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**Kinds of Biological Individuals:**

**Sortals, Projectibility, and Selection**

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**Abstract**

Individuality is an important concept in biology, yet there are many non-equivalent criteria of individuality expressed in different kinds of biological individuals. This paper evaluates these different kinds in terms of their capacity to support explanatory generalizations over the systems they individuate. Viewing the problem of individuality from this perspective promotes a splitting strategy in which different kinds make different epistemic trade-offs which suit them for different explanatory roles. I argue that evolutionary individuals, interpreted as forming a functional kind, face difficulties of individuation and explanatory power that are mitigated by relying on more structurally based properties and non-evolutionary kinds.

1. *Introduction*
2. *Kinds of Biological Individuals*
3. *Evolutionary Individuals and Functional Kinds*
4. *Evolutionary versus Non-Evolutionary Kinds of Individuals*
   1. *Physiological individuality*
   2. *Ecological individuality*
   3. *Developmental individuality*
5. *Conclusion*

**1. Introduction**

The concept of an individual has special theoretical roles in the life sciences beyond its generic role as an ontological category. Biological individuals are the primary objects of natural selection, they are the bearers of adaptation, fitness, and agency in addition to being the principal units of physiological structure and ecological interaction. It is one thing to recognize these roles, however, and another to provide criteria of individuation that allow us to adequately fulfil them. While theorists have traditionally relied on more or less tacit and intuitive criteria of individuation, recent discussion of biological individuality has put the conceptual development of these criteria explicitly into focus. It is increasingly acknowledged that a wide variety of non-equivalent criteria of biological individuality is available, including physiological integration, genetic homogeneity, immune recognition, metabolic autonomy, being a unit of selection, developing from a unicellular bottleneck, and more. In order to choose between criteria amid this diversity, it is necessary to get clear on the major roles that the concept of individuality plays in biological research. These roles determine the aims that an account of biological individuality is supposed to satisfy.

An account of biological individuality can be viewed as a scheme for mapping a set of criteria of individuality onto a set of theoretical aims, thereby providing rules for applying criteria in a given situation. At least nine major aims have been recognized by theorists and philosophers, corresponding to the main theoretical roles that individuality plays in the life sciences. Criteria of biological individuality should ideally allow one to do the following:

1. Count offspring for measurements of reproductive fitness (Clarke [2011], [2013]);
2. Determine which individuals are bearers of fitness (or of genes and traits having fitness) in order to measure population size (*N*) and track demographic change (Clarke [2011], [2013]);
3. Distinguish the reproduction of a new individual from the development and growth of the same individual (Godfrey-Smith [2009]; Herron *et al*. [2013]);
4. Guide the appropriate choice of selection models, such as models for individual, group, and multilevel selection (Sterner [2015]; Okasha [2006]; Wagner and Laubichler [2000]);
5. Identify and explain evolutionary transitions in individuality (Michod [1999]; Clarke [2011]; Clarke [2013]; Sterner [2015]; O’Malley and Powell [2016]);
6. Determine and predict histocompatibility, fusion, and transplantation outcomes (Pradeu [2010]; Burnet [1969]; Medawar [1957]);
7. Provide biological kinds to be used for classification and inductive generalization (Pepper and Herron [2008]; Clarke [2011]; Sterner [2015]);
8. Determine the appropriate reference system for decompositions into functions and characters, such as homologies and synapomorphies (Wagner and Laubichler [2000]; Cummins [1975]);
9. Determine units of ecological interaction, or the individuals that participate in ecological processes as a whole (Hull [1980]; Huneman [2014a], [2014b]).[[1]](#footnote-1)

With these aims in hand, we can frame the issue of monism and pluralism about biological individuality in simple terms. Monism corresponds to the situation that the set of aims (1)-(9) maps uniquely onto a specific criterion of individuation. By contrast, pluralism corresponds to the situation that there are many mappings between the set of aims (1)-(9), or between particular aims, and different criteria of individuation.

In this paper, I argue for a specific form of pluralism about individuality. Before getting to the arguments for this position, we should consider that monism and pluralism are only well-defined relative to a reference set of aims such as (1)-(9), and that adding or removing aims from the reference set can change the truth-value of these positions. In general, the more aims are accepted as legitimate, the less likely monism is to be true. This raises the difficult question whether there is principled basis for including or excluding aims from consideration. The basis for aims (1)-(9) is a form of descriptive adequacy: not all conceivable aims for an account of individuality are included, but only those that have been most widely discussed in the contemporary literature. Monism and pluralism about biological individuality are here defined over (1)-(9), though different reference sets of aims could certainly be argued for.

In principle monism about individuality could be based on criteria from any area of biology, but in fact it has most often been based on evolutionary considerations (see Hull [1992]; Clarke [2013]). Initially, evolutionary monism draws some plausibility from the fact that several of the above aims are complementary. (1)-(3) can be viewed as aspects of an evolutionary ‘counting problem’ which directly bears on the practices of many evolutionary biologists (Clarke [2012]; [2013]). In cases where individuality is not easily assessed, such as modular organisms, it has been debated whether to count vegetatively produced structural units (ramets) as individuals or only the more inclusive products of sexual reproduction (genets). These alternatives have consequences for predictions of evolutionary dynamics (Tuomi and Vuorisalo [1989]; Clarke [2012]). An account of individuality designed to resolve this counting problem can then use the same criteria to determine whether, faced with a population of modular systems like trees, one applies models for individual selection or group selection (4). The same criteria might also help to identify when a major evolutionary transition has occurred (5) such as the origin of multicellularity or eusociality (Michod [1999]), to predict transplantation or fusion outcomes (6), to establish the right grain of description for generalizing across taxa (7), to determine which systems are bearers of evolutionarily significant traits such as synapomorphies and homologies (8) (Wagner and Laubichler [2000]), and to demarcate ‘interactors’ (9) (Hull [1980]).

A more pluralistic situation would be that an account answering to the counting problem doesn’t provide the criteria most germane to elaborating explanatory biological kinds, determining units of ecological interaction, or identifying bases for decomposition into characters and functions. I will argue that this is the case: the counting problem in evolutionary biology promotes functional criteria of individuality, but functional criteria defined in terms of natural selection face difficulties of individuation in addition to frequently being inadequate on aims (7)-(9).

I begin in Section 2 by introducing a new framework for thinking about biological individuality in which biological individuals are viewed as essentially being countable instances of explanatory biological kinds. Sections 3 and 4 evaluate the functional kind ‘evolutionary individual’ as to whether it satisfies aims from the list (1)-(9). This task is divided into two parts. Section 3 assesses whether evolutionary individuality forms an individuative kind, and Section 4 assesses whether it forms an explanatory kind. I propose a modification to Clarke’s ([2013]) account of evolutionary individuality that would allow it to better resolve the evolutionary counting problem (1)-(3). I then argue that evolutionary individuality cannot be plausibly extended into an evolutionary monism about biological individuality specifically because it does not satisfy (7)-(9) as well as more explanatory, structurally defined kinds of individuals. I close by describing distinctive explanatory roles of these other kinds—‘physiological’, ‘ecological’, and ‘developmental’ individuals—which I take to motivate splitting the concept of the biological individual or the organism into more precisely defined sub-kinds.

**2. Kinds of Biological Individuals**

Biological individuals come in many varieties: there are cells, multicellular organisms, superorganisms, symbioses, clones, and more. The idea underlying aim (7) is that accounts of biological individuality can aid in clarifying and developing these varieties into robust biological kinds. However, the role of kinds is more fundamental than this. As I hope to show, the entire problem of biological individuality can be profitably viewed as a problem concerning a certain class of biological kinds.

