When Traditional Essentialism Fails:

Biological Natural Kinds

Robert A. Wilson

Matthew J. Barker

Ingo Brigandt

Abstract

Essentialism is widely regarded as a mistaken view of biological kinds, such as species. After recounting why (sections 2-3), we provide a brief survey of the chief responses to the "death of essentialism" in the philosophy of biology (section 4). We then develop one of these responses, the claim that biological kinds are *homeostatic property clusters* (sections 5-6) illustrating this view with several novel examples (section 7). Although this view was first expressed 20 years ago, and has received recent discussion and critique, it remains under-developed and is often misrepresented by its critics (section 8).

When Traditional Essentialism Fails:

Biological Natural Kinds[*]

Robert A. Wilson

Matthew J. Barker

Ingo Brigandt

1. INTRODUCTION

A near consensus in the philosophy of biology holds that traditional essentialism is a mistaken view of biological kinds, such as species. Traditional essentialists hold that natural kinds "must possess definitional *essences* that define them in terms of necessary and sufficient, intrinsic, unchanging, ahistorical properties" (Boyd 1999: 146), and the near consensus in the philosophy of biology holds that biological kinds such as species do not possess these essences. We think that this near consensus position is correct (cf. Devitt, unpublished), but

---

[*] Contact: Wilson and Brigandt: Department of Philosophy, 4-115 Humanities Centre, University of Alberta, Edmonton, Alberta, T6G 2E5, Canada; Barker: Department of Philosophy, 5185 Helen C. White, 600 North Park Street, University of Wisconsin, Madison, WI, 53706, USA. Rob Wilson and Matt Barker's work on this paper was supported by two individual grants from the Social Sciences and Humanities Research Council of Canada. Ingo Brigandt's work was funded with an Izaak Walton Killam Memorial Postdoctoral Fellowship by the Killam Trusts, Canada. Thanks to the editors for comments, and to Jessica Moore for proof reading.

that most of the constructive responses to this "death of essentialism" are unappetizing. After recounting why traditional essentialism is a mistaken view of biological kinds, we provide a brief survey of the chief responses to its rejection in the philosophy of biology, and identify problems that each faces. The response that we favour, the idea that biological kinds are *homeostatic property clusters*, is also confronted by *prima facie* problems, but we argue that each of these can be adequately addressed once the view is properly expressed.

The homeostatic property cluster (HPC) view was first expressed 20 years ago by Richard Boyd (1988) in his articulation of a form of moral realism. The view says (roughly) that at least some natural kinds are individuated by property *clusters* that are afforded imperfect yet homeostatic integrity by underlying causal *mechanisms*. It allows that such definitive property clusters are essences, but in a softened sense that departs significantly from traditional essentialism. The HPC view strikes a balance between two desiderata that often pull in opposite directions: natural flexibility and explanatory integrity. It has been articulated with different emphases by Boyd (1989, 1991, 1993, 1999), Hilary Kornblith (1993), Paul Griffiths (1997, 1999), and Rob Wilson (1999, 2005, 2007), and is the subject of recent and ongoing discussions (Brigandt in press; Keller et al. 2003; Mallon 2003; Rieppel 2005a, 2005b, 2006, 2007, in press a, in press b; Rieppel and Kearney 2007) and critiques (Ereshefsky and Matthen 2005; Ereshefsky 2007a, 2007b; Craver 2005). We believe, however, that the HPC view remains under-developed and has often been misrepresented. Here we set the record straight.

2. A FAREWELL TO ESSENTIALISM?

"Essentialism" names a collection of related views. The form of essentialism relevant to debates over biological natural kinds can be called (indeed, has been called) *kind* *essentialism*. As Marc Ereshefsky has recently characterized it in a section headed "The Death of Essentialism" in a reference article on species:

> Kind essentialism has a number of tenets. One tenet is that all and only the members of a kind have a common essence. A second tenet is that the essence of a kind is responsible for the traits typically associated with the members of that kind. For example, gold's atomic structure is responsible for gold's disposition to melt at certain temperatures. Third, knowing a kind's essence helps us explain and predict those properties typically associated with a kind. (Ereshefsky 2007a)

As Ereshefsky's example suggests, this "common essence" is traditionally thought of as some kind of underlying, intrinsic property, something that lies within kind members, making them the kind of thing that they are. Ereshefsky himself thinks that all three tenets of kind essentialism are false of species in particular and of putative biological natural kinds more generally, with the problem rooted in a supposed *pre-Darwinian conception* of such kinds. As Ereshefsky says in concluding this section of his review, "In a pre Darwinian age, species essentialism made sense. Such essentialism, however, is out of step with contemporary evolutionary theory."

