity is a specific kind of stability.

Functional constraints are maintained in time insofar as they are subject to closure. Yet, their stability does not necessarily imply heredity, because it might be the case that an organized system (an ecosystem, for example) does not display relevant reproductive discontinuities. If it does, then heredity designates the stability of its functional constituents due to their being subject to cross-generation closure, seen from the standpoint of intra-generation systems. Accordingly, heredity can be described as the stable recurrence of functional constraints from one generation to the next, which reinterprets from an organizational perspective the 'like-begets-like' phenomenon classically evoked in the literature.

¹⁴ One of the reasons for conceiving cross-generation closure as a particular object (see footnote 9, above) is that it maintains symmetry with intra-generation closure; it therefore provides a conceptually unified grounding for cross- and intra-generation functions.

The idea underpinning this account is that when some of the constraints of an intra-generation system are qualified as ‘hereditary’, this means that their existence within a given generation depends on their conservation within a temporally wider organization. Cross-generation organization is abstracted from time: different instances of the same functional constraints are understood as the same particular object subject to closure. Yet, cross-generation organization can also be interpreted in time, as a unidirectional succession of organized systems endowed with similar functional constraints¹⁵. According to this interpretation, if hereditary objects had not existed in previous generations, they would not exist in the present one¹⁶. However, the recurrence of hereditary objects does not have to happen in every generation, which means that an organizational account of biological heredity can include phenomena traditionally included under the concept of ‘atavism’.

Heredity, as discussed here, is a general concept designating a kind of stability. As such, it does not explain how functions are conserved across generations, which would require describing specific mechanisms and processes for each (class of) hereditary object. Besides, hereditary functions do not contribute in the same way to the maintenance of the organization and, furthermore, do not depend in the same way on it. Accordingly, any explanation of their cross-generation conservation would be different in each case. Explaining how distinct hereditary objects are conserved would require the elaboration of several interconnected models that would result in the establishment of an organizational theory of heredity.

Based on the above definition of heredity, we can define hereditary objects as the constraints of an intra-generation system subject to cross-generation closure. Hereditary objects are defined as functional constraints of an intra-generation system, whose conditions of existence within a given generation rely on their cross-generation conservation due to organizational continuity. As a matter of fact, according to our definition, most functional constituents of

¹⁵ From a theoretical point of view, organizational closure is open to temporal readings in both directions: one can say that previous instances determine subsequent ones, or that more recent ones determine previous ones. Presumably, the second interpretation would not be deemed acceptable, although it would be for reasons that are extrinsic to the theoretical characterization of closure.

¹⁶ The idea that heredity is a requirement for the existence of biological objects should not be confused with the idea that it is a defining aspect of Life. When arguing that biological objects would not exist if they were not included in a temporally-wider organization, we are not implying that heredity (and more generally history) contributes to the definition of biological systems (see also Moreno and Mossio [2015], p. 115, for an analogous claim). One might decide whether a given system under observation is a living one by appealing to criteria that do not include heredity, although a sound explanation of the presence of those criteria in the natural world should presumably appeal to this concept. Accordingly, the organizational account of heredity is, in principle, compatible with accounts advocating non-historical definitions of Life, such as, for instance, Ganti’s ([1973/2003]), Rosen’s ([1991]) and Varela’s ([1979]) ones.

biological systems are indeed hereditary insofar as their conservation exceeds the boundaries of a given intra-generation system. Nevertheless, when functions emerge within a specific generation (and possibly become hereditary thereafter), they constitute ontogenetic innovations.

We use the term ‘hereditary object’ to refer to any elements traditionally conceived as either ‘hereditary factors’ or ‘hereditary traits’. The distinction between factors and traits has been framed as a distinction between non-observable and observable entities, the former being thought of as the cause of the latter (Johannsen [1911]). While the difference between what is and what is not observable no longer holds since the materialization of genes, the possibility of distinguishing between hereditary causes and hereditary effects still underlies the distinction between factors and traits in mainstream biology. However, the organizational framework revolves around the idea of closure - a circular regime in which functional constraints are both causes and effects of each other at the same time. For this reason, the distinction between hereditary factors and traits – between genotypes and phenotypes – is no longer valid.