According to a position known as ‘sortalism’, developed and defended at length by Wiggins ([2001]; [2016]) and Lowe ([2009]), the only criteria of individuation that are determinate enough to settle individuation questions of the type raised by (1)-(9) are those embedded in sortals or kinds (see also Wilson [1999], p. 35 ff.). Sortals are general terms for kinds of individuals that are usually expressed by count nouns (‘book’, ‘human’, ‘leaf’). Sortals can be characterized by contrasting them with property classes, such as ‘red things’ or ‘sharp objects’, as follows: whereas property classes have criteria of instantiation, sortals have criteria of instantiation as well as criteria of identity. Criteria of instantiation specify the conditions under which a property is instantiated—what it takes for something to be red or sharp. By contrast, criteria of identity specify the conditions under which things with the property are identical—what it takes to be the same individual book, human, or leaf. Sortalism holds that the possession of sortals with criteria of identity is necessary for our most basic epistemic dealings with individuals, including singling them out as objects of unambiguous reference, tracking their persistence through time, evaluating their putative identity or distinctness with other individuals, and counting how many there are in a given region. Thus, although it is relatively clear what is red and what is not, the property class ‘red things’ does not provide a criterion of identity for its members. There is often no determinate answer to the question when a red thing begins or ceases to exist, whether two red things are really the same red thing, or how many red things there are in the room (Lowe [2009], p. 13). By contrast, sortals are supposed to have criteria of identity that permit determinate answers to these kinds of individuation questions.

Sortalism has become a well-established view of identity and individuation in recent years. If it is right, then the problem of biological individuality is as much about kinds as it is about individuals. The evolutionary counting problem (1)-(3) could then be posed as a problem of finding a certain type of biological sortal or kind. More broadly, each of the individuation problems expressed in (1)-(9) poses similar epistemic demands requiring the implementation of sortals. Yet many of the biological individuality concepts that are available for satisfying these aims seem to only be property classes. In considering symbiotic associations, for example, often we know that symbiosis is instantiated without knowing exactly how many biological individuals there are instantiating it. This is because there are no clear criteria of identity for symbioses or symbiotic associations as such, though there are criteria of instantiation. Similar considerations apply to concepts like ‘multicellular organism’, ‘clone’, and ‘colony’, which are far from having clear and settled criteria of identity.

Fortunately, it is not necessary to have sortals that are fully determinate in all respects in order to make progress on the main biological individuation problems that have occupied theorists (finding criteria to satisfy aims (1)-(9)). In particular, problems concerning necessary properties and diachronic identity are thought to require ‘essential’ or ‘substance’ sortals, which are supposed to determine the essential properties and persistence conditions of individuals. Counting problems are generally less demanding: their criteria of identity should enable counting but can tolerate more vagueness on transworld and diachronic identity (see Grandy [2016]). Returning to the symbiosis example, sortals for evolutionary individuals and for more inclusive ecological individuals (‘holobionts’) could determine that, in a given region, there are 100 of the former and only one of the latter, without providing strict persistence conditions for the individuals thus counted, and without determining what they essentially are. The majority of individuation problems that make a difference for biological individuality are of this less demanding type. I will refer to the minimal requirement for sortals to enable counting as the need for kinds to be ‘individuative’.

Sortalism usefully re-focuses the problem of individuality on the individuative capacities of biological kinds. But there are additional reasons for thinking this way that do not specifically require a commitment to sortalism. One clear advantage of viewing the problem through the lens of kinds is that it explains how biological individuality can be a matter of degrees—an idea that has met widespread consensus (Michod [1999]; Santelices [1999]; Godfrey-Smith [2009]; Clarke [2013]; Herron *et al*. [2013])—despite the fact that something cannot be more or less of an ontological individual. This difference follows from basic differences between ontological categories and natural kinds (see Lowe [1997]). The ontological category of individuals is typically characterized by a sparse cluster of generic category features, such as being particular, concrete, non-dependent (unlike properties or universals), unified in space, and persistent in time (Seibt [2010]). None of these category features are degree properties, however. Being a particular, or being necessarily uniquely located in spacetime, is not a property an object can have to different degrees. Neither is concreteness, persistence, non-dependence, and unity, at least as standardly understood. This is perfectly consistent with the idea that biological individuality comes in degrees as long as ‘individual’ in biology denotes a scientific kind or class rather than an ontological category. It is consistent because an entity can possess the properties that place it in different kinds to varying degrees while remaining entirely an ontological individual. For example, ramets and genets are both ontological individuals, since they both possess the category features characteristic of individuality. But they might not both belong to the kind ‘evolutionary individual’, or they might have different degrees of evolutionary individuality.[[2]](#footnote-2) It is this latter issue that matters in debates about ramet and genet individuality. The conditions for being an ontological individual, in contrast, are satisfied all too easily. Not just ramets and genets, but indefinitely many different demarcations around a system can grant the generic features of ontological individuality. However, the majority of these ‘systems’ are uninteresting from a biological point of view, and certainly for aims (1)-(9). They are not instances of explanatory kinds.

Another advantage of thinking in terms of kinds is thus to highlight that biological individuality—like natural kinds generally—should have some scientific explanatory value. Just as it not biologically significant that some arbitrary part of an organism possesses ontological individuality, so it is not intrinsically significant whether or not some item is descriptively classified as a biological individual. What matters is the *inferences* this permits about that item. Classifying something as an evolutionary individual, for example, should license nontrivial inferences about its evolutionary dynamics. Classifying a worker bee as an organism should permit different inferences than classifying it as a part of an organism. Otherwise, there would be little at stake in the problem. The situation with kinds in general is the same. I will refer to this requirement as the need for kinds to be ‘explanatory’.

These considerations immediately suggest that different accounts of individuality can be treated as rival classification schemes and evaluated as to their inferential or explanatory power with respect to aims (1)-(9). For purposes of making such an evaluation, it is enough to examine how different kinds of individuals connect to different *projectible properties*. A kind has projectible properties when correlations between properties observed in some of its instances can be reliably extrapolated or ‘projected’ to other instances (Goodman [1954]; Griffiths [2004]). Projection is a form of inductive inference running from properties of different instances of the same kind, where these properties are not definitive of kind-membership. A standard example is provided by chemical elements: in classifying a sample as gold due to its having atomic number 79, one can reliably infer that it will have an atomic weight of 196.96657 based on the atomic weight of other samples of gold (ignoring isotopes), in addition to inferring a number of its other chemical properties. This inference is ampliative and explanatory because having an atomic weight of 196.96657 is not what makes something an instance of gold, but it has a projectible correlation with having atomic number 79.

Kinds of biological individuals, being products of contingent evolutionary processes, should not be expected to be as orderly as chemical elements, but they should furnish some degree of projectibility if we are to have an empirical basis for deciding between rival schemes.[[3]](#footnote-3) Kinds can do this by including projectible properties directly or by another more indirect means—by setting the right grain of description for projectible comparisons between instances of *other* kinds, such as biological taxa. This indirect role is particularly important in the context of comparative biology, as Pepper and Herron ([2008], p. 625) point out:

Imagine, for example, that we are interested in organismal senescence, and we want to correlate lifespan with some environmental factor across a wide taxonomic range. For a given species of coral, should we record the lifespan of a single polyp or of the entire colony?

An individuality kind ideally should allow one to identify the more comparable unit in such situations. I return to this issue in examining the projectibility of different individuality kinds in Section 4.

