

The individuality thesis (3 ways)

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Published online: 25 October 2016
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Abstract I spell out and update the *individuality thesis*, that species are individuals, and not classes, sets, or kinds. I offer three complementary presentations of this thesis. First, as a way of resolving an inconsistent triad about natural kinds; second, as a phylogenetic systematics theoretical perspective; and, finally, as a novel recursive account of an evolved character (individuality). These approaches do different sorts of work, serving different interests. Presenting them together produces a taxonomy of the debates over the thesis, and isolates ways it has been (and may continue to be) productive. This goes to the larger point of this paper: a defense of the individuality thesis in terms of its utility, and an update of it in light of recent theoretical developments and empirical work in biology.

Keywords Individuality · Phylogenetics · Systematics · Natural kinds

Introduction

In the 1970's Ghiselin (1974) and Hull (1976, 1978) proposed the view that species are individuals, and not abstract classes or kinds. This view has generated an expansive literature in both biology and philosophy, and is typically referred to as the *individuality thesis*.

In this paper I spell out and defend an updated account of the individuality thesis, presenting it in three complementary ways. First, as a strategy for resolving an inconsistent triad about natural kinds. This novel framing of a familiar characterization provides a clear taxonomy of an important line of debate, and provides an

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entry point to some of the core philosophical issues at stake. Second, I present the thesis as a theoretical perspective that emerged from debates in biological systematics. Clearly identifying the theoretical foundation of the individuality thesis highlights its utility and fruitfulness. Finally, I offer a novel recursive account of the individuality thesis, taking biological individuals to be lineage generating entities that are both constituted by and constitutive of other biological individuals.

Philosophers of biology have often evaluated the individuality thesis in the context of levels of selection debates (e.g., Hull 1980; Wilson and Sober 1989). This has certainly been fruitful, but can produce too narrow a view that threatens to overshadow important features of the thesis (Haber 2013). The account provided here is more general, grounding the individuality thesis in the theoretical and conceptual foundations of phylogenetic systematics. In practice this aligns with the growing use of phylogenetics in a wide range of conceptual and empirical biological work, and has proven to be fruitful, explanatorily powerful, and predictive.

A natural kinds inconsistent triad

Consider the following propositions:

1. Species are paradigmatic natural kinds;
2. Natural kinds are defined by essential properties;
3. Species do not have essential properties (as species).

Jointly held, these generate an inconsistent triad. There are a number of strategies for resolving this inconsistency, from denying one or more of the propositions, to modifying or revising them. Boyd (1999), for example, embraces the first proposition, contending that it demands replacing the second with a *homeostatic property cluster kinds* view; similarly, Griffiths (1999) and Okasha (2002) advocate revising the second proposition by including historical, extrinsic, or relational accounts of essentialism. These accounts mute the force of the third proposition, and so the inconsistency is avoided.

Another strategy for avoiding this inconsistency is to simply deny the first proposition, *species are paradigmatic natural kinds*. The individuality thesis is the best known of this approach. Ghiselin (1966, 1974) and Hull (1965a, b, 1976, 1978) take an important lesson of contemporary taxonomy to be the discovery that it was a mistake to take species as paradigmatic natural kinds, arguing that this error extends back to Aristotle. Evolutionary theory, they argue, undermines this legacy, and it is a category error to apply essentialist and typological treatments to species. For example, Hull (1965a) draws on the work of Cain, Simpson, and other prominent taxonomists to argue that continuous variation between species is incongruent with an ontology that relies on capturing discontinuous, stable differences. Hull (1976) argues that recognizing that species have a capacity for open ended development means that we shouldn't define them in terms of essential characters, or treat them as classes. Classes, Hull argues, don't evolve; species, as individuals, do. Though there is still a general species category, the species belonging to it ought to be thought of as concrete, historical individuals and not themselves categories, classes, or kinds.

Rather, what biological theory and practice tell us is that species ought to be studied, conceived of, and theorized about as we would other biological individuals.

Sober (1980) adopts a slightly different strategy in defending the individuality thesis. He argues that it is not the essentialist's failure to *account* for variation, but in *how* variation gets accounted for that must be revised. It is an implicit 'natural state model' approach that is the culprit in the first two propositions. This is to treat variation as *deviation* from some natural state; population thinking, in contrast, rejects this normative account of variation, instead treating it as an expected component of the products of natural selection (and one that will itself vary over generations).¹ Sober argues that treating species as individuals with diverse parts is the correct antidote to the natural state model. The individuality thesis rejects the essentialist approach that defines a default, absolute, or privileged expression of characters against which variation *must* be measured. Instead, background variation is a moving target; a population level character of previous generations that, filtered through biological processes, is causally responsible for subsequent expressions of population level variation. Just as relativity theory warranted a rejection of Newton's concept of absolute space (against which all motion may be measured), evolutionary theory warrants a rejection of absolute character space (against which variation might be measured).²

Whether anyone ever jointly held the first two propositions of the inconsistent triad, or what that amounts to, is a matter of historical controversy, and Ghiselin and Hull's original formulations have been criticized for attacking a view without any identifiable champions (Winsor 2003, 2006, among others).³ Compelling as this criticism may be, propositions one and two were certainly jointly held in the twentieth century by philosophers (e.g., Putnam 1975; Kripke 1980), and were *perceived* by many biologists to be close to the typological views advocated by pheneticists and numerical taxonomists, e.g., Simpson (1961) criticizes those typological approaches for including strains of Platonic Idealism.⁴ Though we might ask whether these are accurate or fair portrayals of pheneticism (Lewens 2009), here we can simply stipulate essentialism as a *received view* to which Hull, Ghiselin and others were responding.

