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Diachronic Identity in Complex Life Cycles:

An Organizational Perspective

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Abstract: What does it mean to be the same organism over time? This chapter develops an understanding of diachronic identity of organisms from an organizational perspective. We argue that a necessary condition for diachronic identity is organizational continuity, i.e., the presence of a continuous causal process linking successive organizational regimes, irrespective of material and functional changes. Organizational continuity is not a sufficient condition, however, because it cannot discriminate between the development of the same individual and the reproduction of a new individual. We therefore suggest that there are temporal boundaries of identity when there are changes in the number of continuous organized systems, which occurs through fission, fusion, or a combination of the two. We discuss the utility of the resulting organizational view, as well as its relations with other approaches to biological individuality.

Keywords: biological individuality, closure of constraints, development, reproduction, biological persistence, diachronic identity, genidentity, process ontology

1. Introduction

Questions about diachronic identity have sustained extensive philosophical reflection in general metaphysics and particularly in the context of personal identity. Less attention has been given to diachronic identity of organisms. This is in spite of a recent surge of work on biological individuality in philosophy of biology, which has largely focused on which sorts of parts should be included within the spatial boundaries of individuals, and not on which sorts of events should be included within the temporal boundaries of a life. However, temporal boundaries matter for some of the same reasons that spatial boundaries do.

One biological practice that requires criteria of individuation in space is counting individuals in order to measure population size and demographic change (Clarke 2011). For these purposes, it is often not enough to single out the appropriate individuals at specific times without also connecting them across time. One needs to be able to interrupt an observation period and later return to the system under study, to *re-identify* the same individuals as before, and distinguish them from the ones that are new. Otherwise, one risks double-counting certain individuals and missing others completely.

Similar considerations apply to measurements of reproductive fitness in terms of the number of offspring produced. Offspring number straightforwardly depends on how we individuate offspring. But it is not always obvious whether a biological system at a given time is the beginning of a new life or just a later developmental stage of the parent. This is especially the case in life cycles involving metamorphosis, metagenesis (alternation of generations), vegetative reproduction, fusion, fission, and symbiosis, as we will see. It is also important to be able to distinguish development, growth, and reproduction because these processes connect to different dynamics of life history evolution (Stearns 1992). A model that

describes trade-offs and local optima for traits such as growth rate, time to reproduction, and mortality schedules will generate different predictions and different error rates depending on which segments of a life cycle it is applied to. For purposes of comparative biology, the formation of a reliable generalization over life history patterns in different taxa demands that the patterns be genuinely comparable. Work on biological individuality can ideally provide a domain theory that identifies which intervals of organismic processes the models should apply to.

In attempting to provide diachronic criteria of identity we encounter a first difficulty that modes of development and reproduction differ markedly across different biological taxa. It is entirely possible that there are no shared criteria of identity that apply to the class of “organisms” as such, but only local criteria for different taxonomic groups. A second, related difficulty is that organisms can have very different properties at different stages of the same lifetime. In fact, many of the properties emphasized in proposed criteria of individuality are not present throughout the lifetime of the systems they are supposed to individuate (see Clarke 2011; DiFrisco 2018b). Accounts of individuality face this difficulty when they are based on fitness (e.g., Folse and Roughgarden 2010), the capacity to undergo selection (Clarke 2013), and cooperation and conflict (Queller and Strassmann 2009). An organism during its post-reproductive lifespan has no fitness, its cooperation or conflict has no evolutionary effect, and it cannot undergo selection (excluding grandparenting effects). Yet post-reproductive organisms nonetheless exist, and they have effects on biological processes other than evolution. Non-evolutionary features of organisms such as histocompatibility and symbiotic interaction can also be time-variable in development. When the properties that are supposed to determine individuality change over developmental time, they need to be embedded in the context of a life cycle structure. Then we can still count something as an individual when those properties are absent.

Intra-lifetime variability sets up a general dilemma: if the criteria for continued persistence are too demanding, then developmental processes involving dramatic material and functional transformations like metamorphosis may count as a reproductive process involving the production of a new individual. If the criteria are too relaxed, then many reproductive processes will be re-cast as development of one and the same individual.

This chapter examines diachronic identity conditions for organisms specifically in light of the second problem of intra-lifetime variability. We argue that a suitable necessary condition for organismic persistence can be found in spatiotemporal continuity together with the presence of a causal structure known as *closure of constraints*. This dual condition is called *organizational continuity*. Organizational continuity is sufficient for diachronic identity only when there are no changes in the number of organized systems that are organizationally continuous with one another. Such changes can occur through events of fission or fusion, which call for special analysis. In explicating this qualification of sufficient conditions, we find that one also needs to take into account the way in which different temporal boundaries can be promoted by different biological perspectives—e.g., evolutionary, developmental, or physiological—with their distinctive modeling and generalization strategies. We close by considering how the proposed organizational view can plausibly satisfy the above biological roles for diachronic identity conditions, and highlight open questions for future work.

2. Organizational continuity

Spatiotemporal continuity is widely considered by philosophers to be necessary for diachronic identity of objects. An object cannot pass in and out of existence, or disappear from one location and immediately re-appear in another, while remaining numerically the same object.¹ Spatiotemporal continuity alone does not entail contiguity of the spatial parts of an object—

commonly called “unity” in philosophy and “cohesion” in perceptual psychology—but only that the spatial regions an object occupies are connected across time. For example, a biological population can be considered an object whose parts are not topologically connected, but it can nonetheless be tracked across time in virtue of the spatiotemporal continuity of its scattered parts. Unity is often considered to also be necessary for object identity, though we will remain neutral on this issue.

Mere spatiotemporal continuity however, without any specification of the relata that are supposed to stand in the relation of continuity, is not a sufficient condition for identity. This is because any object or event is spatially continuous with its immediate environment and temporally continuous with what precedes it and what succeeds it. Some background determination about the *sort* of item to be tracked—such as a horse, a computer, or a thunderstorm—is needed to get a grip on its spatial boundaries as well as the kinds of change it can undergo while remaining the same thing of that sort. For example, while relying on the criterion of spatiotemporal continuity, an observer may trace different paths through spacetime if she is tracking items in her perceptual field under the sortal *house* versus *set of bricks*. The application of a suitable sortal, together with the condition of spatiotemporal continuity, can be viewed as determining the identity of entities in space and time. This is the position defended in contemporary forms of substance ontology, from Strawson (1997), to Wiggins (2001), and Lowe (2009). Roughly, x and y are the same individual iff they are spatiotemporally continuous *and* they fall under the same sortal.