Two main categories of hereditary objects can be distinguished within a given intra-generation system. First, since hereditary objects can be subject to both cross and intra-generation closure, they comply with the organizational definition of function also within the intra-generation system. Let us call them ‘intra-generation hereditary functions’ (one example being a vascular system). There are two variants of this category: intra-generation hereditary functions can recur in each generation, as is presumably the case in most biological situations (epigenetic marks, enzymes and the vascular system are relevant examples); and intra-generation hereditary functions can also persist across generations, as may well be the case with bird nests and beaver dams. The difference lies in the fact that while reproduction generates different instances of the functional element in the first case (for example, two successive intra-generation systems – two beavers – have two distinct vascular systems), it does not in the second (these two successive intra-generation systems may share the same dam). Nevertheless, both variants must be maintained by each successive intra-generation system through a continuous material turnover, which means that even persistent intra-generation hereditary functions are not the same material objects across generations. This is consistent with the fact that the conservation of functional constraints goes with the

continuous turnover of their material constituents. Indeed, from an organizational perspective, biological heredity does not consist in the transmission of material objects per se¹⁷.

Second, hereditary objects can be subject only to cross-generation closure, which means that they are organizational functions only within the cross-generation organization. Let us call them ‘cross-generation hereditary functions’. Cross-generation hereditary functions include reproductive constraints that are typically recurrent objects involved in the reestablishment of the organization across generations.

The organizational view contrasts sharply with ones that associate heredity with replication (Dawkins [1976]). In the wake of earlier important philosophical contributions (Lewontin [1993]; Griffiths and Gray [1994]; Fox Keller [2000]), our view states that the persistence of hereditary objects – including DNA sequences – cannot be conceived of outside a systemic context. It also revives earlier perspectives, such as that proposed by Nanney ([1956]), which contest the localization of heredity in any particular entity, but rather conceive it as ‘the behaviour of a dynamic system’ (Gayon [1992], p. 433).

¹⁷ It is worth noting that the fact that heredity does not consist of the transmission of material objects does not necessarily mean that it – in general – does not rely on the transmission of some material structures. As a matter of fact, as we mention above – following Griesemer ([2000]) – reproduction implies fission which, in turn, implies the transmission of some material structures from parents to offspring (this is Griesemer’s material overlap). Nevertheless, even though fission implies some material overlap (an issue that we do not discuss in detail here), defining heredity as the cross-generation conservation of functions allows for the possibility that some specific hereditary objects – behaviour, for example – may be conserved from parents to offspring without any material transmission.

Table 1: Core concepts of the organizational account of heredity

Concept	Definition
<i>Constraints</i>	Parts of biological systems that exert control over the flow of matter and energy while being conserved with respect to the specific transformation on which they act, at the relevant time scale
<i>Organization</i>	Causal regime that consists in the mutual dependence (closure) of a set of constraints
<i>Reproduction</i>	Organizational discontinuity due to fission that draws the boundary between two biological generations
<i>Intra-generation system</i>	System that realizes a single or a succession of organized regimes within the boundaries delimiting a biological generation
<i>Organizational continuity</i>	Continuous chain of organized systems connected through constraint dependencies
<i>Cross-generation organization</i>	Causal regime that consists in the realization of organizational closure including at least two different intra-generation systems
<i>Heredity</i>	Conservation of functional constraints across generations
<i>Hereditary object</i>	Part of an intra-generation system subject to cross-generation closure
<i>Intra-generation hereditary object</i>	Hereditary object subject to both cross- and intra-generation closure (for example: genes, organs, some artefacts)
<i>Cross-generation hereditary object</i>	Hereditary object subject only to cross-generation closure (for example: reproductive traits)

4 Implications and objections

The organizational account of biological heredity has a number of significant implications which may prompt objections. A full assessment of its empirical relevance and explanatory power – compared to that of other, more inclusive frameworks – is a task beyond the scope of this paper. We take here just a few preliminary steps in that direction by highlighting some

conceptual consequences – which are particularly relevant to the current debate – derived from the adoption of organizational principles when dealing with biological heredity.