Framing the individuality thesis as a strategy for resolving an inconsistent triad helps identify what is at stake, the central move, and how the thesis is situated in a

¹ Amundson (2000) provides a similar argument, from the perspective of evolutionary-developmental biology.

² My rejection of an absolute phylogeny against which all histories are measured is an extension of this argument (Haber 2012b).

³ Sober (1980) can be read as offering a similar critique as Winsor, though one that ultimately defends the individuality thesis. Stamos (2005) argues that Winsor and other critics are mistaken about pre-Darwinian commitments.

⁴ See Rowe (1987), discussed below, and Will et al. (2005) for more contemporary phylogenetic critiques of typology as embodying essentialist thinking. To their credit, even the foremost champions of numerical taxonomy, Sokal and Sneath (1963), saw the force of this criticism, and actively sought to distance their "empirical approach" (Sokal 1962) from charges of essentialism. In their 1963 monograph, they acknowledge that typology in the context of "Platonic Idealism" is "untenable in the context of modern biological theory" (p. 266), and reject the applicability of Aristotelian logic to biological taxonomy due to its essentialist commitments (pp. 12 and 19).

larger philosophical debate.⁵ Yet this does not provide a lot of positive details of the thesis, namely, what it means to stop thinking about species as paradigmatic natural kinds, but rather as individuals. Unpacking what that commitment entails has been and continues to be a research problem. The utility lies in identifying how the individuality thesis informs and is informed by empirical, theoretical, and conceptual research projects, and in designing those projects to fill out the relevant details.⁶ In other words, we can also treat the individuality thesis as a fruitful theoretical perspective.

The individuality theoretical perspective

The individuality thesis was initially offered in terms of species, i.e., that species are individuals (and not natural kinds or classes) (Ghiselin 1974; Hull 1976, 1978). Much of this took place in the context of the emergence of phylogenetics. Though philosophers of biology have tended to focus on the aspects of the individuality thesis that related to evolutionary theory (most notably the levels of selection debates⁷), systematists, in contrast, tended to see a very different (and more general) role for the the individuality thesis (O'Hara 1993). As such, we can treat the individuality thesis as a theoretical perspective derived from phylogenetic systematics, defined by three central commitments: the *parity*, *history*, and *part/whole* commitments (Haber 2013, 2016). This recalibrates the project in phylogenetic terms, rather than cast in the interests of philosophers (e.g., as a strategy for resolving the natural kinds inconsistent triad). Construed thusly, the biological project becomes filling out the details of these commitments, and identifying further downstream commitments or research problems. Let's look at some of the foundational work and subsequent debates in phylogenetic systematics in order to extract those commitments, and to see how they continue to generate productive research problems, explanatory resources, and predictions.

At its broadest level, the commitment to parity is to treat all levels of the biological hierarchy as belonging to the same general ontological category, without specifying what category that might be. So if one thinks that species are classes, sets, or individuals, the same would be held of organisms, cells, and entities at other levels of the biological hierarchy. It is a rejection of the view that species are of a different ontological category. In one of the earlier descriptions of the individuality thesis, Hull (1978, p. 338) is clear on the sort of views this commitment entails: "Regardless of whether one thinks that "Moses" is a proper name, a cluster concept or a rigid designator, "*Homo sapiens*" must be treated the same way".

This commitment to parity is derived, in part, from viewing the biological hierarchy as an evolutionary system, and the more inclusive parts of that hierarchy as the products of the recursive and successive causal interactions of their

⁵ There are other strategies available for resolving this triad, e.g., Walsh (2006) may be read as denying the third proposition by providing an Aristotelian account of contemporary developmental biology.

⁶ An exemplar is the impact of Wilson and Sober (1989), "Reviving the superorganism", which extends the individuality thesis to social insect colonies in the context of level of selection debates (Haber 2013).

⁷ Thanks, in part, to Hull (1980).

component parts. Though the successive levels will diversify, the more inclusive parts may still be treated as belonging to the same ontological category as the components parts of the system. A phylogenetic expression of that commitment is to distinguish between two projects: *systematics*—describing biodiversity in terms of the evolutionary relationships of taxa, i.e., how the parts of the biological hierarchy are causally related as an evolutionary system—and *classification*—the logical ordering of ontologically distinct and exclusive categories (Hennig 1966, 1975; Griffiths 1974; Wiley 1981; de Queiroz 1988). Hennig (1975, pp. 245–6) illustrates this distinction by way of analogy to how we might consider the rivers of Europe. On the one hand, they may be classified according to conditions they exhibit, such as navigability, salinity, etc. Alternatively, one might seek to reconstruct the drainage system of those rivers, in order to understand how they relate to each other in those systems, and which are parts of the same drainage basins.