From this point of view, the problem of organism identity can be framed as a problem of finding an adequate definition for the sortal *organism* or for specific kinds of organisms. We propose to approach the issue of organism identity in a different way, by first shifting from the descriptive question to a more basic explanatory one. Rather than asking which concept of the organism determines the organism’s persistence, we take a step back and ask which causal structure determines its survival. If we can understand the sorts of physical features and interactions that explain, from the bottom up, how organisms survive—taking “organisms” or “individuals” in an initially loose sense—then we gain insight into how organism identity ought ultimately to be conceptualized.

Biological organisms are physical systems that exhibit a type of macroscopic order based primarily on the energy provided by chemical reactions. In order to maintain their internal structure and energetic functioning against the global thermodynamic tendency toward entropic dissipation, organisms must continually occupy states far from chemical equilibrium by absorbing chemical or radiant energy (Ruiz-Mirazo and Moreno 2004). Unlike other macroscopic dissipative structures, however, organisms exhibit not only physical *order* but also functional *organization*. We use here ‘organization’ in a theoretical specific sense, to refer to a specific causal regime in which groups of differentiated parts collectively maintain each other through their reciprocal interactions. The survival of organized systems as wholes depends on the overall activity of their parts. Hence, these systems can be said to be *self-maintaining* in a given environment (Moreno and Mossio 2015).

As thermodynamically open systems, organisms are traversed by flows of matter and energy in the form of complex chemical and physical transformations (processes or reactions). These transformations are controlled through the coordinated activity of system components, which are theoretically characterized as *constraints*. Constraints are material structures that asymmetrically act on transformations without being directly affected by them, and that remain conserved during the course of those transformations. For instance, the developed cardiovascular system of vertebrates constrains blood flow without being altered by it.ⁱⁱ At smaller spatial scales, enzymes change the kinetics of chemical reactions without being consumed in the process (see Montévil and Mossio 2015 for further details).

In order to constrain a transformation, the constraint must be conserved at the time scale of the transformation it constrains. Yet on longer time scales, biological constraints also degrade and must be replaced or repaired. The cells that compose the vascular system must be nourished, and enzymes undergo degradation and denaturation over time and must be replaced. In general, the repair or replacement of a constraint occurs by means of another metabolic process or complex of processes, which is itself channeled under other constraints. For example, lipid membranes constrain the diffusion of enzymes and metabolites in such a way that the appropriate intracellular concentrations are maintained, but new lipids are also produced through the chemical reactions controlled by enzymes. Once we have reciprocally maintaining effects of a group of constraints, the notion of organization enters the picture. A system is “organized” in the relevant sense when the continued existence of a set of constraints depends on the effects that they *collectively* produce on the overall thermodynamic flow. If this occurs, the set of mutually dependent constraints can be said to realize *closure*. The mutual dependence between constraints, theoretically designated as “closure of constraints,” is what allows organized systems to maintain themselves over time.ⁱⁱⁱ From the organizational perspective, we can view organisms or biological individuals as being organized systems (as a necessary condition), while recognizing that not all conceptions of the organism will have this feature.

Closure of constraints plays a central role in explaining the survival of organisms, viewed as organized systems, as it explains how their parts are functionally arranged in such a way that the system can maintain itself dynamically over time. Accordingly, it seems reasonable to hold that, conceptually, closure of constraints is necessary for organism identity, since any organism that lost this property would quickly perish. Let us propose, then, that *a necessary condition for diachronic identity of organisms is that they continually exhibit closure of constraints*. Any temporal interval where this property of *organizational continuity* is not present then marks a temporal boundary of an organism’s life, either due to death or non-existence before life.

What does it mean for a system to continually exhibit closure of constraints? A first interpretation might be that the particular material structures that act as constraints in the system—i.e., membranes, enzymes, vascular systems—are conserved over time. This would be a problematic requirement on organismic persistence, however. The material composition of organized systems changes over time—indeed, it *must* change if the systems are to survive, because functional constraints degrade and must be repaired or replaced.

A second interpretation might be that continually exhibiting closure of constraints means that a group of constraints, functionally individuated by their causal roles in self-maintenance, must persist despite continual material turnover of components and realizing structures. As argued elsewhere (Mossio et al. 2009), constraints subject to closure can be said to ground biological functions. Diachronic identity would therefore be a matter of conservation of *function* rather than of material structure. The trouble with this solution is that material turnover is not the only kind of constitutive change that organisms undergo. In organisms that develop, i.e. single- and multi-celled eukaryotes, the constraints involved in self-maintenance can themselves arise, transform, and disappear within a lifetime—even if they are defined in abstract functional terms. A dramatic example of developmental transformation is metamorphosis.

