A Category-theoretic Interpretation of the Homology Concept in Biology

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Abstract

Homology is a fundamental but controversial concept in biology, referring to the sameness of biological characters across organisms. Despite its crucial role, its ontological nature has been a subject of intense debate, with a dichotomy between individualist and natural kind views. This study proposes a category-theoretic framework to reconcile these views by emphasizing the processual nature of homology. We first review major philosophical views of homology with their respective advantages and disadvantages. Next, we highlight the dynamic and evolving nature of homologs through two thought experiments. Through mathematical formulation, we then show that the individualist and natural kind views represent ordered set- and groupoid-like aspects, derived from a primary category-theoretical model based on a process-first dynamic view of homology. Our model covers a wide range of phenomena linked with homology, such as atavism, deep homology, and developmental system drift (DSD). Furthermore, it provides a unified perspective on the ontological nature of homology, overcoming the longstanding dichotomy between individuals and kinds in Western philosophy.

Keywords: homology, category theory, ontology, individual, natural kind

1 Introduction

Homology is a key concept in biology (Suzuki 2021; Wagner 2016). It refers to a special sense of the sameness of biological characters, but there has been an intense debate on what exactly this "sameness" means, involving both scientists and philosophers (Assis and Brigandt 2009; Brigandt 2009; Darwin 1859; de Beer 1971; Ereshefsky 2009; Hall 1994, 1999; Lankester 1870; Müller 2003; Owen 1849; Spemann 1915; Wagner 1989).

Behind this conflict, there is a fundamental ontological dichotomy between individuals (or particulars) and kinds (or classes, universals), which has long been granted in Western philosophy. For example, Aristotle divided actual things (*pragmata*) into particulars and universals in "*De interpretatione*" (Aristotle 1966, p. 47, 17a38–39). In the age of scholastic philosophy, the well-known "universals debate" took place (Klima 2000/2022). Even among analytical philosophers, the problem of natural kinds has been intensely discussed (Kripke 1980; Putnam 1975; Quine 1969).

Also in the philosophy of biology, the dichotomy between individuals and kinds appears as several conceptual issues. In particular, the ontological nature of biological species has been actively discussed. Some have proposed that a species is an individual as a historical entity (Ereshefsky 2002/2022; Ghiselin 1997), while others prefer to regard it as a sort of natural kind (Boyd 1999; Brigandt 2009; Griffiths 1999).

Compared to this species problem, a unique point in homology is the lack of clearly defined units. A species typically consists of distinct biological individuals or organisms as its units or members. Here, the boundaries of these units are clearly defined. In contrast, the units of homology (i.e., homologs) are body parts of biological individuals. In this case, the boundary of a homologous unit (i.e., which and how many portions of the body should be included in a homolog?) is not defined *a priori*. In philosophical terms, the problem of individuation is involved here. Because of this undefinedness, the ontological status of homologs is more uncertain and puzzling than that of species.

In this paper, we propose a novel perspective that the equivocal nature of homology can be understood by the category-theoretic formulation of a process-oriented view of homology, which can derive both the individualist and natural kind views as its specific cases. To demonstrate this, we first review major philosophical views of homology, pointing out their respective advantage(s) and disadvantage(s): the essentialist, individualist, and neo-essentialist homeostatic property cluster (HPC) natural kind views (Section 2). Next, we introduce two thought experiments to highlight the weakness of a major view that regards homologs as a HPC natural kind (Section 3). Still, we admit that homologs indeed show certain features as HPC natural kinds, along with the features as parts of an ontological individual. To explain this, we then mathematically interpret the individualist and HPC kind views, characterizing them as special cases of ordered-sets and groupoids, respectively (Section 4). With this mathematical formulation, we emphasize that both mathematical models of the individualist and HPC kind views are deduced from the category theory. This finding leads us to seek alternative views of homology. In Section 5, we review such alternative views that are newly proposed in highlighting processual and dynamical aspects of homology. In particular, we find that the view proposed by Suzuki and Tanaka (2017) shows strong affinity to the arrow-based category theory because it is more process-oriented. In this regard, we subsequently propose a mathematical formulation of these process-oriented

homology views in terms of the category theory (Section 6). Finally, we discuss biological and philosophical implications of our model, suggesting that our analysis opens a new horizon of process-first ontology, going beyond the dichotomy between individuals and kinds.

2 Different philosophical views of homology

In this section, we critically review major philosophical views of homology (i.e., the essentialist, individualist, and neo-essentialist HPC natural kind views) as summarized in Table 1.

Table 1 Different philosophical views of homology.

	Argument	Major advantage(s)	Major disadvantage(s)
Essentialist view (pre-Darwinian)	Homologs share an archetype or an essential nature.	... fits the traditional portrayal of scientific inquiry.	... fails to capture the evolving nature of biological entities.
Individualist view (Darwinistic)	Homologs are parts of an ontological individual.	... captures the dynamic and historical aspect of homologs as evolutionary phenomena.	... fails to capture serial homology; has no room for inductive generalization.
HPC natural kind view (evo-devo-associated)	Homologs share a homeostatic property cluster and its basal mechanisms as a natural kind.	... enables inductive generalization.	...focuses too much on homeostaticity, possibly leading to an oversight of the evolving aspect of homology.

2.1 Essentialist view

In history, Richard Owen was the first to define the homology concept in a more or less modern way. According to him, a homologous organ is "the same organ in different animals under every variety of form and function" (Owen 1843, p. 379). Here, the concept of homology was contrasted with that of analogy, the sameness of function; an analogous organ is "a part or organ in one animal which has the same function as another part or organ in a different animal" (Owen 1843, p. 374). Despite the difference in form and function, homologs are the same because they share the "essential nature" of animal body parts (Owen 1849, p. 70). Here, an essential nature specifically means an archetype, the predetermined pattern that provides a basis for modifications in each organism (Owen 1849, p. 2). This is a typical conception of the essentialist view of homology.

This essentialist view matches the traditional portrayal of scientific inquiry (Locke 1689/1690, Book III; Kornblith 1993, Chap. 2). Scientists first categorize scientific entities or phenomena into a natural kind. Then, they list invariant, intrinsic properties that the natural kind entails. These "defining" properties comprise necessary and sufficient conditions, which participate in the laws of nature. Finally, scientists

reveal the "essence" of the natural kind that explains the properties mentioned above. Through such a process, scientists successfully make explanations and predictions of the natural world.

Such a portrayal has a strong affinity to the practice in physics and chemistry. For example, gold can be distinguished from other kinds of metals in many aspects, including physical (e.g., the density, melting point, thermal conductivity, and malleability) and chemical (e.g., chemical corrosion resistance). Scientists have shown that the properties of gold can be explained by its microstructural essence—the chemical element Au (more specifically, its nuclide, electron configuration, crystal structure, etc.). Actually, biological species were taken to be the best examples of natural kinds before the findings of chemical elements, because they had long been regarded as invariant (Bird and Tobin 2008/2024).

2.2 Individualist view

However, biological entities do not fit such an essentialist attitude because of their evolving nature. The idea of invariant biological species was challenged by the transmutation theories, especially that of Charles Darwin (Darwin 1859). In Darwinian evolutionary theory, species are historical entities that transform and ramify through time. Their genetic structures diverge as well. Therefore, there is no invariant, intrinsic property, or essence of a species. In this way, essentialism failed, and the "death of essentialism" was pronounced (Ereshefsky 2002/2022).

Along the same lines, the Darwinian zoologist Edwin Ray Lankester criticized the essentialist view of homology, redefining the concept of homology (or homogeny in his own words). According to him, homologous (or homogeneous) structures are "genetically related, in so far as they have a single representative in a common ancestor" (Lankester 1870, p. 36). In other words, homologs are defined by historical continuity of descent from a common ancestor (Wagner 1989, p. 51). This "historical homology concept" was widely accepted among evolutionary biologists (Wagner 1989, pp. 53–54).

In the philosophical context, Michael Ghiselin discussed the ontological status of species and put forward the individualist view (Ghiselin 1997). He argued that species are not natural kinds but ontological individuals. Based on this assumption, he also suggested that "homologies are relations of correspondence between parts of wholes [individual organisms] which are in turn parts of larger wholes [evolutionary lineages, e.g., species]." (Ghiselin 1997, p. 205). Here, ontological individuals are characterized as they (1) are concrete rather than abstract, (2) engage in process, (3) have no defining properties (i.e., essential properties), (4) have no instances, (5) are spatiotemporally restricted, and (6) do not function in laws (Ghiselin 1997, 2005).