The utility of thinking about individuality in terms of kinds can now be carried over to the issue of monism and pluralism by re-framing it in terms of kinds. In this framework, monism about individuality can be defined as the view that ‘biologicalindividual’ is an individuative and explanatory kind—that is, it enables counting and is inferentially rich with respect to (1)-(9). By contrast, pluralism would be the view that ‘biological individual’ is not an individuative and explanatory kind, and that either (a) it is a class containing heterogeneous individuative and explanatory kinds (such as ‘evolutionary individual’, ‘physiological individual’, ‘developmental individual’), or (b) no subclass of ‘biological individual’ is an individuative and explanatory kind. To constitute an individuative kind, as we saw, it is not enough for biological individuals to share some property or other. The shared property must be an ‘extension-involving’ sortal property that enables unambiguous counting (see Wiggins [2001], p. 89). Similarly, to constitute a mere class, it is enough for biological individuals to share some property or other, whereas to constitute an explanatory kind, biological individuals must (at least) share *projectible* properties. Below, I will put these requirements to work in support of a pluralism of type (a). In a kinds-based framework, countability and projectibility provide additional guidance for determining which things are biological individuals, over and above the more free-floating notion of ‘criteria’. In this framework, there are biological individuals wherever there are countable individuals instantiating biological properties that are projectible in a sense relevant to (1)-(9). I will refer to this characterization as ‘kind pluralism’ and the characterization from Section 1 as ‘criteria pluralism’.

A final motivation for approaching the problem of individuality as a problem concerning kinds is that it facilitates posing metascientific questions about how broad classes of kinds—such as evolutionary, historical, developmental, physiological, and ecological kinds—interact on the issue of biological individuality, which has been done to some extent for biological characters (see Griffiths [1994], [1996]; Wagner [2001]). In securing projectible information, different classes of biological kinds balance different epistemic trade-offs between generality and depth. More structurally based kinds such as cell and tissue types are comparatively deep but narrow. Historically based kinds like homologies tend to be more fine-grained and informative than functional kinds (Griffiths [1994]; Ereshefsky [2012]). However, one distinctive feature of functional kinds which makes them indispensible to biology and the social sciences is that they can pick out important similarities between structurally and historically heterogeneous instances, which allows them to target diverse mechanisms that are relevant for complex, higher-level processes such as evolution or cognition (Enç and Adams [1992]; Sober [1999]). When the material differences between instances don’t matter, this is a considerable virtue. When they do matter, functional kinds can be shallow and uninformative. This is the central predicament for functional kinds of individuals.

**3. Evolutionary Individuals and Functional Kinds**

Much of the discussion of biological individuality has taken place in the context of evolutionary biology, where uncertainty about individuality seems to have the greatest effects. The main problem arises once we recognize that there are many properties that biological systems possess that can influence their capacity to undergo selection, including spatial contiguity, genetic uniqueness, genetic homogeneity, reproductive bottlenecks, sexual reproduction, germ-soma separation, functional differentiation, and more. Early accounts of evolutionary individuality have tended to single out one or a few of these properties as definitive of evolutionary individuality, such as being a product of sexual reproduction (Janzen [1977]) or passing through a unicellular bottleneck in development (Dawkins [1982]). However, none of these properties is really necessary for an object to participate in evolution by natural selection, and none is universal across different taxa. Eusocial insect colonies lack spatial contiguity, many plants and fungi lack strict germ-soma separation, sea sponges and slime moulds lack reproductive bottlenecks, identical twins and clones can lack genetic uniqueness, and chimeras lack genetic homogeneity. Yet in each case we seem to have something like an evolutionary individual.

Given this fragmentary situation, two kinds of synthetic approaches are possible. First, one can single-out a material property or set of properties as definitive of paradigm individuals, and identify other individuals based on how closely they approach that paradigmatic state (Godfrey-Smith [2009], [2013]; Santelices [1999]; Folse and Roughgarden [2010]). Second, one can abstract from material properties altogether and define individuality in terms of the functional effect that these properties have which makes them belong to the same kind—namely, the effect of increasing the capacity of an object to undergo selection as a whole (Clarke [2012], [2013]).[[4]](#footnote-4) According to this approach, evolutionary individuals constitute a multiply realizable functional kind. I focus on the second, functionalist approach.

The main motivation for adopting a functionalist account like Clarke’s ([2013]) is that many of the properties considered important for biological individuality are materially diverse, and yet similar in their functional effect on the process of natural selection. By defining individuality directly in terms of this effect, one not only reconciles conflicting accounts that are based on different specific properties, but also attains a level of generality that cannot be matched by the strategy of identifying paradigmatic properties. The paradigmatic properties identified by Godfrey-Smith ([2009], [2013]), for example—bottlenecks, germ-soma separation, and integration—are not the only actual properties that influence evolutionary individuality, and new ones could still evolve.

In Clarke’s ([2013]) account, specific properties like bottlenecks or genetic uniqueness are said to have their functional effects on the capacity to undergo selection by acting either as policing mechanisms or demarcation mechanisms, or both. Policing mechanisms decrease the capacity of the parts of an object to undergo selection, and demarcation mechanisms increase (or maintain) the capacity of the object to undergo selection. The capacity to undergo selection at a given level is then analysed in terms of Lewontin’s ([1970]) three necessary conditions for evolution by natural selection:

1. phenotypic variation: members of a population vary in traits;
2. differential fitness: different rates of survival and reproduction probabilistically depend on the possession of different traits;
3. heritability: offspring traits depend on parent traits.

Bottlenecks can act as policing mechanisms by ensuring that the cells in a developing system are genetically homogeneous, except for the inevitable mutations. Genetic homogeneity among cells tends to reduce selection at the cell level by reducing the phenotypic variation between cells as well as restricting the variation between cells that is heritable. Other policing mechanisms can include germ-soma separation, immune response, programmed cell death, DNA repair, worker policing in eusocial colonies, and more (see Clarke [2013], p. 423). Similarly, sexual recombination can act as a demarcation mechanism by making offspring genetically unique, thereby increasing their heritable variance with other objects in the same population. Other potential demarcation mechanisms include mutation, lateral gene transfer, polyploidization, immune response, skin and cell membranes, and inter-colonial aggression, among others (see Clarke [2013], p. 426).

With these definitions in place, Clarke ([2013], p. 429) proposes that a necessary and sufficient condition for a system to be a biological individual is that it possesses at least one policing mechanism and one demarcation mechanism. For simplicity I will refer to this condition by saying that the system is ‘capable of undergoing selection as a whole’. In its application, this condition turns out to be quite permissive: the class of evolutionary individuals can include both bounded organisms and groups, colonies, units at different levels within the same system, and sometimes even very many partially overlapping sub-sets of parts of an individual (see Sterner [2015]). This may be a virtue in cases where different boundaries appear to present strict alternatives, as in debates over whether ramets or genets are evolutionary individuals, when in fact both ramets and genets can undergo selection as a whole to different degrees and even at the same time (Clarke [2012]). The account deals with such situations by maintaining inclusive conditions of membership in the kind ‘evolutionary individual’ and recapturing evolutionarily significant differences as differences of degrees of evolutionary individuality. These degrees are presumably determined by the number of policing and demarcation mechanisms at work in an individual and some measure of the magnitude of their effects.

A functionalist account of individuality like this one can be expected to face some of the same problems as functional definitions of genes and traits, and more broadly, as the attempts to generalize evolutionary theory in the functional terms of units of selection (Lewontin [1970]), replicators and vehicles (Dawkins [1982]), or replicators and interactors (Hull [1980]). Accordingly, the issues I raise are broadly in line with Griesemer’s ([2005]) sustained criticism of these attempts at ‘generalization by abstraction’. The core difficulty with a purely functional account is this: in abstracting away from the material properties that can make something an evolutionary individual, one abstracts from the sortal properties that allow one to individuate concrete objects, as well as from the projectible properties that informatively explain what makes something function as a unit of selection.