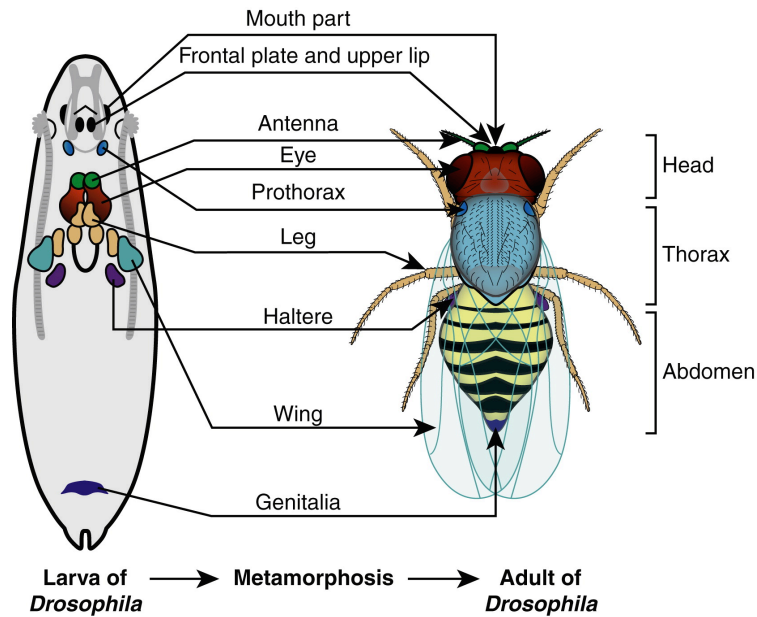


Fig. 1. Material and functional change during metamorphosis in *Drosophila*. Many adult body parts are formed out of the set-aside cells in corresponding imaginal discs in the larva. Image reprinted from *Current Biology*, 20(10), Silvia Aldaz and Luis M. Escudero, “Imaginal Discs” PR429-R431, Copyright (2010), with permission from Elsevier. <https://www.sciencedirect.com/journal/current-biology>

Metamorphosis is a life history pattern characterized by successive life stages that differ markedly in their physiology, morphology, ecological niche, and reproductive capacity (Bishop et al 2006). Although the evolutionary origins of metamorphosis are not well understood, one of the hypothesized adaptive effects of metamorphosis as a life history strategy is to permit the same organism to possess dramatically different functional specializations at different stages of its life. In metamorphic life cycles, functions or constraints often fail to be conserved over entire lifetimes. Moreover, intra-lifetime functional variation is not restricted to functions that are unnecessary for metabolic self-maintenance, such as camouflage or reproduction. The adult forms of many butterflies, moths, and mayflies lack mouthparts for eating, yet mouthparts—mechanical constraints on the flow of food energy—are necessary for self-maintenance in the larval forms.

Of course, many functional constraints *are* conserved over the course of development, particularly those having to do with core metabolism. One might try to reconfigure the criterion of functional conservation in light of developmental change by claiming that only those functions that are necessary for self-maintenance *throughout the entire lifetime* need to be conserved. This amendment, however, is self-defeating. If we say that the boundaries of a lifetime are determined by closure of constraints, but exhibiting closure of constraints means conserving functions that are necessary throughout the entire lifetime, then we already have to know what the temporal boundaries are in order to apply our proposed necessary condition for temporal boundaries. This solution is therefore circular or uninformative. Moreover, it is objectionable for departing from the explanatory role of closure of constraints. The set of constraints that are conserved throughout a lifetime will often be a *subset* of the set of constraints that realize closure at different stages. This conserved subset is not identified in terms of its special role in explaining survival, but by the fact of being conserved. But the main reason for proposing closure of constraints as a necessary condition for organism identity in the first place was that it is necessary for explaining survival. A subset of constraints that does not realize closure at the specific stage when it exists is not the relevant

set of constraints for explaining survival. For example, the set of constraints in the mayfly larva that includes those that realize closure *minus* the mouthparts is not the relevant *explanans* for the survival of the larva. The relevant *explanans* is the *whole* set of constraints that realizes closure at that stage. Subsets of constraints that happen to be conserved throughout a lifetime should not be construed as essential for tracking organism identity.

In order to continually exhibit closure of constraints, or to possess organizational continuity, an ontogenetic trajectory does not have to conserve anything in particular, neither structures nor functions. Nor do the different stages of life need to resemble each other. Being the same organized system over time, we argue, is based on a specific causal dependence relationship. If a system continually realizes closure of constraints, then at any given moment the organization of its parts is causally dependent on the effects of functional constraints that have operated at a previous moment. The organism at t_2 does not need to have the same set of constraints with the same inter-relationships as the organism at t_1 , but some of the constraints at t_2 must be causally dependent on those at t_1 . The *particular* set of constraints and their inter-relations—which we refer to as a *regime of closure*—can change over time as long as later regimes causally depend on earlier regimes. Hence, what must remain the same over time is closure construed as a general theoretical *principle* and not as a specific regime of closure (on this specific point see Mossio et al. 2016).

Note that organizational continuity implies spatiotemporal continuity, so by affirming the former as a necessary condition we include the latter. This implication stems from general physical relationships between causation, space, and time. In order for causal influence to propagate from x to y (without intermediaries) they cannot be separated by a temporal gap during which neither x nor y exists. Similarly, for the physical forces involved in biological interactions (primarily the electromagnetic force), interaction requires spatial proximity. This point might be taken to imply that organizational continuity also requires spatial proximity, but the implication is not obvious, and under-determined by current biological theories of organization. The causal influence implied by constraint relationships must propagate between the parts, under specific spatial and topological conditions that depend on how a given system realizes organizational closure, and on the level of organization being considered. For instance, while it seems to be generally accepted that unicellular organisms cannot realize closure unless their parts are contained within an unbroken spatial boundary, this requirement might be relaxed in the case of ecosystems, viewed as candidate higher-level organized systems, see Nunes-Neto et al., 2014). Nevertheless, it seems reasonable to conjecture that it will generally be difficult to implement the productive relations of dependence involved in closure of constraints in systems whose functional parts do not remain spatially close enough to be able to causally interact with each other.

3. Organizational continuity: Between genidentity and substantialism

The idea of conceptualizing diachronic identity in terms of causal continuity, as opposed to material or functional conservation or resemblance, is not new. It was expressed in its modern form in Kurt Lewin's notion of *genidentity*, which has been promoted by some philosophers of biology as a criterion of diachronic identity for biological individuals (Hull 1978; Guay and Pradeu 2016).

Organizational continuity is a specific type of causal continuity and is thus more restrictive than genidentity. One issue with unrestricted genidentity is that many items are related by causal dependence that we would not want to consider parts or stages of the same individual.