This conception of homology is highlighted in comparison with that of analogy. According to Ghiselin (Ghiselin 1997, p. 208), analogy is also a relation of correspondence between parts of wholes. However, those wholes are not parts of some larger individual but instead are members of a class since analogical characters are not spatiotemporally restricted (Ghiselin 1997, p. 208). Thus for individualists, to put it simply, "homologues are parts of an individual [e.g., a species] rather than members of a kind" (Ereshefsky 2009, p. 228).

Nevertheless, this seemingly clean-cut characterization of homologs as parts of an ontological individual becomes somewhat ambiguous when Ghiselin (1997, 2005) discusses iterative homology, more commonly known as serial homology—homological parts within an organism, for example, left and right eyes/hands/feet of humans ("antimeres") and paired appendages (antennae, maxillipeds, pereiopods, and pleopods) of arthropods ("metameres"). He clearly distinguishes iterative homology from inter-organismal homology ("evolutionary homology" in his term) and suggested as follows (Ghiselin 1997, p. 213):

> If by an explanation we mean relating something to its underlying causal basis, this makes a certain amount of sense for iterative homologues for which the correspondence is between parts that share a common developmental mechanism as well as a history of interconnectedness. On the other hand, since the existence of a common ancestor is a defining property of evolutionary homology, there is obviously something wrong with such a claim.

Given that iterative homology is the relation of correspondence between parts of a biological individual and that evolutionary homology is the relation of correspondence between parts of an ontologically larger individual, Ghiselin's argument sounds strange. One may go back to the original individualist definition of homology and respond that evolutionary homologs have "historical continuity" but iterative homologs do not. However, as Wagner (1989, pp. 55–57) pointed out, homologs themselves in fact lack continuity. Homologous characters, as being phenotypic parts of organisms, are newly generated in each generation. From this point of view, Ghiselin's conception is more careful and sophisticated, but it somewhat obscures the difference between evolutionary and iterative homology.

There is another and more serious issue in Ghiselin's conception of homology; what exactly is the "relation of correspondence" after all? Even if homologs themselves are parts of a spatiotemporally restricted individual, their relation of correspondence itself cannot be an individual. In other words, a biological species is an individual as a branch of the tree of life, while homologs are correspondence between parts of the branches (i.e., between species) or sub-branches (i.e., between biological individuals within a species). In fact, Ghiselin (1997, p. 28) regards relation as a property in terms of ontological categories. This means that homology itself is a (contingent) property of an ontological individual.[1]

However, if this is the case, then how can we recognize the homology (i.e., correspondence) of different parts? To put it another way, how can we find a part homologous to this other part but not to that one? In the case of analogy, the rationale that the parts of biological individuals are analogous is based on the class to which the individual belongs; this class is articulated by the very fact that the analogous parts of its members perform the same function. Therefore, the analogical relation of correspondence is not a contingent but definitive property of the class. In contrast, there is no such rationale for homology because the homological relation of correspondence

[1] In mathematical terms, such a relation of correspondence can be regarded as a groupoid, which can be considered to be a "class" in ontology. Thus, Ghiselin's argument ends up with a notion that homology is a sort of a class. In section 6, we argue that homology can be mathematically formulated in terms of category theory, successfully covering both the tree-like (i.e., individual-like) historical aspect and the abovementioned class-like groupoid aspect.

is just a contingent property or proposition of an ontological individual.[2] As Ghiselin (2005, p. 95) wrote:

> The uniformities that we call laws of nature are formulated as true of classes, and make no reference to any particular individual. Consequently such generalizations of systematics as "all mammals have hair" are purely historical, or contingent, propositions. [...] Homology statements are strictly historical propositions. They are not laws of nature and they lack the necessity that characterizes laws of nature.

As a related issue, lacking the possibility of inductive generalization is also a disadvantage of the individualist view of homology. According to (Ghiselin 2005, p. 95), homology is merely a result of historical contingency. Thus, neither any generalization nor prediction is possible. However, these arguments do not well fit with scientific practices involving the homology concept. Evolutionary biologists often use typological representations to generalize homologous characters (Suzuki 2021). Furthermore, they may predict (or at least imagine) what properties (e.g., internal structure) can be found in a homological character of unknown past or even future species, which is phylogenetically related to known ones, based on such generalization. Of course, this generalization cannot be a natural "law." In other words, it is not always true. However, such a "relatively weak" generalization in fact has a role in biology (Parke and Plutynski 2020).

2.3 Neo-essentialist HPC kind view

In response to the criticism from the individualists, the proponents of the natural kind view adjusted their theory in several ways. Some promote historical or relational essentialism, which treats relational properties (such as genealogy and interbreeding), instead of intrinsic properties, as the essence of a species (de Queiroz 1995; Griffiths 1999; LaPorte 2003; Okasha 2002). However, this position has received considerable criticism. For example, Ereshefsky (2010, p. 683) pointed out that relations such as genealogy and interbreeding do not fulfill the explanatory role, which is a core aim of essentialism, failing to explain the traits typically found among the members of a species.

Another growing part of neo-essentialism is the HPC kind view (Boyd 1999; Brigandt 2009; Griffiths 1999), which moderates the essentialist dogma to encompass biological entities (Table 2). First, classical essentialism holds that a natural kind has a set of invariant and intrinsic properties. In the HPC kind view, on the other hand, a natural kind forms a cluster, rather than a complete set, of often co-occurring properties that can be variable and extrinsic to some extent. Next, a natural kind in classical essentialism has an explanatory role in the laws of nature. However, variable properties in the HCP kind view can no longer contribute to such laws, which do not allow any exceptions. In spite of failing to fulfill such a strict requirement, an HPC natural kind is still helpful to make inductive generalizations that allow some exceptions. Last, classical essentialism presumes that the properties of a natural kind stem from

[2] The obscurity of iterative and evolutionary homology pops up again here. After all, both are correspondence between parts of an individual, either biological or historical. Considering that a historical relationship is also a kind of causal relationships, it seems that there is just a difference in the levels of the organization.

its intrinsic and microstructural essence. Instead, the HCP kind view assumes homeostatic mechanisms, which bring about the co-occurrence of properties and can be extrinsic and/or macrostructural.

Table 2 Classical essentialist and HPC kind neo-essentialist views of natural kinds.

	Classical essentialism	HPC kind neo-essentialism
A natural kind has...	a set of invariant and intrinsic properties.	a cluster of homeostatic properties.
A natural kind plays an explanatory role in...	the laws of nature.	inductive generalizations.
The properties of a natural kind stem from its...	(intrinsic, microstrutual) essence.	basal homeostatic mechanisms.

Some proponents of the HPC kind view argue that their account is metaphysically compatible with that of the individualists, while emphasizing an epistemological advantage of their view in terms of its explanatory role (Assis and Brigandt 2009; Brigandt 2009). In fact, the homology concept is usefully employed to explain the structural or developmental features shared among the members of the homologs. In this respect, the homology concept can be categorized into a broader concept of the developmental types (e.g., cell types). Although typology has been criticized for its essentialist nature, a non-essentialist form of typology (i.e., representational typology) has a certain explanatory role in biology (Love 2008; Suzuki 2021).

However, even if the epistemological advantage of the HPC kind view is granted, it is not negligible that we also commit to its ontological aspect when we adopt that viewpoint. Thus, we need to carefully examine its ontological entailments.

On this point, the predilection for homeostaticity appears to be one of the central issues. Namely, the HPC kind view may focus too heavily on the static aspect of natural phenomena, which results in ignoring their dynamic aspect. Although this attitude is indeed useful for inductive generalization, it is crucially unsuitable for evolutionary entities because they are dynamic in nature (refer to the discussion using two thought experiments in the next section).

Another issue is the nature of the homeostatic mechanisms, which is the very basis for the explanatory power of natural kinds. Boyd (1999, p. 129, 141–142) assumed that membership of properties in a natural kind is determined by homeostatic mechanisms or causal structure of the world, independent of our conventions or our theorizing. However, the exact meaning of mechanisms of causal structure here is obscure. In fact, Craver (2009) analyzed the HPC theory in light of the philosophy of mechanism and argued that the HPC view is not free from our epistemic interest when we judge whether two mechanisms are the same or different (i.e. when we carve out natural kinds).