Unlike previous responses to the counting problem, which make recommendations like counting ramets (Tuomi and Vuorisalo [1989]) or genets (Fagerström [1992]; Janzen [1977]), the functionalist solution is to count whatever objects exhibit the capacity to undergo selection as a whole. Compared to being a ramet or genet, however, this is a much more complex, relational, and hierarchical property. More troublesome is the fact of being an abstract functional property, which creates an individuation problem. On the functionalist account, evolutionary individuals comprise a functional kind, and instances of the kind are functionally individuated. Functional individuation in this context means individuation by effect: instances fall under the kind if they possess those properties that have the targeted effect, which in this case is highly complex, relational, and hierarchical. Individuation by effect requires not only that the effect can be independently identified, but also that the item that is responsible for it can be uniquely singled out solely in virtue of that effect. The stringency of this requirement has motivated the argument that functionally defined kinds do not on their own provide genuine sortals (see Wiggins [2001], p. 87 ff.).

This point can be illustrated by considering a class that is commonly considered to be functionally defined—artefacts. To single out a hammer or count the number of hammers in a room it is usually not enough to know that hammers are things that can be used for driving nails into tough materials. This functional property needs to be mapped onto at least some non-functional material properties, like having a characteristic shape, material composition, size, hardness, and so on. Clusters of detectable material properties are needed for identifying hammers, even if we might classify a materially very different object with the same function as a hammer.[[5]](#footnote-5) The situation with functional kinds of biological individuals is essentially the same: in order to use them for individuation, we must rely on generalizations that map the functional effects onto identifiable material conditions. Without being mapped onto material conditions, a functional kind of individuals has the surface form of a counting sortal (‘*unit* of selection’) but is only a property class defined by a functional property.

Clarke’s ([2013]) account seems to provide exactly these material conditions in the form of policing mechanisms and demarcation mechanisms. However, the trouble is that policing mechanisms and demarcation mechanisms are themselves functionally defined: both individuating mechanisms ‘are, as a matter of definition, what determine the expression of heritable variance in fitness’ ([2013], p. 429).[[6]](#footnote-6) As a result, the individuation problem gets exported to a lower level. Reproductive bottlenecks often act as policing mechanisms by decreasing genetic heterogeneity between cells, but sometimes they do not. When there is a high mutation rate, genetic heterogeneity can be greater in a multicellular system developing from a bottleneck than in one developing from fragmentation. Germ-soma specialization alone does not preclude selection between competing cell lineages, which may be a reason why complementary factors have evolved, such as maternal control of development, apoptosis, immune system policing, and early sequestration of the germ line (Buss [1987]). Even genetic homogeneity itself can fail to have a policing effect. Genetic homogeneity means there is less genetic variation within a system, but genetic variation is only relevant to the capacity for selection to the extent that it affects fitness. On neutralist theories (Kimura [1983]; Stoltzfus [1999]), most genetic variation does not affect fitness. The same considerations indicate that features like mutation, sexual reproduction, lateral gene transfer—in short, genetic uniqueness—can sometimes fail to function as demarcation mechanisms. Only if the unique genes affect fitness differences in a population do they increase the capacity for selection between genetically unique objects.

Of course, bottlenecks, germ-soma separation, genetic uniqueness, and so on, do *tend* to have individuating effects. Some of these traits may even be adaptations that have the function of focusing selection at a particular hierarchical level. But the fact that they can *malfunction* means that when we identify a bottleneck we have not automatically identified a policing mechanism—if policing mechanisms are functionally defined. As long as a trait is a material entity whose effects depend on contextual influences, mismatch is always possible between its function and its actual causal consequences.

The possibility of mismatch leads directly to a dilemma for functional definitions of individuality. On the one hand, if policing and demarcation mechanisms are identified with specific material properties, then possession of these properties might not be sufficient for the functional capacity to undergo selection as a whole. On the other hand, if material properties like genetic uniqueness are ‘functionalized’ so that only the genetic uniqueness that affects fitness constitutes a demarcation mechanism, then genetic uniqueness *per se* can no longer be used for identifying demarcation mechanisms and thus also units of selection. If we have to know that a material property is functioning properly in order to count it as an individuating mechanism, it is no longer an informative criterion. The main purpose of proposing bottlenecks as a criterion is that it permits *ampliative* inferences about selective dynamics in a population. No ampliative inferences are possible if we have to already know about these dynamics in order to identify functional bottlenecks.

To summarize, then, the argument is the following. Functional kinds like ‘evolutionary individual’ need to be mapped onto identifiable material traits in order to be genuine sortals—in order to enable counting their instances. Since these material traits can malfunction, however, the entities possessing them might fail to be instances of the functional kind. Hence, possession of these traits cannot constitute a sufficient condition for the functional capacity in the way required by the functionalist view of evolutionary individuality.

Note that non-functionalist accounts of evolutionary individuality like those proposed by Godfrey-Smith ([2009]; [2013]), Santelices ([1999]), and Folse and Roughgarden ([2010]), do not face this problem because they are based on more specific material criteria. For the same reason, ‘evolutionary individual’ on these accounts is a more explanatory kind because one can draw ampliative inferences from the possession of specific traits to evolutionary-functional properties. This is also the source of their limitations, for an important insight of Clarke’s account is that none of the specific traits proposed in non-functionalist accounts is truly necessary for being a unit of selection.

A promising way to preserve elements from both types of accounts would be to borrow a strategy from the multiple realizability debate in philosophy of mind and define evolutionary individuality directly in terms of the (inclusive) disjunction of material realizers themselves. Like non-functionalist accounts, this would dispense with the above individuation problem while also making ‘evolutionary individual’ a more explanatory kind. However, as long as the material realizers are construed as sufficient conditions for functioning as an evolutionary individual, this would still not resolve the above dilemma, since they could still malfunction. But the dilemma can be resolved if actual performance of the function is no longer taken to determine conditions for being an individuating mechanism. The result would be that something counts as an evolutionary individual if and only if it possesses at least one property in the disjunction of material properties from each kind of individuating mechanism, whether or not it is actually functioning properly. Instead of constituting sufficient conditions for function performance, these different material properties would be associated with *probabilities* that their bearers undergo selection as a whole to different degrees. An additional step might then be to establish thresholds of probability for a property to count as a significant individuating mechanism in a given context, in order to keep the disjunction small and manageable. These modifications have the important consequence that assessments of individuality become operational but fallible epistemic tools for making inferences about evolutionary dynamics. From the functionalist side, the functional conception of units of selection could be used to guide the discovery and study of specific material properties and aid in the classification of a wide diversity of realizations.[[7]](#footnote-7)

This more ‘bottom-up’ strategy can also be combined with taxic sub-kinds of evolutionary individuals to trade generality for inferential accuracy. Properties like bottlenecks might not be necessary for evolutionary individuality in general, but they might turn out to highly probable for evolutionary individuality in certain taxa. Some material properties are inaccessible to certain taxa due to phylogenetic constraints, while others are not adaptively favoured due to functional constraints. As Buss ([1987]) argues, many of the distinctive policing mechanisms in animals, such as defences against cancerous growth, only evolved in response to the motility of animal cells during development. The same policing mechanisms should not be expected to appear in plants in which rigid cell walls restrict cell motility. Still other policing mechanisms arose in fungi due to their coenocytic, multinucleate condition, such as septation and cell-cycle synchronization (Buss [1987], p. 165). Differences of cellular construction in different domains provide one example of phylogenetic and functional constraints on the appearance of individuating mechanisms. To the extent that constraints of this kind are robust, useful answers to counting problems that arise in evolutionary biology are likely to be taxonomically specific.

Even with these proposed modifications, ‘evolutionary individual’ remains a functional kind because the realizers are only associated with one another in virtue of their probabilistic connection to the same functional capacity. We can now ask—if the development of this functional kind is the right way to resolve the evolutionary counting problem, does it also satisfy the other aims for an account of biological individuality? I argue that it fails to satisfy aims (7)-(9) as adequately as other kinds of individuals.