This view of kind essentialism pervades philosophy of biology. Influential expressions of this rejection of kind essentialism about species include David Hull's "The Effect of Essentialism on Taxonomy: Two Thousand Years of Stasis" (1965) and Elliott Sober's "Evolution, Population Thinking, and Essentialism" (1980). Biologists' reflections on species, especially those of Ernst Mayr, were significant influences on this philosophical work. Mayr took his rejection of "typological thinking" in favour of "population thinking" to be a rejection of kind essentialism (Mayr 1959a, 1959b, 1976, 1982).

Philosophers' and biologists' rejection of kind essentialism has become part of a canonical view of the history of essentialism in the biological sciences. On this canonical view, pre-Darwinian biologists adopted (supposedly from Aristotelian thinkers) *typological* or *essentialist* thinking, something like the view encapsulated by the three tenets of Ereshefsky's kind essentialism. Darwin's *On the Origin of Species* introduced a distinct way of thinking about species. Species were not natural kinds with fixed essences, but *populations* consisting in thoroughly heterogeneous collections of individuals whose phenotypic properties changed over time, and varied across the population at any given time. Such variance itself marked the natural and explanatory states of populations, rather than negligible variance away from or "around" a constant natural state. This "population thinking" also had roots in the 19th-century developments in statistical techniques—something that Sober emphasizes—but it was only with the Evolutionary Synthesis of the 1930s and '40s that population thinking came to revolutionize the ways in which biologists thought about evolution, species, and natural variability.

Historians of biology have recently shown convincingly that this canonical view of the so-called history of essentialism is a contentious construction and is mistaken in significant ways (Amundson 2005; Atran 1990; Camardi 2001; McOuat 1996; Müller-Wille 1999, 2003; Rupke 1993; Stevens 1984, 1994, 1997; Scharf 2007; Wilkins 2004; Winsor 2003a, 2003b, 2006a, 2006b). It is mistaken about key pre-Darwinian historical figures, such as Linnaeus and Owen, as well as at best tendentious about the post-Darwinian and post-Synthetic history of the field. It will take many years for the full implications of these facts to be absorbed by philosophers of biology focused on species, taxonomy, and systematics. Yet the mere fact that the canonical view of the history of essentialism must be rejected, in light of pre-Darwinians holding views of species other than kind essentialism, should give pause to the consensus rejection of kind essentialism that draws on the transition from pre- to post-Darwinian thinking.

3. WHY (TRADITIONAL) KIND ESSENTIALISM IS MISTAKEN

Proponents of the canonical view of the history of essentialism have provided a range of reasons to reject traditional essentialism. These include that it (a) involves a mistaken commitment to Aristotelian definition; (b) invokes an outmoded "natural state" explanation of variation; (c) is incompatible with the evolution of species over time; (d) flies in the face of phenomena such as mutation and drift; (e) is incompatible with anagenetic (non-branching) speciation; (f) requires strict kind boundaries when in fact these are often vague. In our view, none of these reasons gets to the heart of what is mistaken about traditional kind essentialism. In addition, their invocation has sometimes led to the endorsement of views (e.g., that species are not natural kinds) that are at least as problematic as traditional kind essentialism.

Whatever fallout there is from the re-evaluation of the history of essentialism in the biological sciences, there is a fundamental reason why kind essentialism is a mistaken view about biological natural kinds, including species. This reason at least features in the canonical rejection of essentialism about species, even if it has not been given the attention there that it deserves. As one of us has argued previously (Wilson 1999, 2005: ch.3; cf. also Elsasser 1965), biological kinds are *intrinsically heterogeneous* in that the individuals they subsume do not simply differ from one another in the properties they possess, but do so *by nature* or *intrinsically as things of that kind.* Biological kinds, unlike many other natural kinds, particularly those of the physical sciences, subsume individual entities (e.g., organisms) whose variation from one another is a natural part of what it is to *be* a member of those kinds. In the physical sciences, this heterogeneity amongst individuals is abstracted away from or otherwise ignored in treating those individuals as members of a physical kind (a proton, a chemical element, an acid). In the biological sciences, this variation persists across whatever abstractions and idealizations are made, and itself plays an important causal role in many biological processes, not the least of which is natural selection itself. One reason for this is that biological kinds are typically individuated by several causally entwined features that stand in *reciprocal* dynamic relations, as we shall discuss in detail below (sections 5 and 7).