For example, organisms are causally continuous with their waste products as well as any artifacts they produce, but there seems to be no biologically interesting organism concept that includes these things as parts to be tracked through time. Organisms are also causally continuous with their parent(s) and the corpses they leave behind. Guay and Pradeu (2016) propose that temporal boundaries can be drawn where there are relatively fast rates of change, particularly change in “internal organization,” so that a single lifetime can comprise dramatic change as long as it is smooth and progressive. Although this rule would restrict genidentity in many cases, it is also likely to exclude metamorphic life cycles, as these can involve quite abrupt changes in internal organization. It also seems that our ability to measure rates of change is epistemically dependent on our ability to identify and track what it is that is changing, rather than the other way around. Hull’s (1978) writing on biological genidentity relies more narrowly on the idea that changes in “organization” mark the temporal boundaries of individuals, though he does not explicate the notion of organization in much detail. Our account of organizational continuity can be viewed as filling in the idea that biological identity is based on causal continuity (genidentity) and organization. An important difference between the accounts, however, is that Hull (1978) and Guay and Pradeu (2016) use genidentity as a general model of persistence for *all* biological entities, including viruses, parts of organisms, and species. In fact, genidentity can be used as a criterion of identity for any kind of entity (e.g., molecules, stones, galaxies), which means that, as such, it does not restrictively apply to the biological domain. By contrast, organizational continuity applies only to systems realizing closure of constraints, which include, at most, unicellular and multicellular organisms, and possibly symbioses and ecosystems.

Let us now examine the connection between organizational continuity and substance ontology and sortals raised earlier. As Hull (1978) and Guay and Pradeu (2016) point out, the theoretical decision to ground persistence on causal continuity rather than conservation or similarity runs counter to “substantialist” habits of thought, according to which being the same individual over time is a matter of retaining the same “substance,” conceptualized either as matter or form (see Simondon 1995). The most sophisticated contemporary defenders of substance ontology, such as Wiggins (2001) and Lowe (2009), are careful to drop the requirement of material conservation. In Wiggins’ framework, the identity of a substance is grounded in its form, dynamically conceptualized as an Aristotelian *energeia* or activity (Wiggins 2001, p. 80). Every natural entity possesses a *principle of activity* or functioning that at once determines its conditions of identity as well as its membership in a natural kind (Wiggins 2001, p. 72). As Wiggins writes:

A particular continuant x belongs to a natural kind, or is a natural thing, if and only if x has a principle of activity founded in lawlike dispositions and propensities that form the basis for extension-involving sortal identification(s) which will truly answer the question ‘what is x ?’ (Wiggins 2001, p. 89)

To be the same individual over time is thus to conserve the same principle of activity, which implies spatiotemporal continuity and falling under the same sortal.

How does our proposal differ from Wiggins’ activity-based substantialism? Initially it would seem that the principle of closure could be interpreted as a kind of principle of activity for organisms. However, problems arise from the supposition that a principle of activity is not only (1) necessarily conserved across a lifetime but is also (2) *sufficient* to determine the spatiotemporal extension or boundaries of an organism. These two roles pull the notion of a principle of activity in different directions, the first toward a coarser grain of individuation and the second toward a finer grain. There are often radically different modes of activity or functioning in different stages of metamorphosis, from physiological activity to morphological change to behavior. In such cases, in order to capture the activity that is

common to all developmental stages, the activity will have to be defined as a quite general one, such as “self-maintaining,” “living,” or “developing.” But it is hard to see how generic activities like these could be sufficiently “extension-involving” to determine the temporal boundaries of organisms, to distinguish parents and offspring, or even to distinguish between organisms belonging to different taxa.^{iv}

In contrast, the conservation of a principle of *closure* over the course of ontogenesis does not entail that each stage displays the same characteristic functioning or activity. The principle of closure is something more abstract; this is why we treat it as a necessary condition and not as providing “thick” sufficient conditions for individuation. Sometimes a principle of closure will correspond to a unitary *regime* of closure that picks out temporal boundaries without difficulty. This is relatively more likely to be the case in organisms that do not undergo massive functional changes during ontogenesis, e.g., non-eukaryotes and some eukaryotes, and in direct developers. But in our proposal the concept of a regime of closure is not attributed an individuating role as a condition of persistence.

These features of our account entail a significant departure from core principles of the substantialist model advanced by Wiggins and assumed by many others. Against substance-based sortalism, there are unlikely to be sortals for organisms that, by specifying a distinct principle of activity, determine the spatial and temporal extent of a life cycle at one stroke. Instead, theoretically useful sortals for organisms are more likely to resemble sortals for *events*, events being inherently temporally extended and typically time-heterogeneous. Event sortals do not single out events by specifying a property or activity that remains the same throughout the event, but rather a characteristic sequence or series of stages or temporal parts, each with their own distinctive qualities, activities, and in the present case, regimes of closure.

Ontologically, the key dynamic category that binds together stages into the same life cycle is not *activities*, but *developments*. Activities are homeomerous or “like-parted,” in that what is happening in any sub-interval of the duration of an activity is itself the same kind of activity. Every sub-interval of the burning of a candle is also a burning. Developments are heteromerous or “non-like-parted” in the sense that what is present in any sub-interval of the development is not the same kind of development (on this distinction see Seibt 2008). The larval stage of holometabolous development is not itself a metamorphosis. This implies that the sortals capable of determining boundaries for developments will be complex, specifying a normal or typical series of stages as well as a relation that makes them stages of the same process (see DiFrisco 2017, 2018a). In fact, this is what we see when biology texts introduce life cycles so that they can be identified by field workers (Gilbert 2010): not a conserved property or activity, but a normal sequence of stages of a specific sort of causal process.

The idea of organizational continuity is therefore more germane to a process model than a substance model of organism identity. To put this idea to use, however, we need more than just a necessary condition for organism persistence. The next section examines sufficient conditions and introduces distinctions between developmental and reproductive processes.

4. Development versus reproduction

One of the primary ways in which reflection on organism identity matters is in connection with the biologically important distinction between development and reproduction. The distinction is particularly difficult in complex life cycles of non-vertebrate multicellular entities such as plants, fungi, colonies of various kinds, and various invertebrates, where we

see processes like metamorphosis, metagenesis, apomixis, symbiosis, fission, and fusion (see Fusco and Minelli in press, chs. 1-2, for many examples of borderline cases).