4.1 Heredity as a specific kind of cross-generation stability

The first implication is the conceptual distinction between heredity and other forms of cross-generation stability. Indeed, by drawing a principled boundary between the biological system and its environment, the organizational account allows us to distinguish between different kinds of stable objects. This distinction entails the one between biological heredity, which specifically refers to the cross-generation stability – as conservation – of a biological system's constituents, and the stability – as transmission – of environmental entities across generations. The distinction between different stable entities calls in turn for different explanations of their persistence or recurrence over time. One might argue that these considerations are irrelevant, insofar as a good theory of heredity needs to explain the stability of traits, not factors. However, within an organizational framework, the very distinction between factors and traits is meaningless and the stability of all hereditary objects is accounted for by appealing to the same explanatory principle. The various categories of stable entities generated by the organizational account are distinguished from each other through the interplay of two criteria: their theoretical status of constraints or resources, and whether or not they are dependent on the activity of the (considered) successive organized systems.

Dependent organized constraints

The first category of stable entities is that of 'hereditary objects', which have been defined as constraints subject to cross-generation closure. As such, hereditary objects are constituents of the biological organization that, in turn, draws the boundaries of the biological system in functional terms. From an organizational perspective, the biological system is the organization of constraints subject to closure.

Organized constraints may be hereditary or not. When they are, their presence within a given intra-generation biological system depends not only on their being subject to intra-generation closure, but also on the organizational continuity linking intra-generation systems across reproductive discontinuities and to cross-generation closure. As suggested in section 3, various biological entities such as nuclear genes, traditional organs (heart, liver, etc.), the metabolic capacities performed by *Buchnera aphidicola* in pea aphids and bird nests all fall

under the definition of organized constraints and, in the appropriate circumstances, of hereditary objects. The organizational characterization of hereditary objects seems to be essentially consistent with the spirit of both Griesemer's and Jablonka's accounts. Griesemer mentions that the 'evolved component mechanisms of development', whose reproduction with material overlap constitutes inheritance, are assumed to be 'organized physical parts of parents' (Griesemer [2000], p. S359). Similarly, and more specifically, Jablonka requires that, for an entity to be hereditary, it must carry information, in the sense of eliciting a functional response from a receiver endowed with an interpretative system, which results from evolution by natural selection (for instance, an organism) ([2002], pp. 582-3). She adds that an entity involved in inheritance processes should be both a source and a receiver of information and that information is heritable 'when it leads to the reconstruction of some aspects of the internal organization of one entity in another' (p. 589). This suggests that by being part of successive evolved biological systems, heritable information contributes to the reconstruction of these systems, which in turn participate in its maintenance over time. The idea that hereditary objects are subject to cross-generation closure seems to adequately capture these insights, while deriving them from organizational principles.

From the organizational perspective, hereditary objects are defined functionally, not materially. Accordingly, an important conceptual distinction should be made between 'functional conservation' on the one hand and a phenomenon that can be called 'environmental transmission', on the other. The heredity of functional elements from one generation to the next implies that they play the same role in both generations, precisely because their function is conserved. By contrast, the idea of transmission refers to a transfer of entities enabled by a 'donor' in favour of a 'recipient', such that they are exploited by either the former or the latter (but not both).

Independent constraints

The second category of stable objects comprises independent constraints, which are objects that contribute to maintaining the conditions of existence of the biological system by channelling the flows of matter and energy, although their own existence does not depend on the activity of this system. Independent constraints are not organized ones, which implies that they are not functional and hence not constituents of the biological system.

Independent constraints are parts of the stable environment. In contrast to hereditary constraints, their own cross-generation stability does not depend on the stability of an

organized system in which they would be integrated. The cave in which mammals may shelter is an example of a stable independent constraint¹⁸. It plays a role in the maintenance of the animal by controlling energy flows (for instance, by contributing to maintaining an adequate ambient temperature, or by hiding the animal from predators), while its existence does not depend on the organization of constraints that constitutes the mammal itself.

The cross-generation persistence of independent constraints can be understood as a kind of environmental stability, conceptually distinguishable from heredity. Independent constraints are conserved objects, which means that they might be shared and simultaneously exploited by different generations: for instance, a family of mammals (parents and offspring) may share the same cave for a while. If the cave is not shared (or not anymore), it can be transmitted, in the sense that parents may make it available to offspring in each generation. One might say that the offspring ‘inherit’ the cave from their parents; however, we argue that this would not be a case of biological heredity because the cave is not maintained through cross-generation closure. Transmission explains the availability and exploitability of the constraint for offspring, while its cross-generation conservation is, by hypothesis, independent.