This ontological parity does *not* entail biological similarity or symmetry between or even within levels. Quite the contrary. Though there is a recursive character to the way that lower level individuals will cohere as parts of larger ones, there is a broad diversity of both modes and degrees of cohesion (Hamilton et al. 2009; Neto 2016).⁸ These cohesion generating relations (CGRs) will be sensitive to the biology of those individuals, and the systems of persistence and recurrence that have evolved at various levels of the hierarchy. That variation, though, is not random, and studying these patterns of variation inform us about the processes, mechanisms, etc., that evolved alongside the system. One important way to accomplish this is by studying how the parts of the system stand in relation to each other, and how their interactions generate the system itself (and its parts). This explains the utility of *individual thinking*—conceiving of an object in terms of how its parts relate—and the limits of *kind thinking*—conceiving of an object in terms of how it is similar to other objects (Ereshefsky 2010). On the former, whether the parts in question are in some respect similar is secondary to how they stand as causally implicated parts of the same system. On the latter, whether properties are shared across parts due to the way they are causally related is secondary to the expression of those properties; it prioritizes *one* pattern of variation (similarity) over all others.

What the phylogenetic approach demands is not merely studying patterns of variation, but the pattern of *recurrence* of those patterns; how these patterns of variation transform, diverge, and diversify as they are transmitted across generations. In this way, phylogenetics is concordant with Sober’s description of population thinking. Patterns of variation are caused by prior variation, filtered through a multitude of biological processes. These produce patterns of descent carried by lineages at different levels. This diachronic component is central to phylogenetics, and reflects a commitment to history.

This historical component has also been interpreted by systematists as a commitment to linking identity to ancestry (i.e., lineages), rather than characters expressed by parts of that lineage. Those characters may transform, after all, though

⁸ Generalizations about the production of these sorts of successive cohesions are often provided in terms of evolutionary transitions (e.g., Maynard Smith and Szathmáry 1998; McShea 2001; Okasha 2006; Godfrey-Smith 2009; Clarke 2014).

the lineage persists, so conceptually divorcing these avoids conflating identity and diagnosis. Operationally, this amounts to distinguishing between arguments over theoretical species concepts, and identifying those criteria used to determine the boundaries or number of species (i.e., species delimitation) (de Queiroz 2007). Jody Hey captures this sentiment well: “As scientists we should not confuse our criteria for detecting species with our theoretical understanding of the way species exist” (2006, p. 449).

An example of application of the commitment to history is Kevin Padian and Jack Horner’s defense of the hypothesis that birds are dinosaurs. Their argument is that the transformation of the lineages from extinct dinosaur taxa to modern birds does not warrant a change in identity, appealing to the historical continuity of the lineages and the way the parts of that clade relate to each other. Notably, they centrally appeal to the *utility* of what they call *transformation thinking*,⁹ and the explanatory resources, predictions, and other fruitful research problems that this generates, in contrast to what they call a ‘typological’ approach (Padian and Horner 2002). They argue that anchoring identity in lineages better reflects and reinforces other biological theories and empirical work,¹⁰ e.g., it permits open-ended development of taxa, where any characters may transform over evolutionary time (Hull 1976).

Underlying Padian and Horner’s argument is a commitment to a broader distinction shared by systematists between a taxonomic ‘definition’ and ‘diagnosis’ (Rowe 1987). The former concerns identity; the latter those characters typically expressed by taxa that aid identification. The interpretation of this distinction is grounded in the commitment to treating taxa as individuals, understood as a rejection of the view that taxa possess *any* defining characters (Rowe 1987, p. 208):

If taxa are viewed as nominal classes, as in phenetic systems, they may then possess defining attributes such as morphological or biochemical characters.¹¹... However, if taxa are viewed as individuals in the phylogenetic system, Ghiselin (1984) quite rightly pointed out that they may not possess defining characters because characters may transform without affecting the individuality of the taxon.

Moreover, viewing taxa as individuals informs biologists of how much a biological entity may change without becoming a new entity (Rowe 1987, p. 210):

In contrast [to the phenetic system], ancestry rather than overall similarity must be the basis for a phylogenetic system. Thus, because snakes were born of Tetrapoda, they remain tetrapods despite their lack of limbs. In this way

⁹ Similar to what O’Hara (1997) calls *tree thinking*.

¹⁰ Padian expresses this commitment to history in other places as well, e.g., “First, taxa in a phylogenetic system are defined by their ancestry in several different ways. ... Second, whereas taxa are defined by their ancestry, they are diagnosed by synapomorphy” (Currie and Padian 1997, p. 543).

¹¹ Notice the identification of pheneticists as the foil here, associated with relying on intrinsic defining characters. It is this perception of essentialist thinking in phenetics that is the target of Hull, Ghiselin, and other phylogeneticists.

taxa are properly defined by the only attribute they possess that cannot change during the course of evolution, their ancestry.¹²

Thus birds are dinosaurs (Padian and Horner 2002) and rattleless rattlesnakes are still rattlesnakes (Meik and Pires-daSilva 2009). These identity claims are not intrinsic properties of those individual taxa, but a consequence of what individual clades they are a part of, i.e., they are relational, historical parthood claims, reflecting hypotheses of taxonomic relationships. This transformationist approach reflects how closely tied the contemporary individuality thesis is to the development and application of phylogenetic systematics.