To refine the HPC theory, some authors have tried to replace homeostatic mechanisms with other concepts. For example, Khalidi (2018) proposed natural kinds as nodes in causal networks. In this view, co-occurrence of properties is not assumed to rely on any homeostatic mechanisms. Instead, natural kinds are regarded as clusters

of core causal properties, which give rise to clusters of derivative properties as non-natural kinds. Nevertheless, Onishi and Serpico (2021) indicated that this view fails to overcome Craver's (2009) challenges, just as the original HPC theory does.

On the other hand, Slater (2015) abandoned any mechanistic or causal notions for natural kinds and put forward the stable property cluster (SPC) account. However, as Onishi and Serpico (2021) pointed out, the SPC theory fails to account for some inductive inference in science, which is an important epistemic and practical aspect of natural kinds.

In addition to interest-relativity, another related issue appears to be involved in the HPC theory and its variations: the notions of determination and causation are mixed up. For example, Boyd (1991, p. 141) wrote, "kinds such that the unity of the property-cluster which defines them is *causal rather than conceptual*" and "[t]he natural definition of one of these *homeostatic property cluster kinds* is determined by the members of a cluster of often co-occurring properties and by the ("homeostatic") mechanisms that bring about their co-occurrence" (italics original). Khalidi (2018, p. 1389) presented a similar view, saying; "it is usually specific stable combinations of some set of (determinate) properties that have a rich set of effects, giving rise causally to the instantiation of a multitude of other properties." These authors assume that a natural kind is determined by a cluster of properties, which are causally interconnected with their basal mechanisms and/or other associated properties. They seem to presuppose the linkage of determination and causation here.

As Kment (2010) pointed out, David Hume introduced two important ideas about causation. One is the determination idea ("causes determine that their effect obtains") and the other is the difference-making idea ("a cause makes a difference to whether its effect obtains: without it, the effect would not have obtained"). As many readers of Hume have remarked, contrary to what Hume suggests, these ideas are quite different. In Kment's (2010, p. 82) words:

> To say that the causes together nomically determine their effects is to say that, given the laws, the causes are jointly sufficient for the effect. By contrast, to say that the effect would not have obtained if any of causes had not obtained is to say that causes are individually necessary in the circumstances for the effect.

As we have discussed above, natural kinds and laws of nature were tightly coupled in classical essentialism. Despite that the HPC theory and its variations weaken this assumption and instead appeal to inductive generalization, they still stick to the notion of determination, which presupposes certain laws. In fact, Onishi and Serpico (2021, p. 65) pointed out that three indeterminacies are involved in the HPC theory and its variations as follows:

- The Boundary Problem: Indeterminacy regarding factors that should be included among the components of kind-defining mechanisms;
- The Degree of Abstraction Problem: Indeterminacy regarding the degree of abstraction at which kind-defining mechanisms are characterized, from very detailed to very schematic; and

- The No One-to-one Problem: Indeterminacy regarding a kind-defining mechanism that arises from non-linear causal pathways between etiological mechanisms, constitutive mechanisms, and property clusters.

Therefore, the HPC theory and its variations cannot maintain determinacy. Kment (2010) argues that what justifies us in using patterns of difference-making to test causal claims is the determination idea. We think determination is too much for this justification. Especially in biology, it is often stressed that there is no universal law (Beatty 1997; Parke and Plutynski 2020). Therefore, causation in biology does not imply determination in a strict sense (i.e., the causes may not be nomically sufficient for the effect). Still, biologists successfully use causal claims in their research. Biological processes in general, and evolutionary processes in particular, are surely causal but not deterministic because they are inherently stochastic.

Also in the case of homology, homologs are often based on surprisingly different mechanisms. One example is developmental system drift (DSD), where homologous characters are generated through non-homologous developmental processes (Haag and True 2021; McColgan and DiFrisco 2024; True and Haag 2001). For instance, the developmental mechanisms for somitogenesis are highly variable in both vertebrates and arthropods (DiFrisco and Jaeger 2019; Peel and Akam 2005). Another example is that homologous parts can often be regenerated through different mechanisms from that found in development (Aztekin 2024). Finally, it is known that a phenotype originally produced in response to environmental cues can later be genetically fixed to appear. This process was first described by Waddington (1953) as genetic assimilation. These phenomena indicate that homologs are not determined by their generative mechanisms in a strict sense.

2.4 Summary

As we have seen above, there are now two major views on the ontological status of homology—namely, the individualist and HPC kind views—each with distinct advantages and disadvantages.

The individualist view argues that "homologies are relations of correspondence between parts of wholes [individual organisms] which are in turn parts of larger wholes [evolutionary lineages, e.g., species]" (Ghiselin 1997, p. 205). It successfully captures the dynamic and historical aspect of homology as an evolutionary phenomenon. However, it struggles to account for the notion of serial or iterative homology well. A more serious issue in the individualist view, or at least in Ghiselin's version, is the ontological status of the "correspondence." Furthermore, this view does not allow inductive generalization of homologs because the properties of an individual and its parts are merely contingent by definition.

In contrast, the HPC kind view has the epistemological advantage of enabling inductive generalization, while it involves some serious ontological issues. In our view, it makes unnecessarily strong ontological commitment to homeostaticity and determination, which seems to be inherited from classical essentialism. In particular, an excessive focus on homeostaticity may result in overlooking the evolving aspect of homology. To emphasize this point, we present two thought experiments in the next section.

3 Two (too?) simple thought experiments

Homologs in particular—and biological entities in general—are participants in dynamic processes. Therefore, the features of homologs can be changed drastically through time. The following two experiments illustrate this dynamic aspect of homologs.

3.1 Decrease of shared properties

Let us think about a branching lineage of homologs (Fig. 1). At first, an ancestral homolog A possesses certain properties: a, b, and c. Its descendants inherit these properties with modification and deletion as well as the acquisition of new properties. For example, the descendant homolog B retains ancestral properties a and b, but c is modified into c'. Moreover, a further descendant C loses b and its descendant D newly acquires d. In a similar way, each lineage of descendants experiences specific changes during the evolutionary process. As a result, it is possible that the most recent descendants D, F, and H have only a as a shared ancestral property.

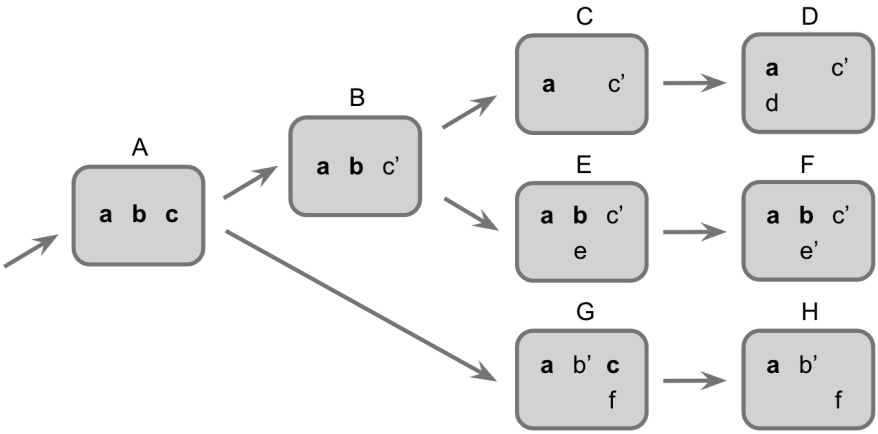

Fig. 1 Schematic diagram of homologs with decreasing properties. Round gray squares represent homologs, and characters (a, b, c, ...) denote homologs' properties. The primes ($'$) indicate evolutionary modification of the properties.

This thought experiment demonstrates that the number of shared properties decreases as we compare more distantly related descendants. Then, as the HPC kind view focuses on such shared or homeostatic properties to recognize a natural kind, the "natural kindness" becomes weaker and weaker as homologous characters evolve—even though they are indeed homologous in a genealogical sense. Here, this example calls attention to the discrepancy between weakening natural kindness in the HPC view and actual consistent generation of homologs.

3.2 Gradual but complete replacement of properties

The following case demonstrates the difficulty of the HPC kind view more clearly. Here, an anagenetic evolution of a lineage of homologs is considered (Fig. 2). At first, an ancestral homolog A has certain properties: a, b, and c. Then, a descendant of A (labeled as B) inherits two of the ancestral properties, b and c, and acquires a new property d, followed by the descendant C with inherited c and d and novel e. Finally, the descendant D succeeds d and e from C, and newly obtains f. In this sequence, the properties of the homologs are gradually but completely replaced, such that the ancestral A with a, b, and c, shares no properties with the descendant D with d, e, and f.