As we saw earlier, amid this tangle of generative biological processes, principled attempts to distinguish between development and reproduction face a general dilemma. On the one hand, if criteria of diachronic identity are too strict, they will not be able to include dramatic transformations such as metamorphosis within the same lifetime. On the other hand, if they are too permissive, they will often be unable to close the temporal boundaries of a lifetime, and reproductive events will be tracked as developments of one and the same organism. Organizational continuity is a quite permissive criterion of identity, given that it does not require conservation or resemblance. Accordingly, it can be expected to face difficulties marking reproductive events—or more precisely, fission and fusion.

To a first approximation, one might hold that organizational continuity provides both necessary *and* sufficient criteria for diachronic identity. The idea would be that any temporal interval where continuity is broken marks a temporal boundary of an organism's life, either due to death or birth, which appear to be straightforward from an organizational perspective. An organism dies when it loses the property of closure of constraints, as this is responsible for its capacity to maintain itself far from equilibrium, and is born when a closed regime appears. Any corpse or parts that remain after death, as well as any preceding material constituents will be spatiotemporally continuous but not organizationally continuous with the organism.^v

To see why this solution generally does not work, recall that organizational continuity between two successive stages is present as long as both stages instantiate the principle of closure of constraints, the stages are spatiotemporally continuous with one another, and the later stage is causally dependent on constraints acting in the previous stage. The problem is that these conditions are satisfied not only between stages of metamorphosis, but also when the earlier stage is a parent and the later stage is an offspring. Parents and offspring are organized systems, they are spatiotemporally continuous with one another, and the offspring is dependent on constraints exerted by the parent, at least in the sense that the very generation of the former depends on constraints exerted by the latter. Hence, parents and offspring are organizationally continuous with one another.^{vi} If organizational continuity were not only necessary but also always sufficient for diachronic identity, then parents and offspring would count as continuations of the same organism.

This has the unwelcome consequence that whenever a parent continues to exist after reproducing, we would have a spatially scattered system comprising both parents and offspring as parts. This system lacks the right causal connections between parts to count as an individual organism in its own right, so we have to choose which system to track as a continuation of the pre-reproductive parental stages. Each tracking path satisfies organizational continuity equally well, however. A similar problem follows from treating fusion solely in terms of organizational continuity (see Fig. 1). Two fusing systems may each individually be organizationally continuous with the fused system, but they cannot both be the same as the fused system, because before fusion they do not together comprise an individual organism.

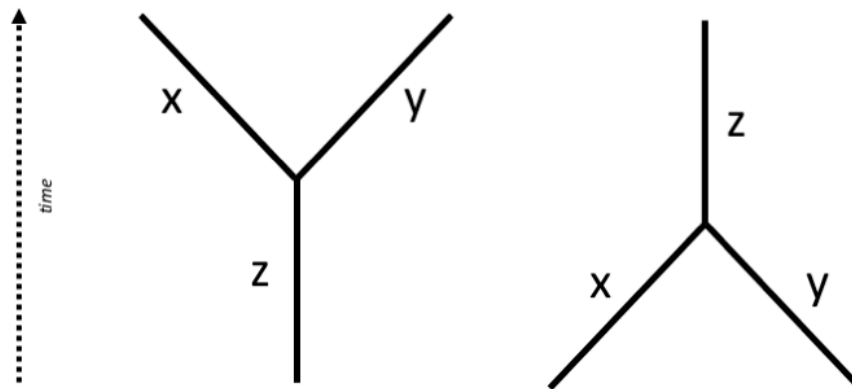


Fig. 2. Fission (left) and fusion (right).

To address this problem, we can modify our criterion by proposing that organizational continuity is sufficient for diachronic identity *unless there is a change in the local number of organized systems that are organizationally continuous with one another*, either via an event of multiplication (fission) or reduction (fusion). When a spatial separation of this sort appears or disappears, then we have a temporal boundary and a change of identity.^{vii}

The issue of spatial separation raises complex problems that go beyond the scope of this chapter, as it would in some sense require a full-blown organizational account of biological individuality. Nonetheless we can say the following. In general, spatial separation occurs when the involved systems do not realize a global closure with mutual dependence. In borderline cases where it is unclear whether there is one organized system or two, the critical consideration is whether the putatively distinct systems are functionally interdependent in virtue of constraint relationships. If organized systems share functional constraints, then the repair and replacement of the constraints depends ultimately on the action of other constraints in each system. In this case, they are not actually separately closed, and the wider system that includes them both is the one that realizes closure of constraints. By contrast, mere causal dependence without constraint relationships does not make the involved systems parts of the same organized whole.

We can clarify and sharpen this characterization of temporal boundaries by seeing how it deals with examples of fission, fusion, and life cycles that combine both.

4.1 Fission

In general, fission occurs when two or more spatially separated organized systems result from a preceding single one, with which they are all organizationally continuous.

Fission allows drawing a temporal boundary in a straightforward way: the preceding system ceases to exist and two new individuals appear. However, this interpretation is not the only possible one, and we need some way of determining whether one of the systems which result from a fission event is a continuation of the life of the preceding system, i.e., whether a parent persists after reproduction.

To tackle this issue, we propose that parent and offspring can be discriminated by the presence of transitory *asymmetrical dependence* relationships. In reproduction, the materials

that will constitute the offspring begin as parts of the parent(s). This is expressed in Griesemer's (2000) condition of "material overlap." Eventually what begins as a part of the parent breaks the symmetry of dependence: it depends on the parent but the parent does not depend on it. When there is a transitory relation of asymmetric causal dependence during the process of multiplication of organized systems, the dependent system can be identified as the offspring, whereas the non-dependent organized system is the parent. If an asymmetry is not present but there is still multiplication of organized systems—e.g., in binary fission—then neither of the resultant systems is a continuation of the parent and both are offspring (new individuals). In most organisms the asymmetrical parental dependence is quite short-lived on the scale of the organism's lifetime, and tends to cease either when there is a physical separation between bodies or the formation of a metabolic boundary such as an egg. Note the loose connection to spatial contiguity implicit in this characterization of multiplication. In order for causal influence to propagate from parent to offspring, they must be at least partially contiguous. But they can remain contiguous without the parent continuing to exert constraints on the constitutive self-maintaining processes of the offspring, such as when eggs are carried around by the parent, or when plants like Aspen trees are connected by underground runners.