Yet it is not merely systematists that hold these commitments. It will be a general feature of biological individuals that they may transform in radical ways without becoming a new individual. It is not the result of a transformation, gain, or loss of some essential defining character that new individuals are generated; identity, and the generation of new individuals, is instead the result of causally distinctive, historical biological processes (Griesemer 2000; Pradeu 2012; Godfrey-Smith 2009, 2016). If these processes also generate new (or recurrent) forms, that can be explained as the outcome of that process. For lineages to persist, those processes will be selected that successfully balance the production of diversity¹³ against the maintenance and transmission of similarity across generations.

A transformationist account of those processes is precisely what those working in the individuality theoretical perspective provide. At the level of species, divergence is not measured in terms of differential expression of characters, but the degree to which they are separately evolving, persistent lineages (e.g., de Queiroz 2007). An advantage of this account is that it recognizes that when two lineages are in early stages of divergence, they may be counted as distinct stem species despite expressing nearly identical characters. Organismal reproduction, likewise, is not defined by the recurrence of form, but participation in a developmental process (Griesemer 2000; Godfrey-Smith 2015, 2016). On these accounts, whether and to what degree offspring resemble their parents is a *product of* rather than *defining of* reproduction, and something for which we can provide evolutionary and developmental explanations. This transformationist view may also be applied to characters and homologies (Wagner 2007, p. 478; favorably citing Ghiselin 2005):

Consistent with modern views of homology, character identity is not tied to particular manifest features, like structure, composition and shape. Instead, homologues have a single historical origin, form a lineage of descent with modification, and can go extinct.

On this view, the generation of new homologies and identity of characters is decoupled from expressions of form or structure. Instead, character identity is in

¹² Though whether it is taxa or taxon names that are defined remains a debate in taxonomy (Stuessy 2000; de Queiroz and Cantino 2001; Haber 2012a). Regardless, taxon *identity* is tied to ancestry, though see Pedroso (2014) on why this does not entail origin essentialism.

¹³ Diversity may be produced by mutation, acquisition of exogenous genetic material, developmental plasticity, etc.

terms of the shared history of developmental modules¹⁴ (Ereshefsky 2012; Wagner 2016). In all these cases, the new individuals will be related to one another. How similar they are will be a function of the evolved processes by which they were generated.

Finally, Ghiselin and Hull both hold that biological individuals have parts, not members (in contrast to classes or sets). Again, systematists provide a sophisticated interpretation of this claim (Rowe 1987, p. 209):

Hull (1976) pointed out that populations, species, and higher taxa need not be made up of similar organisms, but that in a genealogical system they must be made up of related organisms. He also pointed out that taxonomists traditionally have not imposed this requirement upon taxa; rather it has followed from the nature of the evolutionary process itself.

First, note that the use of the term ‘system’ reflects the distinction drawn by Hennig and Griffiths against ‘classification’. This systematization is not a logical ordering, but a description of the way the biological parts of a genealogical system are related as *biological* parts, i.e., it is a mistake to conflate the parthood claims here as claims about mereology (Haber 2016).

Second, though Rowe is describing a *genealogical* system, there are other ways that parts of a biological individual may be related (as biological parts). This is an empirical research problem; it is something we may discover about, say, the products of evolution, or immunology, or development. Understanding ways that various parts might relate as *biological* parts provides the resources for offering explanations or discovering features of a system (Ereshefsky 2010). Moreover, these various parthood relations provide different theoretical notions of identity. It is why we need to know what individual some thing is a part of in order to provide a full accounting of that thing. For example, discovering that two developmental modules are part of the same character lineage tells us that they are homologous, i.e., that the traits they cause to occur are identical, regardless of similarity of form or structure produced (Ereshefsky 2012; Wagner 2016).

Sometimes the parts of these various individuals will coincide, sometimes merely overlap. The pattern of recurrence of concordance of historical part/whole lineages provide important sets of individuating conditions.¹⁵ The more persistent the recurrence of concordance, the greater the degree of diachronic cohesion between those lineages; the mode by which that recurrence is maintained tells us along which dimension that cohesion is being expressed, and what sort of individuals constitute the lineages. And though no single lineage will provide a privileged perspective of phylogeny against which all others must be measured (Haber 2012b), important clusters of lineages will persistently recur over time as a result of biological processes and mechanisms. These clusters will be better or worse at tracking various biological features, processes, etc., of interest, which can be exploited to study those features.

¹⁴ Importantly, the evolutionary lineages formed by these developmental modules may be discordant with the lineages of their containing organisms. This is one way these evolutionary systems generate complex and gradient boundaries and identities.

¹⁵ Thanks to Celso Neto for this observation.

For example, if we seek to track the objects on which selection act, then we should seek out objects whose parts persistently share fitness in the right way (Okasha 2006), or that share a fate due to an evolved bottleneck (Godfrey-Smith 2009). The more tightly the lineages of these parts recur, and insofar as we can explain that recurrence by mutual participation in the causal processes of lineage generation and persistence, the greater those lineages will together express a degree of individuality.