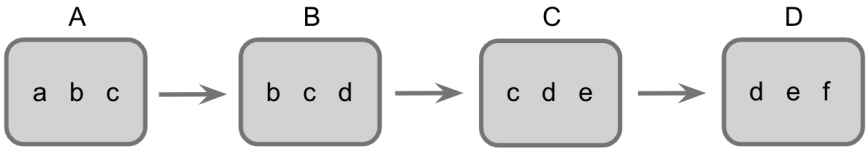

Fig. 2 Schematic diagram of homologs with properties that are gradually but completely replaced. For the explanation of items and characters, see the legend of Fig. 1.

As all properties are replaced completely, there is no homeostatically conserved property, despite the continuous generation of the homologs. The HPC view thus appears to be inapplicable.

Some may insist that homology does not hold in this case. Of course, this is an idealized and extreme toy model, but similar cases are indeed found in nature. The abovementioned DSD is a good example; in a DSD, the developmental mechanisms under homologs are drastically substituted. Another example is genetic assimilation, where the same (i.e., homologous) characters are produced initially via epigenetic, and later genetic, mechanisms. Therefore, the present toy model is not just an armchair speculation, and homology does hold here.

Other HPC advocates may instead argue that there should be other homeostatic properties because the homologs are certainly generated. Still, the aforementioned examples of DSD and genetic assimilation indicate dynamic changes in generative mechanisms for these homologs, undermining the existence of "basal" mechanisms in the HPC view in such cases. Thus, the present toy model again shows the discrepancy between weak natural kindness in the HPC view and the actual consistent generation of homologs.

3.3 Conceptual implications from these thought experiments

The two thought experiments proposed here illustrate the dynamically evolving nature of homology, where the properties and their generative mechanisms of homologs can change drastically, highlighting the disadvantage of the HPC view even if it has some epistemological advantage.

An important point here is that we do not intend to negate and abandon the HPC view but to show its negative tendency to overlook and truncate these dynamic

changes to abstract (quasi-)static snapshots. We instead seek an alternative way to embrace the processual aspect of homology (e.g., genealogical continuity of homologs) in the following part of the present paper.

Still, homological characters indeed show certain natural kind(-like) features, and scientists successfully explain and predict lineage-specific biological phenomena based on homology. How could this be possible? To explain this, it is useful to conceptualize the individualist and HPC kind views in terms of mathematics as discussed below.

4 Mathematical interpretation of the individualist and HPC kind views

From a mathematical perspective, the two current views of homology (i.e., the individualist and HPC kind views) appear to highlight ordered set-like and groupoid-like aspects of homology, respectively. This mathematical interpretation helps us extract formal frameworks of the two views, leading to an alternative way to formulate homology using the mathematical notion of category. For this purpose, we first introduce some basic mathematical definitions regarding category theory.

4.1 Definition of category, preorder, and groupoid

In mathematics, a category is defined as a mathematical system composed of entities called objects and arrows (or morphisms) satisfying the following four conditions.[3]

Condition 1 (arrow, domain, and codomain)**.** *For any arrow f, there exists an object called $dom(f)$ and another object called $cod(f)$, which are called the domain of f and the codomain of f, respectively.*

When $dom(f) = X$ and $cod(f) = Y$, we denote it as

$$f : X \longrightarrow Y \tag{1}$$

or

$$f : X \xrightarrow{f} Y \tag{2}$$

Arrows are also denoted in any direction, not only from left to right, as above.

Condition 2 (composition)**.** *For any pair of morphism f, g satisfying $dom(g) = cod(f)$,*

$$Z \xleftarrow{g} Y \xleftarrow{f} X \tag{3}$$

there exists an arrow $g \circ f$

$$Z \xleftarrow{g \circ f} X \tag{4}$$

[3] The description in this subsection is adapted to a large extent from Saigo (2021).

called the composition of f, g.

For the composition of arrows, we assume the following conditions:

Condition 3 (associative law)**.** *For any triple f, g, h of arrows satisfying $dom(h) = cod(g)$ and $dom(g) = cod(f)$,*

$$(h \circ g) \circ f = h \circ (g \circ f) \tag{5}$$

holds.

Condition 4 (identity law)**.** *For any object X, there exists an arrow called identity arrow $1_X : X \longrightarrow X$. For any arrow $f : X \longrightarrow Y$*

$$f \circ 1_X = f = 1_Y \circ f \tag{6}$$

holds.

By the correspondence from objects to their identity arrows, objects can be considered as special kinds of arrows by identifying each object X with its identity arrow 1_X.

In sum, the definition of a category is as follows.

Definition 1 (category)**.** *A category is a system composed of two kinds of entities called objects and arrows, equipped with domain/codomain, composition, and identity, satisfying the associative law and the identity law.*

In a category, we can define the "operational" sameness between objects via the notion of invertible arrows (isomorphism).

Definition 2 (invertible arrow, i.e., isomorphism)**.** *Let C be a category. An arrow $f : X \longrightarrow Y$ in C is said to be invertible in C if there exists some arrow $g : Y \longrightarrow X$ such that*

$$g \circ f = 1_X, f \circ g = 1_Y \tag{7}$$

An invertible arrow in C is also called an isomorphism in C.

There are many categories whose collection of arrows is too large to be a set. In the present paper, we focus on small categories:

Definition 3 (small category)**.** *A category C is called small if the collection of arrows is a set.*

The groupoid and preorder are special cases of small categories.

Definition 4 (groupoid)**.** *A small category is said to be a groupoid if all arrows are invertible.*

For example, a set of shapes and homeomorphisms (invertible continuous maps) between them form a groupoid (Fig. 3A). A coffee mug and a donut are homeomorphic and mutually deformable (i.e., this deformation is invertible). Therefore, these two shapes are objects of a groupoid. In the same vein, a ball, a bowl, and a cube and homeomorphisms between them collectively form another groupoid.

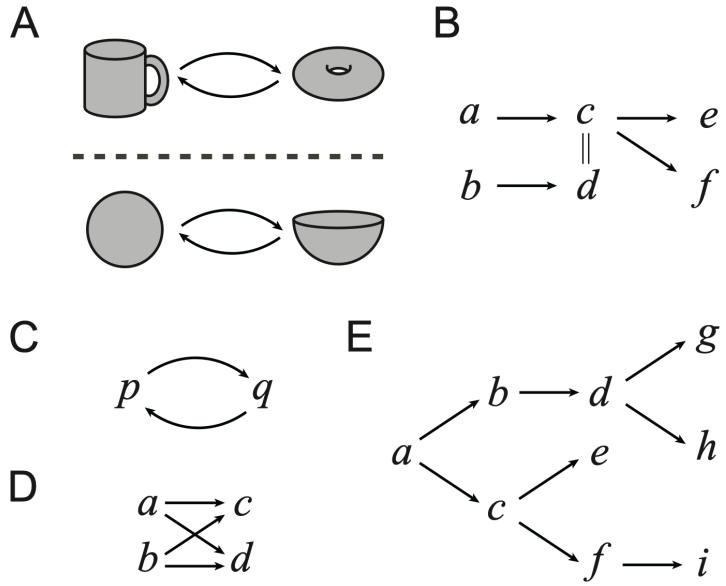

Fig. 3 Schematic representation of groupoid, order, equivalence relation, and meet-semilattice. (A) Homeomorphic shapes in topology as an example of groupoids. A coffee mug, a donut and homeomorphisms between them form a groupoid, while a ball, a bowl and homeomophisms between them form another groupoid. (B) An example of ordered sets. (C) Equivalence relation. (D) An example of ordered sets that are not meet-semilattice. (E) An example of meet-semilattice.

Definition 5 (preorder)**.** *A pair* $(P, \rightsquigarrow)$ *of a set* P *and a relation* $\rightsquigarrow$ *on* P *satisfying*

$$p \rightsquigarrow p \tag{8}$$

for any $p \in P$ *(reflexivity) and*

$$p \rightsquigarrow q \text{ and } q \rightsquigarrow r \Rightarrow p \rightsquigarrow r \tag{9}$$

for any $p, q, r \in P$ *(transitivity) is called a preordered set. The relation* $\rightsquigarrow$ *on* P *is called a preorder on* P*. The preordered set* $(P, \rightsquigarrow)$ *can be viewed as a category whose*

objects are elements of P when we define the relation $p \rightsquigarrow q$ between p, q as the unique arrow from p to q. Conversely, we can define a preordered set as a small category such that for any pair of objects p, q there exists at most one arrow from p to q.