**4. Evolutionary versus Non-Evolutionary Kinds of Individuals**

Initially, again, the criteria used to count evolutionary individuals seem to be readily transferable to the other theoretical aims. Characterizing individuality in terms of selection seems appropriate for guiding models of multilevel selection (4). Similarly, evolutionary transitions in individuality are arguably transitions in evolutionary individuality (5) (although see O’Malley and Powell [2016]). Regarding the aim of securing biological kinds for inductive generalization (7), classification based on evolutionary processes promises the most ‘ultimate’ and long-range classification of biological systems. If the task is to determine the right reference system for decompositions into evolutionarily relevant characters (8) like synapomorphies or homologies, evolutionary individuals ought to be the relevant reference systems for the job. Likewise for function ascriptions (8), depending on the account of functions. Finally, if evolutionary individuals are the systems that undergo selection as a whole, and the ecological interaction of interest has to do with selection, then evolutionary individuals should also be units of ecological interaction (9).

Nevertheless, many theorists have found it useful to distinguish between evolutionary individuals and organisms, where organisms are characterized in more structural or physiological terms rather than in terms of selection (Sober [1991]; Wilson [1999]; Dupré and O’Malley [2009]; Pradeu [2010], [2016]; Godfrey-Smith [2013]; although see Hull [1992]; Queller and Strassman [2009]; Clarke [2013], [forthcoming]). In addition to the reasons commonly given for this conceptual distinction, we can see that functional-evolutionary and structural-physiological kinds have different explanatory capacities. Evolutionary individuals form a kind that is better suited for the evolutionary counting problem, for the latter favours a high degree of generality which can be won by functional abstraction from materially heterogeneous instances. However, this same feature of evolutionary individuality hinders its capacity to discriminate differences that matter for securing projectible comparisons across individuals, as in aim (7).

How much projectible information can be gained by classifying an object as an evolutionary individual? The main source of projectibility for evolutionary individuals lies in the connection between the material properties and functional properties of specific individuals. For example, when a biological system has germ-soma separation, we can infer a policing effect on its parts. Given that the class of evolutionary individuals includes items as diverse as viruses, colonies, and subsets of parts of organism, however, projectible properties between *different* evolutionary individuals will be in short supply. The properties that are robustly shared between different instances are functional properties related to selection. But these properties are partly what makes them evolutionary individuals in the first place, and so they generally do not permit ampliative inferences.[[8]](#footnote-8) There are reliable connections between some material properties, but different evolutionary individual can have material properties that are ‘wildly disjunctive’ and dissimilar.[[9]](#footnote-9) This situation is to be expected for functional kinds in general, since the main reason to use functional kinds in the first place is to group together structurally heterogeneous instances. If those instances shared many important structural properties, they would likely be better traced under a structural kind (see Kim [1992]).

As mentioned in Section 2, kinds of individuals can also provide projectible properties indirectly in combination with other kinds such as taxa. Perhaps, then, there are brighter prospects for indirect projectibility via evolutionary individuality. Consider how this might work in the context of comparative biology. European honey bees (*Apis mellifera*) form eusocial colonies in which worker bee reproduction is suppressed in favour of queen reproduction.[[10]](#footnote-10) While queens and male drones have some degree of evolutionary individuality, it is whole colonies that constitute the primary evolutionary individuals and the focal level of evolutionary dynamics. But there are also solitary and sub-social species of bees, such as in the genus *Osmia* (mason bees) and *Xylocopa* (carpenter bees). Females in these species sometimes live together, but they can each reproduce independently. The evolutionary individuals here are single bee insects rather than groups of insects. In a comparison between *A. mellifera* and various species of *Xylocopa*, then, the systems with comparable degrees of evolutionary individuality would be whole *A. mellifera* colonies and single, physically discrete *Xylocopa* insects.

The projectible comparisons that can be made between *A. mellifera* colonies and *Xylocopa* insects are comparatively few, however, and mostly have to do with coarse-grained reproductive properties. Both *A. mellifera* colonies and *Xylocopa* insects exhibit germ-soma division in some form. This takes the standard form in *Xylocopa*, whereas in *A. mellifera* the queen functions as an ovary, the workers as somatic cells, and drones as sperm cells. Workers also tend to enforce this reproductive division of labor by removing any worker-laid eggs, which is analogous to immune system defences against uncontrolled cell division within single insects. Workers attack foreign workers, foreign queens, and queens that are no longer recognized in a form of extended immune allorecognition. The production of new queens is strictly regulated by factors like compartmentalization of queen brood chambers and nutritional resources in a way analogous to maternal control of development and early sequestration of the germ line in multicellular organisms (Seeley [1995]; Buss [1987]).

However interesting such analogies may be, in general the more projectible comparison is between single, spatially unified insects belonging to *A. mellifera* and *Xylocopa*. Like carpenter bees, honey bees undergo senescence, whereas colonies don’t except in a metaphorical sense. Worker honey bees and carpenter bees share almost all of the same homologies, thus single insects would more likely be the appropriate reference system for targeting evolutionarily relevant characters (aim 8). Their homologous traits also share almost all of the same biological functions (aim 8). By contrast, *A. mellifera* colonies share no homologies with *Xylocopa* insects, and the shared trait functions are largely functions relating to reproduction. Even here, *A. mellifera* colonies may possess germ-soma division, but their component insects also possess germ-soma divisions that are homologous to those of *Xylocopa*. Competition within a colony’s germline, between rival queens, also takes the familiar form of a dominance hierarchy common in groups of social animals.

Similar contrasts could be provided in other cases where both colonies and solitary organisms from related taxa can be evolutionary individuals, including social versus solitary ascidians, bryozoa, hydrozoa, and more. Whether an evolutionary individual is a colony or a spatially unified organism affects its other properties, including its functional properties. For example, possibly due to constraints on the production of variable phenotypes, there is much less functional division of labor in eusocial colonies than within their component organisms, as measured by numbers of caste types versus cell types. The demand for behavioural complexity despite this structural limitation is partially compensated by a preponderance of temporary and behavioural specialization (polyethism) in workers over the more permanent and morphological specialization (polymorphism) in the soma of unitary organisms (Seeley [1995], p. 240; Wilson [1985], p. 1494). This organizational strategy is no doubt favoured by fact that the colony soma is itself comprised of multicellular organisms, which enjoy much greater physiological autonomy than the more rigidly specialized and interdependent cells, tissues, and organs of unitary organisms. To ignore these structural differences because the somatic metazoans are not evolutionary individuals would be to miss out on important features of eusocial colonies that affect their distinctive ecological and evolutionary dynamics.

The contrast between eusocial versus non-social bees suggests that, for the purposes of comparative biology, having a similar degree of evolutionary individuality often will not be as sound a basis for informative comparisons as more structurally-based factors. At the limit, the idea that a classification based on evolutionary individuality will be the most explanatory one assumes that the force of selection overcomes differences due to structure and level of organization to produce convergent similarities—an adaptationism about individuality. We have seen some reasons to be sceptical of this assumption, but whether or not is empirically supported, it is unnecessary. There is nothing to prevent recognizing similarities as well as differences between things like colonies and unitary organisms, but this requires utilizing kinds other than just evolutionary-functional kinds. This requirement often lies implicitly in the background of biological discussions of functionally defined kinds. Lewontin’s ([1970]) original paper on units of selection is largely preoccupied with assessing whether biological entities at different hierarchical levels function as units of selection—molecules, organelles, cells, gametes, ‘individuals’, kin, populations, and higher. In order for such an inquiry to make sense, these entities cannot be individuated by their functioning as units of selection. Instead, they are individuated by first-order properties that are not directly defined in evolutionary terms, with higher-order functional properties superimposed and dependent on them. The same order of kind-dependence must underlie Hull’s ([1980]) and Dawkins’s ([1982]) framework for replicators and interactors or vehicles (see Griesemer [2005]).