A lot of room for disagreement remains over precisely what sorts of processes generate diachronic, persistent recurrence of lineages, e.g., whether holobionts that reliably reconstruct concordant lineages over evolutionary time express individuality to the same degree as entities that maintain that concordance through endogenous parts and processes (McFall-Ngai 2002; Bordenstein and Theis 2015; Moran and Sloan 2015 provide a sample of the range of interpretations on holobionts). The upshot is that being a part of an individual may be characterized synchronically or diachronically. The degree to which more inclusive individuals expresses individuality will be along multiple dimensions, and be an expression of the degree of interaction of its parts.

Moreover, biological part/whole relations evolve, and evolve in more or less concordant ways with other biological part/whole relations (e.g., Danforth 2007). These may generate complex systems (e.g., Rieppel 2009; McShea 2001), with shared parts that belong to multiple more inclusive individuals (e.g., Maddison 1997; McFall-Ngai 2002), more or less tightly expressed along different dimensions (e.g., genealogical, metabolic, immunological, etc.), and that are multiply decomposable (Wimsatt 1974; Haber 2012b).

A commitment to parity, history, or the part/whole commitment alone does not get you the individuality thesis; it is the commitment to all three that is its hallmark. Boyd's (1999) HPC Kinds account reflects a commitment to parity, and may be applied across the biological hierarchy, yet would hardly be mistaken as equivalent to the individuality thesis (and entails a weaker commitment to linking ancestry and identity). Coupling the parity and history commitments means extending the association of lineages and identity beyond species and higher taxa to other sorts of biological individuals. What this reveals is that the way something like the HPC Kinds view and the individuality thesis come into conflict is subtler than as straight competitors; there is a richer story to tell when we have access to the resources available by treating the individuality thesis as a theoretical perspective.

A recursive account of biological individuality

Explicit in the discussion above is the recursive character of biological individuality, suggesting a recursive account of the individuality thesis:

Biological individuals are lineage generating entities that are both constituted by and constitutive of other biological individuals.

This captures the central commitments described by the theoretical perspective above, and central elements of the foundational work on phylogenetics. Yet, we might fruitfully add some stipulations, consequences, and constraints to this account. For example:

1. Individuals need not be *wholly* constituted by other individuals.
2. Individuality will come in degrees.
3. To halt the regress, a concept of maximal and minimal individuals is needed.¹⁶

Let's briefly consider these in the interest of drawing out the utility of this account.

First, there is nothing here demanding that individuals *exhaustively* make up the parts of more inclusive individuals. To the contrary, non-biological parts might be important as well, e.g., termite colonies may include non-biological parts central to their persistence (Turner 2000; Bouchard 2008). An advantage of the individuality thesis is that it provides the resources to account for non-biological (or biological but exogenous) parts. If those parts are causally implicated in the process of the generation or persistence of lineages, then our accounts of those processes (e.g., speciation, reproduction, etc.) must accommodate those parts (e.g., Dupré and O'Malley 2009; Dupré 2010; Pradeu 2012). The utility lies not in adjudicating disputes over whether these are proper biological parts, but in providing a framework for those disputes.

The use of 'constituted' in the recursive account reflects a commitment to a 'constitutive hierarchy', rather than an aggregate one. The former entails that the levels of a hierarchical system are products of successive, recurrent interactions of parts at less inclusive levels; it is an emergent system with causally interactive parts that produce (and, in some cases, maintain) the constitutive hierarchy. Aggregate hierarchies, in contrast, are mere collections of elements, where that aggregation might be along causal or non-causal lines (Wimsatt 2007). As described by Rieppel (2009, p. 312):

A more inclusive level of an aggregational hierarchy represents just an aggregate of the included elements, whereas a more inclusive level of a constitutive hierarchy is more than the mere sum of its parts: the organism that is a complex whole has properties that cannot simply be reduced to the sum of the properties of its parts, i.e. organs or cells.

Rieppel has in mind the emergence of what he calls *enkaptic* hierarchies—those that arise by way of recursive, successive lineage splitting¹⁷—but a more general account of constitutive hierarchies would include any hierarchy that is the product of the causal interaction of its parts. This permits views such as Pradeu's (2012) *immunological individual* that emerges from the active incorporation of microbial individuals through development, in addition to cellular lineage splitting. This demystifies emergence by linking it to causal mechanistic processes, and decoupling it from debates over reduction (Wimsatt 2007).¹⁸

The distinction between constitutive and aggregative hierarchies maps on to the distinction between systematizing and classifying groups (Griffiths 1974; Hennig

¹⁶ On a pragmatist account we could eliminate this stipulation, instead letting the recursive definition play out as a tool and seeing how far down (or up) it may go and still be useful. (Thanks to Ken Waters for this observation.)

¹⁷ Fagan 2016 provides another candidate enkaptic hierarchy in her account of stem cells.

¹⁸ This is not to say those causal processes and interactions will always be well understood.