While they do not count as hereditary objects from an organizational perspective, independent constraints could, on the contrary, be included in heredity by those accounts that conceive it as the stability of multifarious developmental resources. Insofar as heredity (inheritance) is defined as the ‘transfer of essential developmental resources vital to the reconstruction of the next generation’s life-cycle’ (Stotz [2017]), woodpecker habitats (nest sites), for instance, could perfectly well be considered inherited (Griffiths and Stotz [2013], p. 136). Similarly, independent constraints can be understood as hereditary by those accounts that characterize heredity as the transmission of information, especially if what is meant by ‘transmitted information’ is not explicitly defined¹⁹. In this view, for instance, habitat patches are considered to be inherited (Danchin *et al.* [2011], p. 490), as are the selective environments that have been modified by organisms (Mesoudi *et al.* [2013]). Also, when heredity is generally associated with the transmission of non-genetic factors influencing offspring phenotype, natal sites of salmon (Mameli, 2004, p. 46) and ‘habitat quality’ (Bonduriansky and Day [2009], p. 105) are both included in the concept.

¹⁸ Of course, the question of whether a given entity is or is not a constraint, and whether it is or is not dependent, is a scientific one that depends on the theoretical model and empirical evidence being used.

¹⁹ By requiring that entities involved in heredity be both receivers and sources of information, Jablonka’s framework ([2002]) seems to exclude the possibility of (what we call) independent constraints being hereditary, although they can be sources of information.

Dependent resources

The third category of stable objects includes dependent resources, namely the stable sources of matter and energy whose availability depends on the activity of biological systems. In contrast to constraints, which are functional objects conserved while exerting a causal role, resources are defined as material objects that are consumed by biological systems. As such, from an organizational perspective, they are not constituents of the system, but rather belong to the environment.

Dependent resources contribute to the stability of biological systems and their persistence depends on the activity of these systems. They exhibit cross-generation stability, in the sense that the same kind of resources, although not the same particular resources²⁰, are available across generations. Food supplies are typical examples of stable dependent resources: beef, for instance, might be available across generations through agricultural devices, while hatching plants eaten by new-born insects recur because of the parents' egg-laying strategy.

Like the persistence of independent constraints, that of dependent resources can be understood as a kind of environmental stability, different from heredity. As material objects consumed by biological systems, dependent resources are not conserved by definition, but rather regenerated across generations. If a piece of meat is eaten by a given generation, it is not conserved for the next one. If descendants receive resources from their parents and consume them, they will be unable to pass them on. Unlike constraints, specific resources cannot be available to both parents and offspring: they are lost to one generation when given to the next. As a result, there is no continuity between the material resources exploited by successive generations. Their cross-generation regeneration depends on the conservation of hereditary functions such as foraging behaviours or imprinting mechanisms. Blue tits and great tits, for instance, have access to the same kind of nutritional resources across generations because offspring inherit, through learning processes, the capacity to channel them (Slagsvold and Wiebe [2007]).

The exclusion of dependent resources from heredity converges with the intentions of Jablonka's account ([2002], p. 581). However, while we find her explanation of why food cannot be understood as a source of information (and therefore a potential hereditary object)

²⁰ Given that resources are characterized as material objects, it follows that – in contrast to organized constraints, which are identified functionally – their material turnover across generations prevents their successive instances being considered instances of the same particular object.

unconvincing²¹, the organizational perspective distinguishes between constraints and resources in a straightforward and principled way. Griesemer's account also seems to attempt to exclude resources from heredity by requiring, as mentioned earlier, that inheritance be about organized physical parts of parents. Yet, in the absence of an explicit characterization of what an organized part is, the implication remains to some extent underspecified. The organizational account makes a useful contribution in this respect. Conversely, the exclusion of resources diverges from those approaches that conceive heredity as the recurrence of a set of developmental resources or as the transmission of genetic and non-genetic factors. According to these accounts, extended heredity explicitly includes the trans-generation stability of food resources (Griffiths and Stotz [2013], p. 136) and hatching plants of insects (Mameli [2004], p. 52), as well as, more generally, multifarious nutrients (Bonduriansky and Day [2009], p. 105).