Note that order and equivalence relation are obtained from preorder by adding antisymmetricity and symmetricity, respectively.

Definition 6 (order)**.** *A preordered set satisfying*

$$p \rightsquigarrow q \text{ and } q \rightsquigarrow p \Rightarrow p = q \tag{10}$$

for any p and q (antisymmetricity) is called an ordered set.

In other words, the entities in an ordered set have predecessor-successor or equal relations (a schematic image of ordered sets is shown as Fig. 3B). An example of order is the inclusion relation ($\subseteq$) of subsets. If A is a subset of B, which is in turn a subset of C, then A is a subset of C (transitivity). If A is a subset of B and B is a subset of A at the same time, then A is equal to B (antisymmetricity).

Definition 7 (equivalence relation)**.** *A preordered set satisfying*

$$p \rightsquigarrow q \Rightarrow q \rightsquigarrow p \tag{11}$$

for any p and q (symmetricity) is called an equivalence relation.

An example of equivalence relation is geometric congruence and similarity. If a figure A is congruent (or similar) to B, then B is congruent (or similar) to A as well.

This equivalence relation can also be regarded as a special case of groupoid because p and q are in invertible relationships (Fig. 3C). In other words, groupoid is a generalized notion of equivalence relation.

In the following subsections, we propose that the individualist and HPC natural kind views of biological homology are mathematically interpreted as highlighting its ordered set-like and groupoid-like aspects. Based on the fact that both ordered set and groupoid are special cases of category, we further discuss that these two views can be generalized in terms of category theory.

4.2 Ordered sets and the individualist view

The individualist view highlights the historical continuity of homologs as evolutionary entities, meaning that homologs form a sequence, which sometimes bifurcates as a tree. The semilattice, a special case of ordered sets, is useful for mathematically describing such tree structures. Although there are two types of semilattices, join- and meet-semilattices, here we introduce only the latter one because of its affinity to the evolutionary tree.

Definition 8 (meet-semilattice)**.** *A (partially) ordered set is a meet-semilattice if the greatest lower bound exists for its all pair of elements p and q. The greatest lower bound is called the meet of p and q, denoted as $p \wedge q$.*

The reason why we need semilattice is that ordered sets may not be able to represent the last common ancestor. Fig. 3D shows an example of ordered sets that are not meet-semilattice. Here, the elements a and b are lower bounds of c and d. However, it cannot be specified which element, a or b, is the greatest lower bound of c and d (i.e., $c \wedge d$). In contrast, the greatest lower bound or the meet exists for all pairs of elements of meet-semilattice by definition. Here, lower bounds and the greatest lower bound can be interpreted as common ancestors and the last common ancestors in a phylogenetic tree. Based on this point of view, meet-semilattice is appropriate to represent tree structures (see Fig. 3E as an example).

Therefore, semilattice can mathematically represent the individualist view of homology, which emphasizes the historicity of homology as an evolutionary phenomenon[4]. Evolutionary morphologists often discuss phylogenetic transformation of homologous structures. As an example, let us think about the tetrapod forelimb, which originally stemmed from the pectoral fin of the fish-like ancestor. While this fin retained its morphology in cartilage and bony fishes retain this fin morphology, it transformed into a limb with digits in tetrapods. Furthermore, the forelimb changed its form variously in different lineages (e.g., the wing in birds, the fin in whales, and the arm in humans). Such divergent evolution is well captured by the ordered set, or more precisely, by the semilattice.

4.3 Groupoids and the HPC natural kind view

In contrast to the individualist view, the HPC natural kind view focuses attention on the groupoid-like aspect of homology. This attitude stems from classical essentialism, which holds that 1) members of a natural kind share "defining" properties as the necessary and sufficient conditions to be its members, 2) the members share the essence for being a member of the natural kind, and 3) having all the "defining" properties is logically equivalent to having the essence (i.e., if an entity shows all the "defining" properties, it must contain the essence, and vice versa). Subsequently, the HPC natural kind view mitigated or even abandoned some of these strong postulates, but in our view, it still retains the essentialist attitude. To clarify this point, we first construct a sort of category for understanding these classical and HPC natural kind views as follows.

Let E ("the set of entities") and P ("the set of properties") be sets, and M ("the set of *meaningful* subsets of properties") be a set of subsets of P (i.e., a subset of the power set of P) which is closed under intersection (i.e., "$X \in M$ and $Y \in M$" implies "$X \cap Y \in M$").

For each map $\Sigma : E \longrightarrow M$ (for each $\epsilon \in E$, $\Sigma(\epsilon)$ is interpreted as "a certain set of the properties satisfied by ϵ"), the category $C[\Sigma]$ is defined as follows:

[4]Note that the semilattice here represents lineages of homologs, not organisms or species. We can construct a phylogenetic tree of any evolutionary entities, including body parts and genes (cf. orthologous and paralogous genes).

- Object of $C[\Sigma]$: any element of E. ("an entity");
- Arrow of $C[\Sigma]$: any triple (β, μ, α) consisting of $\alpha, \beta \in E$ and $\mu \in M$ satisfying $s \subseteq \Sigma(\alpha) \cap \Sigma(\beta)$. ("a relation between α and β mediated by a subset of properties they have in common") [Remark: In general μ can be empty].;
- Domain/codomain: $dom(\beta, \mu, \alpha) = \alpha, cod(\beta, \mu, \alpha) = \beta$;
- Composition: $(\gamma, \nu, \beta) \circ (\beta, \mu, \alpha) = (\gamma, \nu \cap \mu, \alpha)$; and
- identity arrow: $1_\alpha = (\alpha, \Sigma(\alpha), \alpha)$.

(Associative law follows from the associativity of $\cap$. Unit law is easy.)

This category becomes a dagger category, that is, a category with an operation † satisfying

- $(x \circ y)^\dagger = y^\dagger \circ x^\dagger$;
- $(1_X)^\dagger = 1_X$ for any object X; and
- $(x^\dagger)^\dagger = x$.

by defining $(\beta, \mu, \alpha)^\dagger = (\alpha, \mu, \beta)$. However, it should be noted that dagger categories are not necessarily to be groupoids. Note that the arrow (β, μ, α) is invertible if and only if $\mu = \Sigma(\alpha) = \Sigma(\beta)$.

In the classical essentialism, a natural kind is defined by suitable Σ satisfying the Property (Classical) below:

Property (Classical). *$\Sigma(\alpha) = \Sigma(\beta)$ if and only if α and β belong to the same kind, where $\Sigma(\epsilon)$ is a certain set of properties satisfied by ϵ.*

In this case, α and β belong to the same kind if and only if it is isomorphic in $C[\Sigma]$. In other words, the core (i.e., the subcategory consisting of all invertible arrows) of $C[\Sigma]$ has all the information of classification.

In addition, the classical essentialism assumes an essence underlying this Property (Classical). In other words, it is because α and β shares an essence that $\Sigma(\alpha) = \Sigma(\beta)$ holds and they are the same at the ontological level.

Mathematically, the HPC theory can be formulated in a similar way. All we need to do is change the "interpretation of symbols" in modeling classical essentialism. First, we re-interpret $\Sigma : E \longrightarrow M$ as a mapping from entities to the *meaningful* subsets of properties in a sense that these properties are *co-occurred frequently* in some entities. This leads to the next re-interpretation of $\Sigma(\epsilon)$ as "a certain set of the properties that are satisfied by e and frequently co-occurring each other in some entities belonging to E", instead of "a certain set of the properties satisfied by ϵ". This means entities are represented as weights of a connection between properties in M (i.e., if two properties co-occur frequently in many entities, then the connection between these properties becomes stronger).

If we accept the ontological principle of the HPC theory that "behind the properties that co-occur there must be a common underlying basal mechanism that generates them," then by choosing proper $\Sigma : E \longrightarrow M$, the structure of the subgroupoid should provide a foundation of natural kinds. In other words, as in the classical essentialism, the HPC view requires suitable S satisfying the Property (HPC) below:

Property (HPC). $\Sigma(\alpha) = \Sigma(\beta)$ *if and only if* A *and* B *belong to the same kind, where* $\Sigma(\epsilon)$ *is a certain set of the properties that are satisfied by* ϵ *and frequently co-occurring each other in some entities belonging to* E*.*

Here, the HPC theory assume "basal mechanisms" underlying this Property (HPC). In other words, it is because α and β shares basal mechanisms that $\Sigma(\alpha) = \Sigma(\beta)$ holds and they are the same at the ontological level.