1975; de Queiroz 1988), and to the utility of Ereshefsky's (2010) 'individual thinking' against 'kind thinking' in systematics. 'Individuality thinking' describes the sorts of inferences and discoveries we draw from understanding the ways that parts of a system are causally related; 'kind thinking', in contrast, is to draw reliable inferences based on how members of a kind are projectably similar. In a constitutive hierarchy, individual thinking will capture the causally relevant interactions between parts that clustering of similarities will miss.

The recursive account places lineages at the core of thinking about individuality: Biological individuals are lineage generating entities. This will obviously not be the end of the story, but requires some account of lineage generation and persistence. Here we see an alignment with treating the individuality thesis as a theoretical perspective. In both cases, fruitful research projects are generated by characterizing the production of new individuals in terms of lineages (and the processes that maintain or generate those lineages). These may be in terms of higher taxa or species (e.g., Padian and Horner 2002; de Queiroz 2007), organismal reproduction (e.g., Griesemer 2000; Godfrey-Smith 2015, 2016), or the production of new homologies or characters (e.g., Wagner 2007, 2016; Ereshefsky 2012).

An advantage of the recursive account is that it provides a clear strategy for considering whether some entity is a biological individual or not: determine whether or not it is a lineage generating entity, what its parts are, and what it is a part of. Filling in those details for a variety of entities will help develop fruitful research questions, which will generate explanatory resources and predictions.

Characterizing biological individuals encourages examining a diverse range of biological entities, and asking whether the processes that they engage in require an expansion or revision of what processes count as reproductive or lineage generating, e.g., Ereshefsky and Pedroso (2015) ask how we must revise notions of reproduction if we include biofilms as lineage generating entities. Clearly there will be debates over how to best characterize these processes and diversity of modes of persistence and generation, and some entities will express these evolved processes to a greater or lesser degree. But I take that to be a mark in favor of the individuality thesis, not against it. The individuality thesis will be consistent with narrow interpretations that restrict lineage generation to homogeneous individuals (Godfrey-Smith 2009), but also more expansive ones that treat holobionts as lineage generating entities (Zilber-Rosenberg and Rosenberg 2008; Bordenstein and Theis 2015). It is broad enough to include homologies or characters (Wagner 2007; Ereshefsky 2012), and perhaps even some cultural traits (Gray and Jordan 2000). If entities may be said to generate biological lineages, then the resources of individuality thinking are available to study and understand them, though the individuality thesis will be agnostic about *which* processes will count as lineage generating.

Yet, if a biological individual is both constituted by and constitutive of other biological individuals, a regress threatens. Exploring this regress displays the utility of this account.¹⁹

¹⁹ This locates the individuality thesis in the biological tradition of central theorems and concepts whose utility lies, in part, in the limits of its applications, e.g., the conditions of the Hardy–Weinberg equilibrium are never met by natural populations, an understanding of which provides explanatory resources; or,

One way to avoid this regress is by introducing the notions of a *maximal* and *minimal* individuals. This introduces a rich research problem. There is a conceptual aspect (sharpening up the concepts of *maximal* and *minimal* individuality), a theoretical aspect (what is the theoretical foundation or support for these concepts), and an empirical aspect (what are examples of maximal or minimal individuals? How might we study them or what might count as evidence for them?). Let's consider a couple of candidate maximal and minimal individuals to help demonstrate the richness, depth, and breadth of this sort of research problem.²⁰

Minimal individuals will bottom out the recursion, and not have any parts that are *biological* individuals. This presents a challenge, if the mechanisms and bearers of recurrence, innovation, persistence, and reproduction are specialized parts of an individual that typically form lineages. This apparatus will not be present in minimal individuals, at least not as lineage generating entities.

Diachronically, this challenge will dovetail with origin of life studies. Here, minimal individuals will be borderline or transitional ones (see also Gánti 2003). The prediction is that the earliest proto-individuals will have lacked the apparatus to participate in what we might consider basic or primitive biological processes. Or, at least, to do so on their own. By combining (or recombining, as it were), they transitioned to the first genuine biological individuals by bootstrapping off each other's apparatus. These sorts of interactions of parts would be the first cases of emergence of a new biological level of hierarchy. As these new individuals subsequently and successively interacted in ways that new levels emerged, the successive levels would express individuality in distinctive and varied ways, and in greater degrees along those dimensions. Furthermore, they would have inherited the capacity for generating successively complex systems of organization through innovative interactions.

We can also consider minimal individuals more synchronically. Simple viruses are familiar candidate minimal individuals. These lack the apparatus to reproduce on their own, because they do not have other biological individuals as parts. Rather, they must piggyback off of the reproductive apparatus of other individuals. Like their origin of life counterparts, we can view these sorts of viruses as borderline or transitional individuals. This is no knock on them; tree thinking rejects any sort of teleological view being appended to evolved hierarchies (O'Hara 1997). It's merely an observation about the strategies of transmission and persistence that lineages have evolved, and how a minimal individual might be maintained in the presence of individuals of a greater degree. If these viruses descended from individuals with more robust biological apparatus, then they might be viewed as analogous to non-social wasp species that saw a reversal of the colony complex, or parasites that no longer express endogenous traits in exchange for outsourcing functions to exogenous hosts. Regardless, the presence of borderline and transitional individuals is just what we should expect on the individuality thesis. The boundary between

Footnote 19 continued

exceptions to biology's Central Dogma provide fruitful research problems that generate a deep understanding of biological systems.