A related question is whether or not dependent resources can be 'transmitted' *stricto sensu* from one generation to the next. As in the case of independent constraints, parents can indeed play a role in making resources exploitable for their offspring and can 'transmit' them in an intuitive sense. Nevertheless, this transmission would be different from that of independent constraints. In particular, since it is not conserved, a particular resource cannot be first exploited and then passed on. Therefore, transmitted specific resources cannot have the same status in different generations: they cease being resources for a given generation when they are made available to the next. For this reason, it might be preferable to distinguish between the (relaxed) transmission of meat and the (strict) transmission of the cave.

Independent resources

In the interest of thoroughness, we feel we should mention the fourth category of stable entities, namely independent resources, which are basically consumable resources whose cross-generation stability is assumed to be independent from the activity of biological systems. Water falling as rain and oxygen present in the atmosphere are examples of independent stable resources. Just like independent constraints and dependent resources, independent resources are not functional and are not constituent parts of the biological

²¹ In particular, Jablonka ([2002]) argues that, in contrast to informational relations, non-informational reactions do not depend on the form of the source of energy and matter, the form being defined as 'the organization of the features and/or the actions of the source, and specifically those aspects of organization with which the receiver reacts' (p. 582). What we find unconvincing is the discussion (and examples) of why the interaction between an organism and food cannot also depend on the form (and related variations) of the latter.

system. Rather, they are parts of the environment that play a role in the stability of biological phenomena across generations. In contrast to independent constraints, independent resources do not exhibit conservation, precisely because they are consumable objects. In contrast to dependent resources, their availability across generations does not rely on the heredity (conservation) of organized constraints. This is why their stability should be distinguished from the three cases discussed previously.

Category switches

To conclude this section, it is worth pointing out that entities may move from one category to another over time, even though they are assumed to belong to only one category at any given moment. The organizational account can therefore deal with the changes entailed by biological dynamics at both an ontogenetic and evolutionary scale. However, describing how such category switches may occur is a fairly complex matter, which depends on the specific categories under scrutiny, the time scale being considered, and whether one is dealing with kinds of entities or particular entities. For instance, it is easily conceivable that certain kinds of independent constraints or resources can become dependent constraints or resources, at both the evolutionary and ontogenetic time scales. Organisms may start maintaining shelters which were previously independent, or learn how to cultivate a given type of food (tomatoes, for example) that was previously only found in nature; these changes can occur across generations as well as within the lifespan of an individual.

Things are less straightforward in the case of particular entities (for example, a particular tomato or a particular nest). Within the organizational framework, particular resources are continuously transformed so as to build constraints, which means that they cannot themselves become constraints²². Particular independent resources can become dependent ones, for instance, if they are found and harvested by a system instead of being immediately consumed. Also, a particular independent constraint may become dependent if the organization of an organism takes over the control of its external boundary conditions. So, for instance, a

²² There might be some tricky cases, such as those in which a given resource is recruited (which implies understanding its consumption as minimal transformation) and used as a functional constraint. One example would be gastroliths, the stones swallowed by some animals to help digestion. In this case, the stones are simply moved from the environment to the digestive system, and one could argue that this represents a category shift of a particular entity, with a resource becoming a constraint. Nevertheless, it seems to us that a precise application of the organizational framework can conceptually discriminate, even in this case, between the resource (the stones lying on the ground) and the functional constraint (a given concentration of stones of a specific volume in the digestive system).

previously independent nest can become dependent over time, if the organism begins contributing to its maintenance.

By offering an explicit definition of each category of cross-generation stable objects, the organizational account provides conceptual guidance for exploring the conditions under which category shifts are possible.

**Table 2: Four categories of objects stable across generations,
from an organizational perspective**

Objects	Examples	Status	Cross-generation stability
Dependent organized constraints	Organs, symbionts, nests	Parts of biological systems (i.e. exerting functions)	Conservation due to organizational closure: heredity
Independent constraints	Hermit crab shell, cave	Non-consumable and useful environmental objects	Conservation not due to organizational closure; exploitability due to environmental transmission (strict sense)
Dependent resources	Hatching plant, farm-breed meat	Consumable environmental objects	Regeneration due to organizational closure; exploitability (possibly) due to environmental transmission (relaxed sense)
Independent resources	Water falling as rain, sunlight	Consumable environmental objects	Regeneration not due to organizational closure

The table summarizes the four categories of objects stable across generations, from an organizational perspective. The upper category (highlighted in darker grey) includes objects that are understood as hereditary by the organizational account, as well as by most other conceptual accounts. The middle categories (in lighter grey) consist of objects with respect to which there is a divergence between the organizational account (that excludes them from heredity) and other accounts (that include at least some of them). The lower category includes objects that no account characterizes as hereditary (see text for details).