In this way, the HPC theory has a mathematical basis similar to classical essentialism in terms of understanding homology through "subgroupoids." It thus retains the strong commitment to the sameness among entities or individuals at the ontological level, although at first glance it appears to be a much more relaxed version of classical essentialism.

4.4 Summary

Our mathematical interpretation of the individualist and HPC kind views highlights a sharp contrast between them; the former highlights the ordered set-like aspect of homology, while the latter emphasizes its groupoid-like aspect instead. Nevertheless, both mathematical models are deduced from the category theory. This implies that they share a common mathematical basis but emphasize different facets of homology. If that is the case, is it possible to conciliate them for establishing an integrated theory? To accomplish this, the key is incorporating the processual and dynamical aspect of homology and admitting categorization as a natural kind without strong ontological commitment to the essence or its proxies such as basal mechanisms.

5 New alternative views of the homology concept

To overcome the dichotomy between the individualist and natural kind views, two new conceptions of homology have recently been proposed (Otsuka 2017; Suzuki and Tanaka 2017). They both aim to avoid essentialistic ontological commitments but instead highlight the processual and dynamical aspect of homology, thereby providing a conceptual basis to establish a new mathematical formulation of homology.

First, Suzuki and Tanaka (2017) take a phenomenological minimalist attitude and propose that homologs can be defined as persistently reproducible modules (PRMs). They suggest that homologs are persistently and repeatedly generated in both evolutionary and developmental processes. For example, the right forelimbs of a tetrapod species are consistently formed from generation to generation. Furthermore, a newt can regenerate its appendages, meaning that homologous structures can be repeatedly produced in development.

According to Suzuki and Tanaka (2017), homologs certainly show individualist-like features such as spatial restriction and engagement in temporal processes. Nevertheless, non-individualist-like features are also found; strictly speaking, homologs are not continuous either spatiotemporally or genetically because they are formed and destroyed in each generation without transmitting any genetic information. At the same time, the authors point out a kind-like feature in homology because persistent reproducibility of homologs enables us to inductive generalization. However, they do

not assume any essence or its proxies behind the persistent reproducibility, keeping a distance from the natural kind view.

Concurrently, Otsuka (2017) proposed another concept of homology employing the causal graph theory, in which homology is defined as an isomorphism of causal subgraphs over lineages. His mathematical formulation is as follows (Otsuka 2017, pp. 1130–1131).

> Let $G(a)$ be a causal graph representing a particular developmental mechanism of an individual organism a. Collectively, $G(A)$ is a set of the relevant causal structures for a set of organisms A. We assume usual ancestor/descendant relationships over organisms. If b is an ancestor of a, the lineage between b and a is the set of every individual between them. Given this setup the causal homology is defined as follows.
>
> For two sets of organisms A, B, let G' be a subgraph of all $g \in G(A)$, and G'' be a subgraph of all $g \in G(B)$. Then G and G'' are homologous iff
>
> 1. $G' \sim G''$ (here '$\sim$' means isomorphism);
> 2. there is a set of common ancestors C of A and B; and
> 3. for every d in all the lineages from C to A and C to B, $G(d)$ has a subgraph G''' such that $G''' \sim G' \sim G''$.

With this formulation, Otsuka (2017, p. 1134) argues that a homolog to concrete organs stands not as a universal to particulars in instantiation, nor as a whole to parts in mereological relationship, but rather as a model to phenomena to be modeled in representation. He also advocates the superiority over his account to the HPC theory, pointing out the boundary problem involved in the latter (Otsuka 2017, p. 1135).

In summary, both Suzuki and Tanaka (2017) and Otsuka (2017) attempt to overcome the dichotomy between the individualist and natural kind views, in pursuit of a third alternative. They aim to avoid strong ontological commitment to individuals or universals and instead take a phenomenological or representational stance. In this sense, they are oriented in the same direction.

Nevertheless, the PRM view by Suzuki and Tanaka (2017) is too conceptual and lacks mathematical formulation. In contrast, the causal graph theory by Otsuka (2017) is well established. However, his theory encounters the same pitfall as the HPC natural kind view in considering the two thought experiments described in Section 3. Let us interpret characters a, b, c, ... in Fig. 1 and 2 as subgraphs instead of properties. In the case of the "decrease of shared properties," for example, the isomorphic causal subgraphs become smaller as the number of shared properties decreases among lineages. Furthermore, in the case of the "gradual but complete replacement of properties," there is no isomorphic causal graph when properties of homologs are completely replaced.

These thought experiments reveal an inconspicuous similarity between the causal graph and HPC theories; commitment to stable causal/mechanistic structures behind phenomena, defined as isomorphic causal subgraphs and basal mechanisms, respectively. In discussing DSD, Otsuka (2017, p. 1136) argues that the drift in genetic or cell materials may not alter topological features of the causal network, that an abstract description of the causal structures buffers the changes in drift, and that a partial correspondence in subgraphs suffices to establish a homology relationship. Nevertheless, the subgraphs for defining a set of homologs are required to remain constant.

Instead, we propose that we should place more emphasis on dynamic changes. Since evolution and development are dynamic processes in nature, we may miss the key aspect of homology if we discount it. In this regard, the PRM view appears more suitable for the basis of our new mathematical formulation because it is more process-oriented.

6 Mathematical formulation of the process-oriented homology views in terms of the category theory

Now, we present a new mathematical formulation of homology based on the PRM view proposed by Suzuki and Tanaka (2017). This can be accomplished by generalization and extension of the causal graph model by Otsuka (2017), considering free categories of graphs at a higher level with lower-level causal graphs (here representing individual organisms) as vertices, representing evolutionary changes among generations.

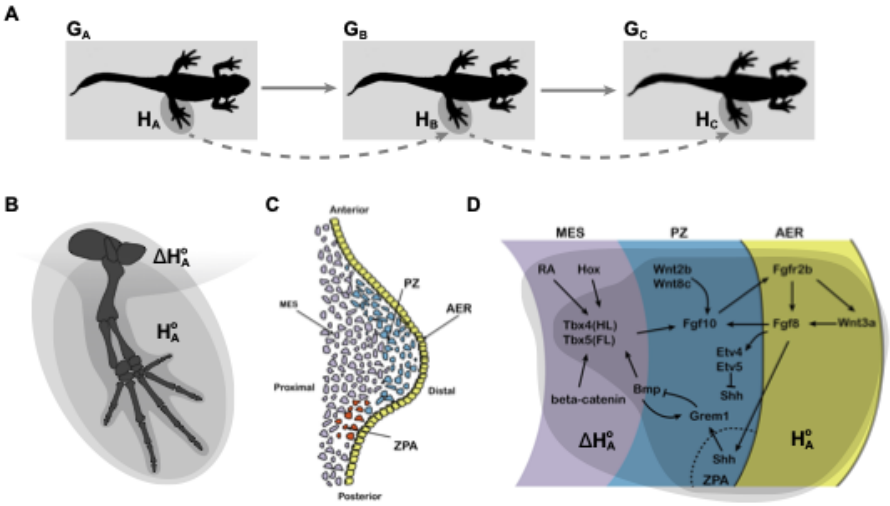

Fig. 4 Category-theoretical formulation of homology. (A) Homologs as persistently reproducible modules (PRMs), based on Suzuki and Tanaka (2017). The transgenerational relationships of the entire individuals and the homologs of interest are represented as solid and dash lines, respectively. (B) Schematic image of a morphological module. The hindlimb and its fringe are denoted as H^o_A and ΔH^o_A, respectively. (C, D) Schematic diagram (C) and genetic regulatory network (D) of a developing limb, modified from Jin et al. (2019), licensed under CC-BY. The developmental module for a limb bud and its fringe are denoted as H^o_A and ΔH^o_A, respectively.

First, we consider a pair (G_A, H_A) of the graph G_A, representing an entire network of morphological characters or developmental mechanisms of an individual organism A, and its subgraph H_A of interest as a vertex of the "meta-level" graph as described below. This means that the correspondence of the homologs is interpreted as meta-level intergenerational relationship (the dashed lines in Fig. 4), where these homologs are defined as subgraphs of individulas-as-entire-networks. Here, subgraph H_A is the

union[5] of the subgraph H^o_A of the homology of interest[6] and its "fringe" ΔH^o_A; the latter denotes a directed graph consisting of the vertices that are not in H^o_A but directly connected to the vertices of H^o_A, as well as the edges between them.