²⁰ This mirrors a strategy adopted elsewhere by Griesemer (2000) and Godfrey-Smith (2015).

living and non-living will be like other biological boundaries: gradient, not categorical.

This view about minimal individuals also generates downstream research questions. An approach advocated by Darwin was to seek out transitional and borderline cases in order to understand how some character might have evolved (Darwin 1964 [1859]). Viruses opportunistically use resources of other individuals (and the shared environment) in order to reproduce. This is not unique to viruses, though it can be easy to overlook this aspect of other, more complex individuals. If early individuals emerged by using exogenous resources, then it would hardly be surprising if this character were retained (though modified) by descendent individuals.

Thinking about maximal individuals is similarly fruitful. On one hand, it might be easier. *The* maximal individual would be all life on earth. This was Darwin's conjecture, though he left open the possibility that life on earth represented multiple origins. Of course, treating life on earth as a single individual is complicated by microbial challenges to tree of life studies, and the growing evidence that rather than a single root there was something much more complex occurring (Doolittle 1999; Doolittle and Bapteste 2007). Yet, even granting this, there is good evidence that life on earth *does* constitute a single system, albeit one that has parts that are more or less invested in or insulated from lateral gene transfer and may lack a single common origin, at least as traditionally understood.²¹

Recognizing lateral transfer as a mode of lineage generation shifts microbial networks from being a challenge to an embodiment of the individuality account. Studying the patterns of how these discordant lineages are transmitted, recur, diversify, and diverge provide identity conditions in much the same way as other taxonomic cases. Identity is still tightly tied to lineages, though the degree to which it might be contingent that individual lineages coalesce might be greater. But this is just what we ought to expect on the individuality view. There are a range of successful strategies that might evolve for lineage generation, persistence, divergence, and diversification, which will produce a spectrum of ways these will be expressed. Microbial networks may be far messier than, say, for polar bears, but this reflects different evolved strategies and the degree to which the more inclusive lineages express individuality.

There may also be more localized maximal individuals. A mule, for example, might not be a part of a more inclusive lineage as a lineage generating part, though it is a non-reproducing part of two distinct lineages. It is also constituted by cellular lineages, and, from an evolutionary perspective, is an end point for them. In this way, they are part of a local maximal individual that will not become a part of any more inclusive individual; that local system has maxed out as a result of biology, and lack the apparatus to generate further lineages. Recognizing why things like sterile hybrids represent local maximums provides insight into how lineages persist, diverge, coalesce, and diversify, and provides a way of accounting for non-reproducing individuals.

²¹ As Jay Odenbaugh observed in comments on this manuscript, "mammals having more than one parent doesn't deny their individuality, so presumably it needn't in the case of the whole of life".

Polar bears

Let's turn to an example to see how the individuality thesis may be applied: the relation of the Polar bear lineage to the Brown bear clade (Fig. 1). This is a case of divergence, followed by introgression (that may be ongoing, in response to anthropocentric ecological pressures). Among the challenges here are (a) how to describe a system with gradient boundaries such as this; and (b) how to assign identity when transformation of characters may occur after divergence yet prior to introgression and possible convergence.

There are numerous challenges here, including what this relation tells us about the speed of speciation and adaptive transformations, how to identify when the Polar bear lineage split away as a distinct species, and what status the Polar bear may have as mating behavior changes in response to anthropogenic ecological pressures.

Drawing on the three presentations above, applying the individuality thesis to a case like this means (among other things), that we should resist identifying and delimiting the species in terms of characters, and instead focus on the history of the