4.2 Heredity at various levels of description

The second implication is that the organizational account enables heredity to be thought about at various levels of description.

In this context, biological heredity occurs at any level of description at which an organization of mutually dependent constraints can be outlined, as soon as it exhibits relevant cross-generation discontinuities. As a result, the organizational perspective can be legitimately applied to various sub- or supra-organismic organized systems such as, for instance, organism-artefact systems like the birds-nest or the beavers-dam systems.

At what level of description can a given functional entity be shown to be subject to organizational closure? The theoretical and empirical answer to this question might be difficult and, sometimes, challenge our intuitions. For instance, some hereditary objects might turn out to be functional at the social level. Empirical studies could provide evidence that beaver dams are functional at the level of a community and not at that of an individual beaver. It may indeed be whole groups of beavers that maintain dams and that, in turn, are maintained by them. In other words, the organizational closure to which the dams are subject might include several beavers (in the same vein, rescaling considerations may lead us to conclude that selection for the dam-building trait occurs at the level of beavers' families, see Pocheville [2018]).

In this case, dams cannot be considered hereditary with respect to individual beavers. This is because functional conservation and cross-generation discontinuities must be described at the same level, otherwise the hereditary objects whose conservation is described at one level may be non-functional for the intra-generation systems described at another. For instance, the dam would – by hypothesis – be an independent useful constraint from the standpoint of individual beavers, something which would prevent it gaining the status of hereditary object at this specific level.

The same analysis could possibly be applied to artefacts used in human societies. Persisting buildings such as, for example, high schools, may play a functional role at the social level and therefore be understood as hereditary objects if relevant discontinuities were described at that organizational level. One of the difficulties would be that these supra-organismic organizations may not exhibit cycles that are theoretically equivalent to the life-cycles of single organisms. In this respect, it may prove difficult to adequately describe discontinuities

and therefore distinguish between successive generations (Pocheville [2010] and [2018] argues the possibility of distinguishing between generations through scale separation).

4.3 Non-functional and dysfunctional objects

One possible objection to the organizational account is that, by defining hereditary objects as functional constraints, it seems to exclude non-functional features from the field of heredity. Yet – the objection points out – it is common to include among hereditary objects various traits that are not necessarily functional, such as, for example, morphological traits like eye colour and chin shape. As a result, the organizational account is too restrictive because it is unable to make room for various standard hereditary objects.

We do indeed maintain that, in our framework, non-functional (in the sense of neutral) entities are not viewed as hereditary by definition. If their stability across generations does not depend on their being subject to cross-generation closure, they do not count as hereditary objects. However, we submit that non-functional neutral characteristics may be specific aspects of biological structures that, in other respects, do fulfil organizational functions. For example, although eye colour might not be functional per se (for the sake of the argument), eyes do possess other aspects that contribute to maintaining the organization to which they belong (such as perception of food, for example). The cross-generation stability of eye colour depends on (is linked to) the cross-generation stability of the eye itself. As such, eye colour can be viewed as a subordinate hereditary characteristic.

On a related note, critics might also claim that the organizational account does not grant the status of hereditary object to dysfunctions commonly thought to have a hereditary basis, such as, for instance, short-sightedness and diseases such diabetes or cancer. Here again, the organizational account seems too restrictive. Our response to this objection is straightforward: dys-functioning is, in fact, a way of functioning. We follow here Moreno and Mossio ([2015]), who argue that a dysfunction is an effect that (in contrast to a non-functional one) actually contributes to the maintenance of the organized system, although in a ‘poorer’ or ‘less efficient’ way, according to (quantitative) criteria that we do not explore here. A dysfunction is therefore an ‘impoverished’ function, whose stability is explained in the same way as that of ‘normal’ functions. Providing they exhibit cross-generation stability, dysfunctions comply with the organizational definition of hereditary objects. In particular, many heritable diseases can be described as effects of heritable impoverished functions,

which are constitutive parts of a biological organization. For example, short-sightedness is an effect of the heritable impoverished (set of) functions dedicated to visual perception; diabetes is an effect of the heritable impoverished functions controlling sugar concentration in the blood; and as for cancer, it is an effect of the heritable impoverished functions that control cell proliferation.