A casual way to express the resulting contrast is to say that if you've seen one electron (or copper molecule, or tumbler of hydrochloric acid) you've seen them all, in that although there are differences between instances of any two individuals, these are differences that don't matter when we are looking at kinds in the physical sciences. This is not true in the biological sciences, where differences between instances of many natural kinds are important for explanation and prediction and are not simply abstracted away from in forming generalizations about the kind. If you've seen one tiger (or vertebrate or coral reef) you *haven't* seen them all, for there are differences between instances of any of these biological kinds that remain significant (indeed, in some cases, central) for the regular operation of biological processes and the articulation of biological knowledge. This is true of species in particular, but of biological kinds more generally. This epistemic difference between the objects of the physical and biological sciences signals the need for a conception of natural kinds in the latter that is sensitive to this intrinsic heterogeneity.

The intrinsic heterogeneity of biological kinds is manifest in the centrality of the above-mentioned “population thinking” in evolutionary biology. Natural selection often acts on variation within a population of individuals, and when that variation is exhausted (e.g., when a certain trait goes to fixation such that the population rather than any one individual has instantiated the property of having a certain trait frequency) that particular form of natural selection also ceases. As Sober (1980) has argued, in the physical sciences (and, he argues, in pre-Darwinian biology), variation was understood as deviation from a natural or normal state determined by a kind's essence. While before Darwin (roughly speaking) this variation was to be abstracted away from, in the post-Darwinian era, and especially through the Evolutionary Synthesis, variation came to be viewed as itself crucial to the underlying causal mechanisms at the heart of biological stasis and change. Appreciation of some of these variation-driven mechanisms motivates a focus on populations, not just organisms. This in turn betrays how intrinsic heterogeneity underpins the many ways in which biological processes have a complexity to them that makes for various "levels" of explanation across the biological sciences, and thwarts attempts to specify exceptionless, general laws in the biological realm. The centrality of intrinsic heterogeneity in biological thinking is, we think, reflected in attempts to understand biological kinds as encompassing diversity, and recognition of intra-kind diversity runs deep through the history of thought about the biological world.

Why is the intrinsic heterogeneity of biological kinds a definitive reason to reject kind essentialism? The problem lies not simply with what Ereshefsky lists as the first tenet of kind essentialism—the claim that all (and only) members of the kind have a given essence—but with the entire packet of tenets, which together imply that a kind's essence is *universally instantiated* by members of the kind, is *causally responsible* for that kind's typical traits, and is *explanatorily salient* in accounts of those traits. If biological kinds are intrinsically heterogeneous in the sense described above, then *there are no such universally instantiated traits*, and so the causal and explanatory roles played by putatively corresponding essences do not exist.

There are, to be sure, *typical* traits amongst members of biological kinds, and these form the basis for robust generalizations about those kinds, including generalizations about how they are caused and what they in turn cause. Indeed, our own view of biological kinds is built around such typicality. But for traditional kind essentialism, mere typicality is a death knell. Typical traits need not be possessed by all members of the kind, and they can vary over space and time without affecting whether an individual is or is not a member of that kind. No trait is definitive of the kind.

4. SCRATCHING THE ANTI-ESSENTIALIST ITCH

If kind essentialism about biological kinds is mistaken, as we have argued above, then what view of paradigmatic biological kinds should we adopt? One of the curiosities of the canonical view of the history of essentialism is that in answering this question there has been a myopic focus on just one example: species. Within this context, the standard response to the failure of kind essentialism has been to argue that species are not natural kinds but rather are *individuals* (Ghiselin 1974; Hull 1978). If we step back from the focus on species, we could see this response as being developed in one of two ways to provide a general account of biological kinds.

The first would be to view the failure of kind essentialism with respect to species to be illustrative of biological kinds more generally: all putative biological kinds *are really individuals*, i.e., there are no biological kinds. Call this the *radical view* of biological kinds. According to it, a massive error infects our thinking about the biological world. For we have taken the biological world to be full of not only individuals *but kinds of individual*, ranging from those that are the subject of biochemistry and physiology, to those that feature in the evolutionary and ecological sciences. On the radical view, there are no such kinds. This view is perhaps most plausibly developed in tandem with the view that *there are no biological laws*, and by defending the claim that if there are no biological laws, there are no biological kinds. The radical view holds the failure of kind essentialism to be pervasive across the biological sciences.

The second way to develop the standard response to the failure of kind essentialism about species would be to view the species case as special in some way (whether or not it is unique). This would allow that kind essentialism is correct about at least some biological kinds, even if it is mistaken about species and perhaps some (even many) other cases. Call this the *conservative view* of biological kinds. It is conservative in that it suggests that we need not reject the idea of biological kinds wholesale, but must recognize only that biological kinds of which kind essentialism is true are not as extensive across the biological sciences as has been traditionally assumed.