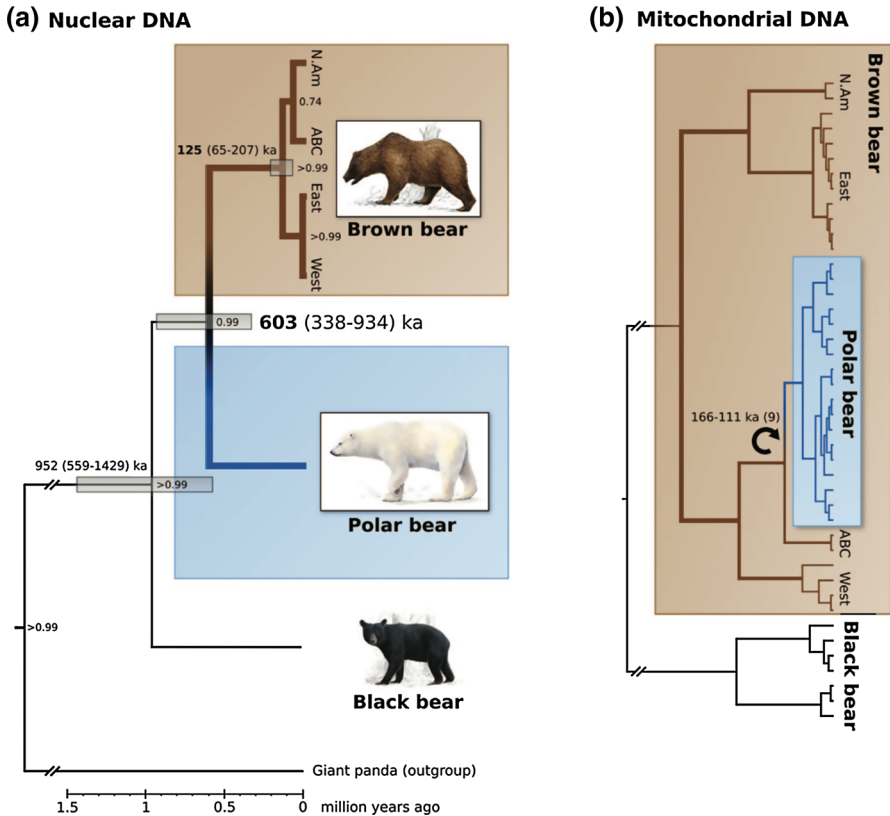


Fig. 1 Roughly 600 ka the Polar bear lineage began diverging from what would generate the Brown bear clade. Around 150 ka, an interbreeding event occurred between a male Polar and female Brown bear. The result of these events are discordant mtDNA and nuclear DNA lineages (Hailer et al. 2012)

lineages. Tree and transformation thinking also encourage a focus on processes, and how those processes produce gradient boundaries and new individuals. Finally, we should track how the parts of the individuals relate to one another in order to provide a characterization of the system.

Applying this, some of the main takeaways we learn from this case include:

1. Speciation is the process of divergence of population level lineages, untethered from any particular character expressed by those lineages (de Queiroz 2007). Whether any particular character is transformed over this process is incidental to the lineages diverging into separately evolving populations (or converging back to a single one). The gain or loss of, say, interbreeding between the lineages, is not, in and of itself, what marks these lineages as distinct, but is one criteria by which we can measure divergence (or *species delimitation*, at the level described in this case).
2. Rather than measure the degree of divergence by character differentiation, it may be expressed, in part, in terms of degrees of shared parts, e.g., organisms or lineages that simultaneously belong to sister taxa. A number of processes (e.g., lineage sorting, hybridization, lateral gene transfer, etc.) will generate lineages that are constitutive of yet discordant with their more inclusive lineages. This provides an important way to measure degrees of distinctive individuality (Maddison 1997).
3. The Brown and Polar bear lineages share parts at different levels in discordant ways, most notably in the pattern of descent displayed by nuclear and mitochondrial lineages. These are, respectively, distinct and shared histories. The degree of overlap in these lineages is one way to measure the degree of divergence between these lineages, and the degree to which either expresses individuality distinctly. This means individuation is not categorical, but gradient.
4. Speciation is a dynamic, temporal process. There is no categorical stopping point when lineages stop diverging, though the characters we might use to measure that degree of divergence will be sensitive to the research problem at hand. Identifying the relevant data and tools to precisely characterize a group of taxa, and developing methods sensitive to various modes of lineage introgression, is an important empirical research project for phylogeneticists (Carstens et al. 2013).
5. The recursive, successive diversification and divergence in the Brown bear lineage following the divergence of the Polar bear lineage 600 ka is an example of the production of the sort of enkaptic system Rieppel (2009) describes as embodying a constitutive hierarchy. As those divergent lineages persist as separately evolving groups (and continue to diversify and diverge as they descend), new markers will be available to continue measuring the degree of divergence of the various taxa in this phylogenetic system.

For these reasons and more, on the individuality thesis taxon identity is disentangled from the expression of characters, but instead tied to ancestry. The Polar and Brown bear lineages are in the process of diverging. And though it is yet

to be determined whether that will generate separately evolving lineages, it has resulted in the production of an ekaptic system of lineages characterized by a unique and complex history.

Conclusion

I have presented three complementary presentations of the individuality thesis. As a strategy for resolving an inconsistent triad about natural kinds, as a theoretical perspective stemming from phylogenetics, and as a recursive account of an evolved character. A lot of work remains, but that is by design and an advantage of this view, i.e., that it generates fruitful research problems. Answering these sorts of questions will require conceptual, theoretical, and empirical work, at the intersection of biology and philosophy.

For example, how many kinds of biological individuals have evolved, and how ought we count individuals of each kind? If causally interacting with other individuals so as to be a part of a more inclusive individual necessitates trade-offs, how will this constrain the kinds of individuals there will be and how we count individuals of each kind? Focusing solely on fitness, for example, we might only count continuously persistent individuals whose parts' fitness is tightly tied together, e.g., Darwinian individuals (Godfrey-Smith 2013). On the other hand, if we focus on other organizational or functional relations, then we will get a more expansive taxonomy of biological individuals, e.g., those that are persistent without being continuous, and must recurrently self-construct over generations (e.g., holobionts or immunological individuals). My presentation here is consistent with both narrow and broad counts of the kinds of biological individuals there are in biology.

Acknowledgments Thanks to Melinda Fagan, Jay Odenbaugh, Anne Peterson, Thomas Pradeu, and the University of Calgary Department of Philosophy. This project was supported by NSF Grant 1557117.

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