The reason why we need to consider the fringe or ΔH^o_A is that, in discussions of homology, it is essential to consider the part H^o_A "within the whole," especially in relation to its fringe (the principle of connections, introduced by Geoffroy Saint-Hilaire 1980; see also Russel 1916; Hall 1994).

To make a meta-level directed graph, let us draw an edge from (G_A, H_A) to (G_B, H_B) whenever A is a biological parent to B, and H_A and H_B are isomorphic. Furthermore, we have a symmetric graph by adding a "child to parent" edge $e^* : (G_B, H_B) \longrightarrow (G_A, H_A)$ to each "parent to child" edge $e : (G_A, H_A) \longrightarrow (G_B, H_B)$. By considering $e^{**} = e$, the operator * means an "involution" on edges. Let us write this symmetric graph as Γ.

For any graph $Q = (V_Q, E_Q)$, where elements of V_Q and E_Q are called vertices and edges of Q, respectively, we can construct a category called the "free category" $C(Q)$ of Q, whose objects and arrows are vertices and "paths" (simply put, a coherent sequence of directed edges), respectively. Here a path means a tuple (finite series) of vertices and edges $(v_n, e_n, v_{n-1}, e_{n-1}, \cdots, e_1, v_0)$ that satisfies the condition $s(e_n) = v_{n-1}, t(e_n) = v_n$, where $s(e)$ and $t(e)$ denote the source (starting point) of e and target (endpoint) of e, respectively. The composition of the two paths $(v'_n, e'_n, v'_{n-1}, \cdots, e'_1, v'_0)$ and $(v_n, e_n, v_{n-1}, \cdots, e_1, v_0)$ such that $v_n = v'_0$ is defined as concatenation:

$$(v'_n, e'_n, \cdots, e'_1, v'_0) \circ (v_n, e_n, \cdots, e_1, v_0) = (v'_n, e'_n, v'_{n-1}, \cdots, v'_0 (= v_n), e_n, \cdots e_1, v_0).$$

The free category $C(Q)$ becomes a dagger category when Q is symmetric. Specifically, our meta-level symmetric graph Γ equipped with the operation *, $C(\Gamma)$ becomes a dagger category with

$$(v_n, e_n, v_{n-1} \cdots, v_1, e_1, v_0)^\dagger = (v_0, (e_1)^*, v_1, \cdots, v_{n-1}, (e_n)^*, v_n).$$

We suggest that *this $C(Q)$ denotes the homologous relationship*. This formulation can be regarded as an generalized version of Otsuka (2017)'s causal model in the sense that it does not require any set of characters shared in all homologs; what it needs is just the isomorphism between each parent and child. As an example, let us consider a lineage of biological individuals A, B, C, and D, where any parent-child pair shows isomorphic relationships: $(G_A, H_A) \longleftrightarrow (G_B, H_B)$, $(G_B, H_B) \longleftrightarrow (G_C, H_C)$, and $(G_C, H_C) \longleftrightarrow (G_D, H_D)$. Then, we can construct $C(\Gamma)$ for (G_A, H_A), (G_B, H_B), (G_C, H_C), and (G_D, H_D), whether or not there is a set of properties shared in all these homologs of interest.

[5] Here, the union (of two subgraphs of a graph) refers to the graph obtained by union of the vertex sets and edge sets of the two graphs.

[6] An important point here is that the scope of H^o_A depends on the level of abstraction. See the discussion below in the main text.

As a specific case, let us consider the hindlimbs of newts (Fig. 2). In a parent newt A, the entire network of morphological characters (or developmental mechanisms) and its subgraph around the hindlimb are denoted as a pair (G_A, H_A). In the same way, the corresponding graphs and subgraphs of offsprings are described as (G_B, H_B), (G_C, H_C), ..., respectively, from generation to generation. Precisely, H_A, H_B, ... are the union of the subgraphs of the hindlimb itself H^o_A, H^o_B, ..., and their fringe ΔH^o_A, ΔH^o_B, ... The vertebrate hindlimb articulates to the pelvic girdle, which consists of the pubis, ischium, and ilium. Thus, the fringe can be regarded as this connection between the hindlimb and the pelvic girdle (Fig. 2B). Without considering this connection, we cannot judge confidently whether it is a forelimb or a hindlimb. This is why we need to consider the fringe of homologs, although other ways of application are also possible (e.g., to focus on the developmental mechanisms instead; Fig. 2D). Finally, the intergenerational (i.e. evolutionary) conservation, or homology, of this relationship is then represented as $C(\Gamma)$.

In a similar way, our model can cover the homological relationship between the hindlimbs of the identical biological individual before and after the regeneration. The fringe in morphological connections here is to be the same as in the intergenerational homology, but that in developmental mechanisms should be different because the regenerative mechanisms are not the same as the developmental mechanisms for the same organ (Aztekin 2024). This suggests that it is better to interpret (G_X, H_X) as a network of morphological characters, instead of developmental mechanisms, for describing regeneration of homological organs.

Moreover, we can consider homology of the different parts in the same biological individual (iterative or serial homology), if we assume different subgraphs H_X, H'_X, H''_X, ..., in the same graph G_X. Let us consider the case of left and right hindlimbs (in short, *Lh* and *Rh*, respectively) of a newt; these two symmetrical organs show the same morphological characteristics based on the same developmental mechanisms, except for the difference due to their bilateral symmetricity. Here, we can assume bilateral edges between these two organs, (G_X, H^{Lh}_X) and (G_X, H^{Rh}_X), and thus $C(\Gamma)$, although they have no historical continuity in a strict sense.

It is also notable that homologs can be differently marked out depending on the level of abstraction. Atavism may well illustrate this point (see also Suzuki and Tanaka 2017, p. 177). For example, adult whales usually lack hindlimbs but their embryos show hindlimb buds temporarily at some period in development. Imagine that a mutant whale accidentally has a pair of hindlimbs in adulthood, as actually reported (Andrews 1921; Ogawa and Kamiya. 1957; Ohsumi and Kato 2008). Here, our model can be applied to this case in two different ways as follows.

If we assume (G_X, H_X) as an entire network of adult morphological characters and its subgraph, respectively, then the "new" hindlimb can be interpreted as a novel structure, because it lacks "child to parent" and "parent to child" edges as the parents of the whale have no hindlimb in adulthood.[7]

Thus, it appears better to focus on development here. By regarding (G_X, H_X) as an entire causal network of developmental mechanisms and its subgraph, respectively, we

[7] Still, we may construct somewhat "weak" $C(\Gamma)$ among the whale and the ancestral tetrapods with a (large) generational gap, assuming homology and its enabling mechanisms behind it.

can construct "stronger" $C(\Gamma)$ of this "new" hindlimb and those of ancestral tetrapods with respect to the conserved developmental mechanisms.

This equivocality of interpretation actually reflects the practice of biologists; an atavistic hindlimb of a whale can be interpreted not only as a somewhat novel structure but also as a true homolog of ancestral hindlimb.

The dorsal fin is a good example that forms a contrast to the case of the hindlimb. The similarity of the dorsal fin between fishes and cetaceans (whales, dolphins, and porpoises) is the result of convergent evolution,[8] thus it is homoplasy. Despite their seemingly resemblance in appearance, the internal morphology and relationship to the remaining body are totally different: the fish dorsal fin contains skeletal fin rays associated with basal skeletal elements called pterygiophore, while cetacean dorsal fin lacks either these bones or even muscles but instead consists of fibrous connective tissues (Huggenberger et al. 2019). Therefore, no $C(\Gamma)$ can be constructed based on morphology. Although it is perhaps possible that certain developmental mechanisms are commonly involved (e.g., Fgf signaling pathway for outgrowth formation; see Abe et al. 2007), it will not exceed the level of deep homology (see below).

The level of abstraction also matters in a more practical situation, when we discuss homology in various levels in the biological hierarchy such as genes, cells, developmental processes, morphological structures, and behaviors.

Notably, non-homologous organs often share some parts of their developmental mechanisms, known as deep homology (Shubin et al. 1997, 2009). For example, the tetrapod limbs and the insect appendages involve shared patterning genes, *Shh/Hh* and *Dlx/Dll* (Held 2017). In this case, if we take the pair (G_X, H_X) for morphological characters, no $C(\Gamma)$ can be constructed because there is no shared subgraph at the level of morphological characters. If we regard that it represents developmental networks, on the other hand, G_X will denote a small but insufficient subgraph (a portion of developmental mechanisms at a "deeper" level) to represent a homolog of interest.