The simplest and most ancestral form of reproduction of organized systems is cell division.^{viii} When cell division is "symmetric" in the sense that cell biologists use the term—i.e. the resultant two cells have roughly the same kinds of components and the same size—it is thought that the parent cell ceases to exist upon division and gives rise to two offspring. Cell division can also be "asymmetric" in the sense that the parental components are unevenly distributed to the daughter cells, which are often different in size. When asymmetric division occurs in the cells of multicellular organisms, such as in stem cells, typically the parent cell is again treated as ceasing to exist upon division. But when it occurs in unicellular organisms, such as budding in yeast, it is more common to treat one of the resulting cells as a continuation of the parent.^{ix} In budding yeast (*Saccharomycetales*), the parent cell can be distinguished by several features—for example, it is usually larger, bears scars on the membrane where the bud formed, and retains the aging factors such as carbonylated proteins and DNA circles (Mortimer 1959; Shcheprova et al. 2008). During the generation of a bud, the parent cell dedicates biosynthesis to the bud, whereas the bud dedicates biosynthesis to its own growth (Shcheprova et al. 2008, p. 728). Arguably this is a form of asymmetrical dependence in our (functional) sense, which marks budding as a reproductive process with an identifiable parent that survives it.^x

It is quite likely, however, that there are similar asymmetrical dependencies that can be found in asymmetrical cell division *within* multicellular organisms, and so additional factors must be invoked to explain their different biological treatment. The most obvious difference is that although somatic cells and free-living cells are both organized systems, only the latter are able to develop and reproduce without being normally subordinated to the reproduction of a higher-level entity. Yeast can have complex life cycles with alternating asexual and sexual reproduction. Unlike somatic cells, they produce not only diploid daughter cells but also haploid "gametes" which fuse with gametes from another yeast to form another genetically unique diploid yeast cell. This process is distinguished from gametogenesis and syngamy in multicellular organisms because the fusion yields a yeast cell that is itself able to reproduce asexually and sexually, without intermediary stages of cell division and differentiation.

Attention to these differences illuminates why it is productive to view the yeast cell, but not a somatic cell, as an organism with a life history that persists through multiple reproductive events. Drawing the temporal boundaries in this way yields a developmental unit that is an informative base for generalization and comparison with other developmental units. For example, yeast cells undergo aging and experience trade-offs between growth rate and

reproductive rate due to antagonistic pleiotropy, like many developing organisms (Christie et al. 2018). If we stipulated that, like in somatic cells, the parent cell ceased to exist after each budding event, then the life cycle of yeast would become less comparable to these other life cycles in terms of aging and life history strategy, as well as in terms of ecological and evolutionary dynamics of alternating asexual and sexual reproduction. A similar pattern of reasoning could be applied to multicellular life cycles that include stages of asexual reproduction, such as fission by fragmentation in sea sponges, budding in hydrozoa, and cyclical parthenogenesis more generally. The result of this reflection is that in some contexts, the presence of asymmetric dependence between organisms is not sufficient to assign the identities of parent and offspring. We also need to take into account how drawing the temporal boundaries in one way rather than another can provide a more informative and inferentially rich classification scheme for that individual, giving access to generalizations and enabling the application of explanatory models of its developmental processes.

4.2 Fusion

Having looked at temporal boundaries in a few salient cases of fission, now we can turn to cases of fusion (cf. Hull 1978; Guay and Pradeu 2016). In contrast to fission, fusion occurs when organizationally continuous systems merge in space in such a way that the persistence of one or both systems is affected.^{xi} An individual x and an individual y merge to form an individual z (see Fig. 1). Fusion is not reproduction, but one kind of fusion—syngamy, or fusion of gametes—is part of the process of sexual reproduction, and all kinds of fusion pose issues of temporal boundaries. The question with fission was whether one of the two individuals that are produced is a continuation of the earlier individual (the parent), and with fusion it is the same except reversed in time. In fusion, one of two outcomes can occur:

- (1) x is the same individual as z and y becomes a part of z during fusion, or y is the same individual as z and x becomes a part of z during fusion; or
- (2) neither x nor y are the same individual as z , and x and y cease to exist upon fusion.

The first case corresponds to parental persistence after fission, and the second corresponds to parental cessation upon fission.

An outcome of spatial merging that is *not* fusion would be:

- (3) neither x nor y are the same individual as z , and x and y persist through merging.

Because this does not involve a disruption of the identities of the fusing entities, we will call this “integration” of x and y .

Continuing the parallelism with fission, what happens to biological individuals when they fuse is determined most basically by whether there is an asymmetrical dependence relation between the fusing systems once they have come together in space. When there is, we have outcome (1): the dependent system becomes *part* of the non-dependent system, and the non-dependent system persists through fusion. In Ceratioid anglerfish, for example, when a male finds a female he will bite into her skin and fuse their circulatory systems indefinitely. Males parasitize the metabolism of the females, which are much larger, in exchange for providing a constant source of sperm. Because the male becomes dependent on the self-maintaining processes of the female once they have merged, whereas the female is not similarly dependent on the male, we have an asymmetrical dependence relationship and thus (1). The female persists through fusion and the male becomes a part of her while (presumably) losing its

individual closure of constraints. In fact, this assessment agrees with the naïve judgment of early investigators, who mistook the fused males as “lumps” on the female’s body and searched in vain to find male exemplars of the group.