What are these non-evolutionary kinds of individuals? I briefly describe three: physiological, ecological, and developmental. This list is not intended to be comprehensive or definitive, but rather to show how non-evolutionary kinds of individuals are individuative, explanatory, and irreducible to evolutionary individuality.

**4.1 Physiological individuality**

The kind of individuality most akin to criteria of individuality in non-biological contexts targets mechanistic or causal cohesion among parts. Physiological individuality is characterized by stable interaction gradients that are present when physiological interactions between parts are stronger or more frequent with each other than they are with parts of the environment. A physiological interaction can be understood as any sort of physical interaction that has actual or potential effects on biological functioning, and that is part of the dynamical regimes of metabolism typical for known living systems, including chemical reactions, weak and strong bonding, catalysis, diffusion, mechanical interaction, inter-cellular signaling, adhesion, electrical signaling, and so on. Physiological cohesion is a specification of a more general causal cohesion criterion of individuality for dynamical systems (Collier [2003]; [2004]), where the relevant interactions are restricted to those of a specific type. Such specifications allow physiological cohesion to provide sortals for counting kinds of physiological objects, such as cells, organs, and organisms (see Collier [2004]). While interaction strength is matter of degree, having a higher ‘centripetal’ than ‘centrifugal’ interaction strength in a given a set of parts is not. Defined over a clearly specified interaction type, it is a property that enables counting cohesive individuals.[[11]](#footnote-11)

Physiological individuality has various theoretical roles in biology, such as demarcating sub-systems in modular body plans, distinguishing organisms from their non-functional by-products (such as fallen leaves or insect exuviae), as well as distinguishing reproduction from growth or development (aim 3) in cases where the offspring’s capacity to reproduce is lacking or only determined later in development (Godfrey-Smith [2009], p. 71). Perhaps the best example of projectible properties associated with physiological individuality is provided by metabolic scaling laws, which capture wide-ranging correlations between properties like body mass, body size, metabolic rate, and lifespan (see Glazier [2014] for a review). Knowing that a physiological individual has a certain mass, one can reliably infer its metabolic rate and average lifespan. The reason these laws are associated with physiological individuality is that the physical patterns and processes that explain them are also structurally tied to physiological cohesion. For example, explanations from surface area models cite the proportionality between body surface area, heat loss, and metabolic rate, and predict that each factor should scale as *M*2/3 where *M* is body mass (Glazier [2014]). Resource transport models explain metabolic scaling in terms of the size-dependent geometry of vascular and respiratory branching networks (Glazier [2014]; West *et al*. [1997]). System composition and resource demand models point to cell- and tissue-specific metabolic rates that scale nonlinearly with body size (Glazier [2014]). Physiological individuality is useful for guiding the application of these scaling laws because metabolic interaction gradients mark exactly those size boundaries that are likely to scale with metabolic rates.

It is not the case that metabolic scaling generalizations can be captured just as easily when we replace the notion of physiological or metabolic individuals with the notion of evolutionary individuals participating in metabolic processes (see Clarke [forthcoming]), as this would be misleading in many cases. Sterile workers in eusocial colonies of naked mole rats are subject to metabolic scaling laws even though they have very low degrees of evolutionary individuality. Many colonial marine invertebrates will have high degrees of evolutionary individuality at the colony level, but colonies frequently exhibit the isometric metabolic scaling relations characteristic of groups of asocial animals. This is thought to be a consequence of their modular, iterative physiology (Hartikainen *et al*. [2014], p. 779). While individual physiological modules exhibit the allometric, nonlinear metabolic scaling characteristic of physiologically integrated organisms, colony metabolic rate is close to being a linear function of the number of modules (Hartikainen *et al*. [2014]), such that the metabolic whole is the sum of its parts.[[12]](#footnote-12)

Intuitively, increased cohesion positively correlates with increased functional division of labor in many cases, which increases the degree of fitness decoupling between parts and whole and thereby probably also increases the evolutionary individuality of the whole (see Folse and Roughgarden [2010]). However, it is important to recognize that these factors are theoretically independent. Division of labor can increase modularity in a way that reduces physiological cohesion between modules. Evolutionary individuals can also be selected for having *less* cohesion. As Sober ([1991], p. 294) points out: ‘Selection at a given level of organization does not have to produce objects at that level that are highly [physiologically] individualistic. And an object at a given level may be highly individualistic even though it is not the result of selection at that level’.

Functional criteria might enter the picture where stricter conditions of physiological individuality are needed. A stricter condition would be organizational closure, the property that each constraint on metabolic dynamics is produced and maintained by the action of other endogenous constraints (Moreno and Mossio [2015]). Like evolutionary functional criteria, this would have to be mapped onto identifiable material properties and structures to be used for individuation. However, since this functional property is internal rather than depending on complex external relations, this condition is more easily satisfied. Organizational closure in unicellular organisms can be detected via its most salient endogenous constraint—the cell membrane. The epithelium is an analogous structure possessed by all eumetazoans (Arnellos and Moreno [2016]; Wagner and Laubichler [2000]).

**4.2 Ecological individuality**

Whereas physiological individuality is a matter of interaction gradients for physiological systems, ecological individuality targets interaction gradients between parts of an ecosystem. Accordingly, the procedure for counting units is the same as before, but it is based on ecological interaction types—for example, trophic exchanges, ecosystemic matter-energy flows, and processes such as decomposition and primary production. While they will often coincide with physiological and evolutionary individuals, ecological individuals can also have little physiological cohesion and can lack heritable variance in fitness as a whole. Ecological individuality is thus particularly useful for demarcating certain symbioses or ‘holobionts’ that do not form physiological or evolutionary individuals. Ecological individuals might also include abiotic parts of the environment as extended phenotypes (Dawkins [1982]), such as a spider and its web or a bird and its nest.

Ecological individuality is closely related to Hull’s concept of interactors, though it need not be restricted to selection-based interactions. Hull ([1980], p. 318) defined an interactor in functional terms as ‘an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential’.[[13]](#footnote-13) This definition leaves open *which* entities are differentially replicated. What is replicated could be the interactor’s genes, or the genes of symbiotic partners comprising the interactor. The mutualistic association between certain plants and nitrogen-fixing bacteria arguably forms a single interactor or ecological individual, as they normally interact with the environment in such a way as to increase each other’s replication, as well as together comprising a causal node in the nitrogen cycle. Communities of microbes such as biofilms can also constitute ecological and physiological individuals. What is less clear is that either of these examples constitute unified evolutionary individuals, though this remains an open discussion.[[14]](#footnote-14) The component symbionts tend to have correlated mortality rates, but they are not transmitted vertically from the same source and they reproduce independently. That makes it difficult to meaningfully assign parent-offspring lineages between successive ‘generations’ of whole holobionts, putting the heritability of holobiont-level properties into question (Booth [2014]; Clarke [2016]; Skillings [2016]).

In some biological contexts it is more illuminating to think in terms of ecological individuals rather than evolutionary individuals, especially when evolutionary processes are not specifically in focus. For example, individual based modelling in ecology is an approach that models ecological processes in terms of organism-level interactions rather than the classical population-level interactions (see Grimm and Railsback [2005]; Justus [2014]). In this context ‘organisms’, or units of ecological interaction (aim 9), are often ecological individuals and not necessarily evolutionary individuals. In modelling ecological processes such as dispersal, foraging, and trophic exchange, researchers generally do not take extra steps to exclude microbial symbionts from their hosts in order to only target evolutionary individuals. Holobionts often physically disperse, forage, and eat (and are eaten) as a whole. Ecological individuals thus provide indirect projectibility in the generalizations deriving from individual based modelling.