In the opposite case, homologous morphological characters can be formed through distinct developmental mechanisms (DSD; see Sect. 2.3). Similarly, it is reported that homologous behaviors are generated by distinct neuronal networks (Newcomb et al. 2012; Sakurai and Katz 2017). Ereshefsky (2009, p. 226) described these phenomena as hierarchical disconnect. Our model can be easily applied to these situations by taking (G_X, H_X) at the level of character itself. In the case of DSD, for example, we can construct $C(\Gamma)$ for morphological characters even if the developmental mechanisms for homologs have been changed.

Our model is compatible with the concept of character identity mechanisms (ChIM) proposed by DiFrisco et al. (2020). In their framework, ChIMs are defined as cohesive mechanisms with a recognizable causal profile that allows them to be traced through evolution as homologs despite having a diverse etiological organization. If this assumption is granted, we can apply our model to a ChIM as H^o_X associated with the input signals and output realizer mechanisms as its fringe (ΔH^o_X) in the entire sets of mechanisms for generating the entire body (G_X).

In addition, both the individualist and HPC natural kind views can be derived from our model. First, it respects the lineage between organisms, representing the

[8] https://en.wikipedia.org/wiki/Dorsal_fin (accessed on October 3, 2024)

ordered set-like aspect of homology as emphasized by the individualist view. Also, it has the structure of a dagger category, which is a generalization of groupoids. Thus, $C(\Gamma)$ encompasses the HPC natural kind view. In addition, if we regard the fringe of the homolog of interest as the mechanisms that generate the homolog, the concept of the basal mechanisms can be incorporated into our model without strong commitment to the sameness at the ontology level behind the phenomena. At the same time, the point that our model does not have such ontological commitment strikingly illustrates how our model differs from the HPC view. We will further discuss this point as well as biological implications in the next section.

To summarize, we demonstrated that homology can be mathematically formulated in the framework of the free category $C(\Gamma)$. Our model serves as the basis for homology, consistent with various extreme cases such as atavism, deep homology, and DSD. Also, is has both ordered set-like and groupoid-like aspects, which are highlighted by the individualist and the HPC natural kind views, respectively.

7 Biological and philosophical implications

7.1 Biological implications

With our model, we intended to explain homology, a special form of the sameness of biological characters. Nevertheless, it may also be applied to other sameness in biology including biological individuals, species, and animal consciousness. Perhaps we need separate papers to discuss these topics in enough detail, so we just draw rough sketches here.

First, a biological individual organism A can be regarded $C(\Gamma)$ of a diachronic series of monoids (cf. Hirota et al. 2023), by assuming H_A as the entire G_A (here, $H_A^o = H_A$ and $\Delta H_A^o = \varnothing$). A monoid in category theory is defined as a category with only one object, meaning that all arrows start from and terminate at the single object (as both domain and codomain). Hirota et al. (2023) suggest that the autonomous self can be interpreted as a monoid or a "hub" through which various self-mediating processes (represented as allows) are mediated. This interpretation enables us to understand why we recognize an individual as an individual, even if the "constituents" of a biological individual are constantly replaced (cf. the "Ship of Theseus" paradox).

Second, a species A at a generation i can be represented as H_{Ai}, which is a subgraph of G_{ToL}, the entire genetic network of life (i.e., the "Tree of Life"). In other words, a species can be regarded as a trans-generational interbreeding network of a population and the Tree of Life is a tree-structured collection of these species as its branches. Thus, H_{Ai} is a time-section of a species A as a branch at generation i. A species is most commonly defined as a group of organisms that can successfully interbreed and produce fertile offspring (the biological species concept), although there are other different species concepts (Ereshefsky 2002/2022). For example, all living dogs and wolves belong to the same species *Canis lupus* and have a potential to have a fertile pup by mating. In this definition, a species is characterized as a series of transgenerational gene pools (here, a gene pool means the total collection of genes shared by biological individuals in an interbreeding population at a specific generation).

Generation to generation, the contents of a gene pool changes constantly by mutation, selection, genetic drift, and so on. If we consider H_{Ai} and the same gene pool at the next generation H_{Aj}, we obtain an isomorphic subgraph $H^o_{Ai} \sim H^o_{Aj}$ based on the shared portion of the gene pool $H_{Ai} \cap H_{Aj}$. Then, we can construct $C(\Gamma)$ that represents genetic continuity of the gene pool through generations.

In contrast, different species (i.e., different gene pools) A and B at a specific generation n have no gene flow between each other, thus no $C(\Gamma)$ can be constructed between H_{An} and H_{Bn}. Still, they evolutionary share common ancestry because all known organisms have a single origin. In this regard, we can assume 'indirect' $C(\Gamma)$ via their common ancestor $H_{(A/B)m}$ at a past generation m; they were the same species at that time after all.

Just as the case of homology we have already shown, our model thereby disentangles the species problem whether a species is an ontological individual or a natural kind.

Last, our model may be applicable to animal consciousness. Recently, more and more authors discuss the evolution of consciousness (e.g., Feinberg and Mallatt 2016, 2018; Ginsburg and Jablonka 2019; Ota et al. 2022; Suzuki 2021, 2022a, 2022b; Veit 2023). Homology is a key question here; for example, are vertebrate and cephalopod consciousness is homologous? If we accept that consciousness is an evolutionary entity generated in specific biological individuals (see also Suzuki 2022a; Suzuki and Tanaka 2017), consciousness of an animal A can be characterized as H_A in the same way as other homologs.

Interestingly, the hierarchical disconnect can also be found in the homology of consciousness (Ota et al. 2022). Feinberg and Mallatt (2016, pp. 118–125) suggested that the "end site" of the vertebrate sensory consciousness was shifted from the midbrain tectum to the forebrain pallium in mammals and birds independently. If it is true, the neural substrates for homologous consciousness were changed during the evolution of these lineages in a similar manner to the DSD. As our model can encompass the cases of the hierarchical disconnect, it provides a powerful conceptual platform for animal consciousness research.

7.2 Philosophical implications

We have shown that homologs have both individual-like and natural kind-like aspects. Are they irregular ontological entities? On the contrary, we suggest that the canonical "individuals" and "classes" *are* special cases. An ontological individual is defined as a highly static diachronic series of monoids (Hirota et al. 2023), as is the case in a biological individual organism. On the other hand, a class is $C[\Sigma]$ that is constructed from isomorphism of properties $H_A, H_B, H_C, ...$, in distinct ontological individuals $G_A, G_B, G_C, ...$, without considering genealogical interconnections.

This idea further leads us to reform of ontology, with emphasis not on static elements or "things" but more on dynamic processes and causal networks. The category theory is a powerful tool to explore this idea. Whereas the set theory regards elements as fundamental factors, the category theory is based on arrows and even elements can be interpreted as arrows. This arrow-first mathematics has strong affinity for modeling dynamical changes of causal networks; a causal network at a time point is represented

as a directional graph composed of arrows, and its diachronic changes are described as "morphisms between categories" such as functors.

An important point here is that the causality in these networks is not necessarily deterministic or mechanistic. As discussed in Section 2.3, biological processes are causal but not deterministic because they are inherently stochastic. For describing such non-deterministic causation, we may employ the concept of the "enabling relation", which means "X enables Y" or "without X, there would be no Y" relationship (De Jaegher et al. 2010; Hirota et al. 2023). Category theory is a powerful tool to represent such kind of causation.

Philosophically, the dichotomy between individuals and kinds has long been taken as a given. However, our analysis opens a new horizon for going beyond this disjunction. We suggest that individuals and kinds are derived aspects of other entities, namely, processes. In fact, such process-first ontology has been promoted by some philosophers of biology (Dupré 2012; Nicholson and Dupré 2018). These philosophical analyses of biological entities, including the present study on homology, may provide a crucial viewpoint to reconsider traditional (especially, Western) philosophical dogmas.

8 Conclusion

In the present study, we attempted to establish an unified perspective on the ontological nature of homology. Through mathematical formulation, we showed that both individual-like and natural kind-like features of homologs can be derived from a process-first ontology based on the category theory. Our model are applicable to a wide range of phenomena linked with homology, such as atavism, deep homology, and DSD. Furthermore, we propose that our analysis leads to the process-first ontology, overcoming the longstanding dichotomy between individusls and kinds in Western philosophy.

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Data Availability

This is not applicable to this article as no datasets were generated or analyzed during the current study.

Declarations

Conflict of interest

The authors have no Conflict of interest to declare.

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