An example of fusion in which neither fusing partner persists through fusion (2)—instead becoming parts of a new organized system—would be syngamy, or fusion of gametes (Hull 1978, p. 346). In syngamy, each of x , y , and z is an organized system, and the gametes x and y do not maintain their respective closure once fusion occurs because their functional components get mixed together. This is what distinguishes syngamy from obligate fusion of anglerfish as a case of outcome (1). During fusion, male gametes do not retain sufficient cohesion as cells or even as unified parts of the female gamete to stand in a stable asymmetric dependence relationship^{xii}. The female gamete is, moreover, dependent on the ingression of the male gamete to initiate an individual process of development, giving an additional reason to consider them parts of a single individual.^{xiii}

What distinguishes between outcomes (2) and (3) is whether x and y cease to be organized systems in their own right during merging. When x and y retain their closure of constraints, then (3) they persist through the merger. Outcome (2) implies that the fused individual (z) is an organized system. But outcome (3) is consistent with the possibility that the merged individual (z) is an organized system (which might actually be taken as a necessary requirement for being an individual from the organizational perspective), or that it is not.

“Integration” can be characterized as a biological relationship in which spatially contiguous partners influence each other’s functioning in a way that benefits either some partners (asymmetrical dependence, as in parasitism or commensalism) or all partners (symmetrical dependence, as in mutualism). When the dependence is symmetrical, integration generates a new encompassing organized system that realizes closure. An example of (3) that creates a new organized system would be slime molds. Slime molds are groups of free-living amoebae that facultatively aggregate and disaggregate depending on the presence of food. The aggregated amoebas each contribute to the self-maintenance of the whole and even undergo temporary differentiation and functional specialization.

4.3 Sexual Reproduction

With the preceding characterizations of fission, fusion and integration in hand, we can now briefly consider life cycles that involve both. Sexual reproduction of multicellular organisms involves a complex succession of events: fission of gametes from parents or parental cells is followed by fusion of gametes (syngamy) which, in many organisms, is shortly followed by integration of the zygote with the mother.

Applying our criteria yields two interpretations of this sort of sexual reproduction (Fig.3). Under the first (A), the zygote is part of the mother due to its continuing asymmetrical dependence. The production of a new individual only definitively occurs when this dependence is broken due to the fission of mother and offspring, for example at birth.

A second interpretation (B) would count the zygote as a distinct individual from the mother on the grounds that its appearance constitutes the start of a developmental process. The asymmetrical dependence is an intermediate phase in the development of functional and spatial separation of the same entity, which allows tracking the zygote as the same individual as the offspring at birth. Under this interpretation, gametes form a new individual by

syngamy, this zygote persists through its integration with the mother, and is the same individual as the eventual infant.

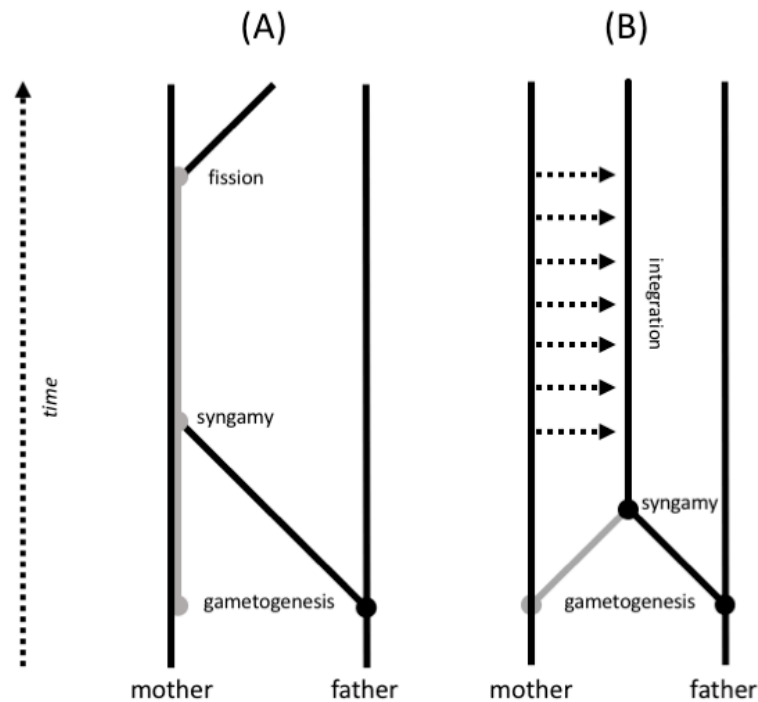


Fig. 3. Differing interpretations of temporal boundaries and parthood in sexual reproduction in placental mammals. Gray segments denote parts of the female parent (f), and circles mark fission or fusion events. Time intervals are not to scale.

The temporary asymmetric dependence of metabolism between parents and offspring should not preclude our ascribing distinct individuality to the offspring in all contexts and for all purposes of inquiry. In line with interpretation (A), the idea that the developing embryo is *part* of the mother (in placental mammals) has been promoted in recent discussion of the “metaphysics of pregnancy” (Kingma forthcoming). However, from an evolutionary perspective, a zygote is already a new evolutionary individual due to its genetic uniqueness and homogeneity (Clarke 2013). This new individual plausibly persists through its integration with the mother during implantation in the uterine wall, though it is not yet a physically separate organized system throughout its existence. The distinction between mother and offspring is even more evident from a developmental perspective. The embryo is undergoing completely different ontogenetic processes and stages than those of the mother. For purposes of applying models of human development, then, it is more productive to think of the mother and embryo as distinct individuals. In the terminology of DiFrisco (2018b), mother and embryo are parts of the same physiological and ecological individual, but they are distinct evolutionary and developmental individuals. Which classification scheme we choose in different classes of cases should be determined by our theoretical framework and its investigative and explanatory aims.

5. Conclusions

In this chapter, we have seen how diachronic identity for organisms can be plausibly grounded in a special kind of causal continuity. In order to capture sameness over time despite radical developmental changes such as metamorphoses, continuity should not be based on conservation of matter, function, form, or activity, but rather on a causal dependence relation called organizational continuity. For two stages of a developmental process to be organizationally continuous with one another, they must be spatiotemporally continuous, must realize closure of constraints (by whatever particular regime of closure), and the later stage must be dependent on constraints exerted in the earlier state. This permissive conception of organism identity entailed a departure from the substantialist model of persistence due to Wiggins (2001) and others, while also enriching and specifying existing accounts of genidentity due to Hull (1978), Guay and Pradeu (2016).