**4.3 Developmental individuality**

Other criteria of individuality for multicellular organisms can be drawn from developmental processes. A developmental individual can be defined as a subset (or superset) of evolutionary, physiological, or ecological individuals that is produced by a series of cell divisions contiguous with a bottleneck, budding, or fragmentation event (see Wilson [1999], p. 99).[[15]](#footnote-15) Identifying a developmental individual thus requires a working grasp of the developmental processes that determine how its parts got there. These processes can specify the extension of countable developmental units, which may be more or less inclusive than individuals of other kinds. Developmental individuals are typically characterized by vertical rather than horizontal transmission of component parts, high levels of genetic homogeneity, and the endogenous determination of cell fates by intercellular regulative mechanisms (Arnellos *et al*. [2014]).

Developmental individuality tends to be more stringent than other criteria of individuality. If a graft is taken from one developmental individual, such as a plant, and fused onto another, the resulting entity may be an ecological and physiological individual but not a developmental one. Eusocial colonies are not developmental individuals except in a metaphorical sense, though their component organisms are. In many cases whole plants are developmental and ecological individuals, but are not evolutionary individuals when sub-parts are the units of selection, and are weak physiological individuals when their physiology is highly modular. Symbiotic associations would be excluded from forming single developmental individuals except in cases where their component parts are vertically transmitted, such as aphid-*Buchnera*, and *Psyllidae*-*C. rudii* partnerships.

Developmental individuality might be viewed as a traditional organism concept to be replaced by more revisionary evolutionary or ecological views (Dupré and O’Malley [2009]; Gilbert *et al*. [2012]). It does have useful theoretical roles, however. Developmental individuality seems to provide the most relevant criteria for assessing factors like whether an entity has a lifespan and undergoes developmental processes such as maturation and senescence. The overlap between developmental and evolutionary individuality arguably determines the central domain of application for life history theory, with its concepts of life history strategy, stages, and trade-offs between fitness components (Stearns [1992]; see Wagner and Laubichler [2000]). In cases where such overlap is missing or only partial, such as evolutionary individuals that are not developmental individuals (eusocial colonies) or developmental individuals that are not evolutionary individuals (workers in eusocial colonies), life history models will have more limited applicability. For example, it is difficult to apply life history models of ageing to whole colonies without simply identifying colony lifespan, reproduction maturation, and senescence with that of the queen (Hou *et al*. [2010]). In polygynous colonies having many queens, this would be problematic. Likewise, since workers generally do not reproduce, reproductive properties such as age-specific reproductive investments, iteroparity versus semelparity, number and size of offspring, and so on, are excluded from the projectible clusters of life history traits of workers. The comparative study of life histories is therefore indirectly supported by the use of the kind ‘developmentalindividual’ and not only ‘evolutionary individual’. A similar requirement of overlap between developmental and physiological individuals can be envisioned for scaling models that correlate metabolic rate with average lifespan (Balaban *et al*. [2005]).[[16]](#footnote-16)

Arguably the major source of projectible information to be gained from developmental individuality comes in the form of homology. Due to the conservatism of development, especially around the maximally comparable phylotypic stage, developmental individuals often most reliably constitute the bearers of homologous traits (aim 8). As mentioned earlier, honey bees and carpenter bees share very many homologous characters, whereas honey bee colonies and single carpenter bee insects share none. The use of developmental individuality for comparative purposes can be taxonomically specific, as in this example, or more general, as in the comparative study of homologies in metazoan development (Buss [1987]).

Further variations on these kinds may be formulated, and progress on the problem of individuality in biology will require deeper investigation as to their inter-relations and relative importance. What is at least clear is that kinds like these capture biologically important distinctions and enable distinctive biological generalizations that are not available from evolutionary individuality alone.

**5. Conclusion**

The diversity of non-equivalent individuation criteria presents an obstacle for conceptual clarity about biological individuality. Given that criteria can be multiplied arbitrarily, the choice between them should be grounded in their capacities to fulfil the main theoretical roles for individuality in biology. My argument has been that the primary way they can do this is by figuring in robust biological kinds, which provide operable sortals and projectible properties. A prescriptive consequence of this approach is that conceptual clarity about individuality only matters to the extent that it affects the individuative and explanatory power of kinds of individuals.

A similar methodological line was pursued by Wilson ([2000]), who proposed evaluating the kind ‘organism’ in terms of its capacity to support empirical generalizations via three routes: homologies in multicellular lineages, evolutionary convergences in the multiple origins of multicellularity, and design constraints on multicellular development. Though he weighed in favour of generalization via homology, Wilson ([2000], p. 301) concluded that none of the routes requires ‘what would have to be a stipulative sharpening of an organism concept’. Thus he claimed that ‘biology lacks a central organism concept [. . .] because the most important questions about organisms do not depend on this concept’ (Wilson [2000], p. 301). The trouble with Wilson’s conclusion is that failure to sharpen the organism concept would seem to require falling back on traditionally vague and intuitive criteria of individuality. Reliance on such criteria hinders our ability not only to individuate organisms, but also to form and apply inductive generalizations in borderline cases where it is unclear whether something is an instance of the kind ‘organism’. Far from being negligible exceptions, the vast majority of multicellular taxa do not fit the intuitive vertebrate-biased notion of unitary organisms (Herron *et al*. [2013]). While it is true that the situation is not improved by a mere stipulative sharpening of the concept, neither is it improved by leaving things vague.

A better solution for this explanation-centred approach is to abandon monism at the level of generality of ‘organism’ or ‘biological individual’ and divide biological individuality into more precise sub-kinds.[[17]](#footnote-17) In accordance with kind pluralism of type (a) described earlier, this would mean that ‘biological individual’ and ‘organism’ are classes containing individuative and explanatory kinds, but are not themselves individuative and explanatory kinds. For the evolutionary counting problem the functional kind ‘evolutionary individual’ is most appropriate, though I have argued it only becomes individuative and explanatory when it is mapped onto readily identifiable material properties. Nonetheless, equating ‘evolutionary individual’ with ‘organism’, a perfectly admissible notion for contexts of use not requiring precision, would amount to a harmful ‘stipulative sharpening’ of the concept. More structurally based kinds such as ‘physiological’, ‘ecological’, and ‘developmental individuals’ are typically more suitable for aims (7)-(9). Splitting kinds of individuals in this way allows theorists to utilize their different explanatory strengths on different aims without incurring the epistemic costs of bundling them together.

While pluralism about individuality currently appears to be a popular position, the sense of this term available from standard framings of the problem (for example, Wilson [1999]; Clarke [2011]; Sterner [2015]; Pradeu [2016a]; Love and Brigandt [2017]) is ‘criteria pluralism’ rather than ‘kind pluralism’. This would mean there are multiple mappings between the aims (1)-(9) that have characterized the individuality problem and the diverse criteria of individuality available from biology. As Pradeu ([2016a]) stresses, however, it is no longer useful to simply argue that there are different criteria of individuality for different questions and scientific contexts. ‘Criteria pluralism’ risks coming out true too cheaply—without offering positive prescriptions for how the concept of individuality can be productively put to work. Of particular significance is the risk that the multiple criteria of individuality turn out to only be multiple criteria of instantiation which define descriptive classes rather than explanatory kinds. Kind pluralism, by contrast, provides two general prescriptions that are of central importance: individuals should be instances of explanatory kinds, and should be countable with sortals. This can make sense of the fact that not all classes of individuals are equally interesting, useful, and operational. In this sense of the term, ‘pluralism’ is an indication that the problem of biological individuality is posed at too high a level of generality, and that theoretical unity can be re-discovered at a finer grain.