When seen as dysfunctional effects, many diseases can be understood as the effects of ‘altered’ functions. However, there may also be another case in which a given biological structure (for instance, a specific genetic sequence) would exclusively be involved in the occurrence of a disease without performing any function at all (not even in a poor way). If this were the case, the structure would not count as dysfunctional but rather as ‘non-functional’ (in the sense of deleterious). Its stability across generations would be linked to that of a functional part (functional DNA sequence, for example), with which it would be jointly reconstructed. It would therefore be treated as a subordinate hereditary object, just like the non-functional neutral objects mentioned above. It is worth emphasizing that stable non-functional objects can produce either neutral or harmful effects. In both cases, they are characterized as subordinate hereditary objects insofar as they do not contribute – in contrast to dysfunctional ones - to the maintenance of the organization.

5 Conclusions: from conservation to variation

The main aim of this paper was to connect biological heredity and organization. We have argued that heredity consists in the cross-generation conservation of functional elements which, in turn, are defined as constraints subject to cross-generation closure. We submit that the organizational account makes a major theoretical contribution insofar as it succeeds in broadening the scope of heredity beyond genes without over-extending this key biological concept. The central implication of the organizational account of heredity is that it discriminates between different forms of cross-generation stability related to different categories of stable biologically-relevant entities. A specific explanation must be provided for each form of stability, as well as their relationships. Heredity designates the specific way in which the (functional) constituents of a biological system remain stable over generations, in contrast to the stability of various elements in the environment.

Before concluding, we would like to go back to the interplay between conservation and variation in relation to heredity. One criticism that may be levelled at the account presented

here is that it neglects the key concept of variation. Heredity does not refer to the general recurrence of traits across generations; rather, it points to the recurrence of those traits for which there is some variability in a given population. This is why heredity is sometimes defined as the transmission of trait differences. Indeed, Mendelian genes were originally conceived as ‘difference makers’ for phenotypes. Moreover, the concept of ‘inherited variation’ is particularly important when heredity is discussed in the context of evolutionary biology, where the focus is on the transmission of trait variations associated with different fitness values.

We submit that the organizational account has no difficulty integrating variation into its conceptual framework. Although the issue really requires a full-fledged discussion (which we leave for a future work), we would like to offer some preliminary considerations here. First, inherited constraints in a given lineage (blood pumping capacity, for instance) can easily be described as functional variations when compared with other instances in a population. Second, we maintain that heredity is a matter of cross-generation stability. A variation occurring in a given generation (with respect to the previous one) is not necessarily hereditary. It only becomes so if it is stabilized from that generation on. Accordingly, the expression ‘inherited variation’ may be misleading: heredity is either about the stability of objects for which there is variability in the population – stability of variants – or about the stability of objects that are variations of previously existing functional objects – stability of ontogenetic innovations.

Biological organization does not prevent variation from occurring. Quite the contrary, in fact: organization is actually a condition for the emergence of functional variation and the element which enables its stabilization over time (Montévil *et al.* [2016]). Here, we follow Kauffman ([1995], p. 71), who has argued that the laws of self-organization underpin the evolvability of living beings, insofar as they ground a dynamical order that allows systems to ‘engage in the Darwinian saga’ (Kauffman [1995], pp. 73-4).

Furthermore, the extension of biological organization beyond the boundaries of typical organisms enables a wider spectrum of variations to be taken into account, while at the same time clearly distinguishing them from environmental modifications. This distinction is particularly important in evolutionary biology, given that environmental modifications and system variations do not have the same theoretical consequences: while environmental modifications are changes in the selective pressure exerted on an entire population, system modifications are individual changes in fitness.

Lastly, the emergence of functional variation over time shows that biological systems involved in hereditary processes do not reproduce faithfully. As time passes, biological organizations undergo continuous modifications. Consequently, the set of functions that are conserved across generations tend to decrease as larger numbers of generations are considered. The main implication is that biological heredity requires the cross-generation time interval at which functional conservation is observed to be specified. Again, the kind of conservation involved in biological heredity has nothing to do with rigid invariance; rather, it points to the delicate and complex balance between novelty and historicity, which is so characteristic of biological phenomena.

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