Organizational continuity is consistent with dramatic developmental change, but it does not differentiate development and reproduction. This is because parent and offspring are organizationally continuous with one another just as the successive stages of parental development are. To distinguish parent and offspring, then, it is necessary to adopt working notions of fission and fusion. We argued that the reproduction of organized systems entails their spatial multiplication, and that the presence of a temporary asymmetrical dependence relationship between systems largely determines whether one of them is a continuation of the life of the parent. With fusion, similarly, the outcome is determined by the presence of asymmetrical dependence as well as by whether the fusing systems retain their separate closures.

With this account in hand, we can now assess it in light of the problems of individuality introduced at the start. On the problem of distinguishing development and reproduction, our account weaves between overly permissive and overly restrictive criteria of diachronic identity while making sense of a wide range of generative phenomena in biology. This provides a productive starting point for thinking about organism identity, but we also saw how, with the examples of reproduction in yeast and placental mammals, alternative temporal boundaries can be promoted from within different perspectives that bring different modeling and generalization strategies. Further work will be needed to sort through this variation in a more fine-grained way, to determine exactly which empirical situations demand which kinds of temporal boundaries.

Other theoretical aims foregrounded by existing accounts of biological individuality can, in most cases, be fruitfully embedded within an organizational account of organism identity. Part of the reason these other criteria can be superimposed on an organizational account is that the latter starts from the biologically basic process of self-maintenance rather than more complex developmental, ecological, or evolutionary processes. There is a clear sense in which, in order to be able to participate in those dynamic processes, a physical system must first be able to maintain itself far from equilibrium with its environment. In many cases, criteria focused on these other processes will individuate subsets and supersets of organized systems across time, and may also single out different temporal segments of biological process, but closure nonetheless explains what keeps it all going physically. An open task for future work will be to account for how these elements ultimately hang together.

The picture of organism identity outlined here has an interesting implication for classificatory practice in biology. Substantialist views lend themselves to a “phenetic” approach in which the identity of organisms and classes of organisms is determined by qualitative similarity, resemblance, or sameness of properties or activities. This type of approach has historically been associated with classification errors in which stages of the same polymorphic life cycle are assigned to different taxa because of their dissimilarity (Hull 1978; Nyhart and Lidgard 2017). The propensity to make this error can be corrected by

shifting from a similarity-based view to a causal continuity-based view of organism identity. Instead of looking for similarity between different stages of development, one looks for the right sort of causal connections between stages of the same four-dimensional developmental process.

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ⁱ The fact that so many authors have expressed the shared intuition that spatiotemporal continuity is necessary for object identity is plausibly a reflection of deep-seated psychological mechanisms that allow us to perceive objects as persistent, an insight explored by Scholl (2007). Thanks for Riana J. Betzler for pointing us to this work.

ⁱⁱ During morphogenesis, however, the structure of the vascular system is influenced by the dynamics of blood flow (hemodynamics), as Alessandro Minelli points out (personal communication). See Yashiro et al (2007) and Kowalski et al (2013).

ⁱⁱⁱ Note that closure of constraints is importantly different from *causal* closure, a notion that is often invoked in discussions of physicalism or materialism. For more on the connection between physicalism and organization see Mossio et al. (2013) and DiFrisco (2017).

^{iv} Curiously, Wiggins maintains that “live things exemplify most perfectly and completely a category of substance that is extension-involving, imports the idea of characteristic activity, and is unproblematic for individuation” (2001, p. 90). This may be true if the task is one of distinguishing organisms from artifacts and other non-living things, but problems of individuality in contemporary biology are more demanding.

^v In practice, it may be that we cannot specify an exact moment of death or birth, but only a temporal interval during which they have occurred. However, the ability to pinpoint an exact time of death does not seem to matter much from a biological perspective.

^{vi} Recently, one of us has argued that organizational continuity among generations is actually a fundamental requirement for biological heredity, understood from an organizational perspective (Mossio and Pontarotti 2019).

^{vii} Note that we are not attempting to define reproduction directly, but to identify temporal boundaries of lifetimes. One such temporal boundary occurs with the spatial multiplication of organisms, which is not quite the same as reproduction. To distinguish reproduction from mere production of a new organized system, it may be necessary that the offspring *resemble* the parent or belong to the same kind (Godfrey-Smith 2009, p. 78). Certainly some form of parent-offspring resemblance, probabilistic dependence, or covariance is necessary in order for reproduction to lead to evolution by natural selection, as Lewontin (1970) pointed out. That being understood, we sometimes still use the term “reproduction” for its familiarity.

^{viii} Many authors think of *replication* as the most fundamental form of reproduction, the paradigm case being replication of nucleic acids. Our characterization is not intended to cover reproduction or replication in non-organized systems such as nucleic acids, genes, or viruses.

^{ix} Some yeasts, namely “fission yeasts” (Schizosaccharomycetes), reproduce asexually with symmetric cell divisions, so what follows does not apply to them.

^x Recent evidence suggests that some paradigmatic cases of symmetrical cell fission (e.g., *E. coli*) may actually involve asymmetries in the retention of ageing components (see Nyström 2007). Thanks to John Dupré for pointing this out.

^{xi} Another phenomenon sometimes included under the heading of fusion is *conjugation*, a merger between cells in which genetic material is exchanged. Conjugation is a form of sexuality without reproduction (see Fusco and Minelli in press). Since conjugation does not affect the persistence of organized systems, we do not include it as a case of fusion.

^{xii} It should be noted that, in this framework, fusion is understood as a functional issue, and refers to the merging of constraints between two individuals. For this reason, the situation in which an organism eats another

organism does not count as fusion, because the eating organism consumes the eaten organism and no functional integration occurs. The theoretical distinction between constraints and processes outlined above is at work here.

^{xiii} Isogamy, an ancestral state of sexual reproduction in which there is no male-female differentiated gametes, fits the interpretation of syngamy as (2) even more naturally. Other examples of fusions (2) would occur during the split-embryo development of certain freshwater fish (*Cynolebias*) (Minelli 2011, p. 11) and the formation of a syncytium.