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1. Detailed arguments that there are genuine biological problems contained in these aims can be found in most of the above references. Here, those arguments are largely presupposed, and aims (1)-(9) are taken as the premise for evaluating different accounts and their proposed criteria of individuality. [↑](#footnote-ref-1)
2. Note that whether a ramet is an evolutionary individual at all (that is, whether it has a non-zero degree of evolutionary individuality, or whether it surpasses a certain threshold of evolutionary individuality) is not a matter of degree. Nonetheless, an object can have more or fewer of the properties that characterize evolutionary individuals, and in this sense can be more or less of an evolutionary individual (see Section 3 below). It is not immediately clear how this feature could be accommodated if ‘evolutionary individual’ were construed as the essential or substance sortal for its instances. [↑](#footnote-ref-2)
3. Some classifications are not intended to enable explanatory inferences, but simply to order objects of study in a useful ‘storage and retrieval system’ (Reydon [2009], p. 170) similar to the indexing system of a library. From (1)-(9), however, it is evident that part of the interest in biological individuality is to discover criteria that support generalizations or inferences of some kind. This is partly why kinds of individuals should not immediately be identified with essential or substance sortals (as in Wilson [1999], p. 35 ff.). The demands of individuation and explanation for biological individuals tend to pull in opposite directions—respectively, towards greater specificity and greater generality. Essential or substance sortals for individuals will likely need to be as determinate as low-level taxa, whereas aims (1)-(9) are about finding generalizations that apply across many taxa. This tension is resolved if we recognize that the forms of biological individuality that are the most plausible candidates for being explanatory kinds are counting sortals but not necessarily essential or substance sortals. [↑](#footnote-ref-3)
4. These functional properties are here understood as properties formed via functional abstraction from properties at a given base level, an operation which isolates only their effects. The base level properties are designated as ‘material’ properties in relation to the operation of functional abstraction, but they can themselves be functional properties in relation to still lower-level properties. For example, germ-soma division is a material property in relation to the functional capacity to exhibit heritable variance in fitness, but it is a functional property in relation to its physical realizations. Note that I do not wish to claim that all functional properties are abstractions over material properties, but only that some are, and that being a unit of selection is one of these. [↑](#footnote-ref-4)
5. Abstract functional descriptions might be individuative for some purposes and in simple contexts, but in more complex contexts they quickly become inoperable. Suppose there is a set of stones of varying weights in a room. From this set, a subset can be used for hammering by one person, but a larger subset can be used for hammering by a second, stronger person, and still a different subset by another person having different attributes, and so on. How many functional hammers are there in the room? There seems to be no determinate answer. Compare this with the scenario where we single-out hammers by their possession of a characteristic shape, composition, and hardness, and stones by physical-structural properties. In separating structural from functional aspects, we can state with greater determinacy that there are *n* hammers and *m* stones in the room, many of which can probably be used for hammering. [↑](#footnote-ref-5)
6. Some remarks in Clarke ([2013]) suggest a more ‘probabilistic’ view of the connection between specific material traits and policing and demarcation effects—in agreement with the view proposed below—but other remarks, such as the above quotation, suggest otherwise. If the probabilistic interpretation is the correct one, then what follows can be read not as a counterargument but as a further development and clarification of aspects of her account. [↑](#footnote-ref-6)
7. One objection to the disjunctive strategy for countering multiple realizability arguments might be deployed here. It is argued that disjunctions of realizers for functional kinds can be infinite, and so cannot be scientifically useful, much less ‘reduce’ the functional kind (Fodor [1974]). There are three reasons to resist this objection in the present context. First, unlike in the context of reductive physicalism in philosophy of mind, here the realizers are not physical properties or states, but are themselves fairly coarse-grained functional properties like bottlenecks, germ-soma divisions, and immune response mechanisms. Germ-soma divisions are called ‘material properties’ in relation to a higher-order functional kind, ‘policing mechanisms’, but they will themselves have multiple *physical* realizations, all of which count as one item in the disjunction of policing mechanisms. Second, it seems unlikely that the disjunction of properties that have appreciable effects on the capacity for selection is truly infinite, or that it is knowable as such, except in some very long-range sense that is far removed from the current biological problems that have motivated reflection on the topic of evolutionary individuality. Third, the disjunction is inclusive, unlike a disjunction of brain states which cannot all be simultaneously instantiated in the same individual. Even if the disjunction turned out to be infinite, then, it would not need to be known in its entirety in order for us to use some of the disjuncts to identify evolutionary individuals. [↑](#footnote-ref-7)
8. One plausible exception is that being an evolutionary individual seems to be strongly correlated with exhibiting adaptation, as a reviewer points out. Since adaptation is a result of past selection processes, however, exhibiting adaptation is more reliably correlated with being a *descendant* of evolutionary individuals. The connection between ancestral selection and descendant adaptation also requires additional background conditions concerning evolvability and environmental stability (see Lewontin [1978]; Wagner and Altenberg [1996]; Godfrey-Smith [2009]). Other background conditions might be similarly added to connect evolutionary individuality with evolutionary transitions. [↑](#footnote-ref-8)
9. As an example of projectible material properties, individuals with germ-soma separation are very likely to reproduce sexually (see Buss [1987], pp. 121 ff. for hypotheses as to why). Individuals developing from a bottleneck are also quite likely to be genetically homogeneous due to the mechanisms of replication and cell division. Since these particular connections are not specified by the kind ‘evolutionary individuals’, however, they cannot be said to make *it* more explanatory. [↑](#footnote-ref-9)
10. Worker bees retain some capacity to produce haploid male drones asexually, though only an estimated <1% of workers in queenright colonies have ovaries that are sufficiently developed to lay eggs (Ratnieks [1993]; Seeley [1995]). One study of approximately 1.8 million worker bees measured the probability of actual reproduction for any given worker as 0.00004 (Visscher [1989]; Seeley [1995]). [↑](#footnote-ref-10)
11. In cases where interaction gradients are more continuous or ‘fuzzy’, it may be necessary to specify thresholds in order to demarcate countable units. Although threshold values are defined by the observer, whether a set of parts meets the threshold is not. This sort of individuation procedure is similar to pragmatically assigning thresholds of effects on selection for traits to count as policing or demarcation mechanisms. [↑](#footnote-ref-11)
12. The applicability of metabolic scaling laws could also be used to assign degrees of physiological individuality to an entity. Interestingly, Hou *et al*. ([2010]) show that eusocial insect colonies are found on metabolic scaling curves much closer to unitary organisms than to asocial groups, possibly due to increased overall energetic efficiency via role specializations. [↑](#footnote-ref-12)
13. Note that in order for Hull’s definition to be individuative, the functional description would have to be mapped onto specific ecological cohesion conditions. Given that cohesion is relative to specific interaction types, an entity can be an ecologically cohesive ‘interactor’ without being very physiologically cohesive. [↑](#footnote-ref-13)
14. See the 2016 special issue in *Biology and Philosophy* on holobiont individuality. [↑](#footnote-ref-14)
15. In complete metamorphosis, more than one bottleneck can occur over the course of the same ontogenetic trajectory. Thus, for certain diachronic identity questions, sortals for developmental individuals will have to be more refined. One could, for instance, specify that the relevant bottleneck or fragmentation events are those in which both putative parent and offspring stages have the capacity for *multiplicative* reproduction (see Godfrey-Smith [2009]; Minelli [2011]). In any case, it seems quite likely that sortals that are determinate enough to specify diachronic identity conditions for developmental individuals will have to be taxonomically specific, unlike the kinds of individuals considered thus far (for example, *Holometabola*, *Trematoda*, or *Rotifera* developmental individuals). The result would be that ‘developmental individual’ can constitute an individuative and explanatory kind without constituting an essential or substance sortal. [↑](#footnote-ref-15)
16. These cases of overlap show how different kinds of individuals can be complementary rather than competing classification schemes. [↑](#footnote-ref-16)
17. Earlier, Wilson ([1999]) pursued a similar splitting strategy, but his proposed sub-kinds were distinguished more for purposes of clear conceptual analysis than with the criterion of explanatory power or projectibility in focus, as he later acknowledged (Wilson [2000]). [↑](#footnote-ref-17)