Both the radical and conservative views face insuperable problems, at the core of which is the simple biological fact that the vast majority of putative kinds to which biologists appeal are neither individuals nor kinds of which kind essentialism is true. Thus developing the standard response to the falsity of kind essentialism about species by replacing, more generally, kinds by individuals, flies in the face of the biological facts just as much as does kind essentialism itself.

The problem with the radical view is relatively easy to illustrate. In addition to species taxonomy, the biological sciences include a huge range of disciplines—from biochemistry to ecology, from physiology to evolutionary biology, and from developmental biology to behavioural biology—and many of the kinds over which scientists generalize in these disciplines are not even prima facie candidates for being considered individuals rather than kinds. Consider particular kinds in ecology, developmental biology and molecular biology. Ecologists often generalize over the kind *predator*. Yet there is no sense in which all predators form an individual. Predators are not predators in virtue of their integration with all other predators, nor are they localized or continuous in any interesting way. The same is true of all adrenergic cells, a type of neural crest cell important in the development of many organisms, and of tRNA molecules, which serve as adaptors that order amino acids as specified by mRNA molecules during protein synthesis. There is no sense in which the adrenergic cells or tRNA molecules in my body and those in yours form part of an individual that we could call Adrenergic Cell and tRNA Molecule, respectively. More tellingly, biologists see the predator, adrenergic cell, and tRNA categories as corresponding to kinds because of their explanatory and predictive value. Individual predators are predators not in virtue of being integrated parts in a larger individual, but in virtue of certain intrinsic and relational properties that they tend to share and which underwrite certain explanations, predictions and generalizations involving them and other organisms.

This objection does *not* turn on supposing a restrictive conception of what an individual is, and so it stands even once one loosens the notion of individual to include reference to *historical entities* (Ereshefsky 2001). For "predator", "adrenergic cell", and "tRNA" do not name historical entities any more than they name individuals *strictu sensu*. However individuals and historical entities are specified precisely, they have in common the idea of being spatiotemporally bounded, continuous particulars, and our point is just that it is incredibly implausible to think that this is what putative kind terms across the biological sciences refer to.

The same is true, though less obviously so, of species. This brings us to the conservative view of biological kinds, which holds that at least *species* are not natural kinds, but individuals. Advocates of the view that species are individuals also proceed under the idea that individuals are spatiotemporally continuous and integrated entities, then argue that species have these properties as well (Hull 1978, 1999). Certainly species members often stand in relations of historical descent and reproduction that in part define what it is to be such a member. But, on the one hand, an appropriate view of biological kinds can capture this, as we shall see. On the other hand, these relations are typically insufficient for the kinds of spatiotemporal continuity and causal integration that seem to us definitive of paradigm individuals, such as organisms (see Wilson 1999; Barker 2005, in press; Barker and Wilson submitted; cf. Hull 1978; Armstrong 1980; Ayers 1999: 229-253; Shoemaker 1979; Slote 1979).

The differences between paradigm individuals and species are apparent upon reflection. The parts of a paradigm individual are spatially contiguous. Given that species consist in spatially separated organisms and *not* the gaps between them, this is not true of species; indeed, rather than being set apart from other entities, different species can spatiotemporally overlap in part because they don't have the boundary of an individual. The spatial gappiness of species also implies that they are not continuous in the way that, say, organisms are. Perhaps most importantly, the kind of cohesion that in part makes an individual an individual is absent in most, if not all species. All present parts of an individual are (at least serially) causally integrated at a time, so that they form a structural and/or functional whole. In species, some conspecifics may be similarly integrated, but many are not and manifest cohesion only in that they independently respond to evolutionary pressures in relatively similar ways—as if they were one, but not such that they are one (Barker in press; Barker and Wilson submitted). If species are not individuals, then even the conservative view of biological kinds is inadequate. Indeed, it would fail even were each species an individual, as the only resources it provides to characterize entities such as predators, tRNAs, and adrenergic cells are the notions of individual and traditional essentialist kinds.

To sum up so far, kind essentialism about all biological kinds is indeed mistaken. But so too are the radical and conservative views of those kinds. Most putative kinds to which biologists appeal are neither individuals nor kinds of which kind essentialism is true. Because the standard response to failed kind essentialism about species is flawed and cannot be developed into a general account of biological kinds, we have occasion to refit our philosophy to our biology, by rethinking rather than abandoning biological kinds. After articulating such a revised notion of natural kinds (the HPC view) in the subsequent two sections, section 7 will offer three detailed examples of kinds from different biological domains (evolutionary biology, molecular genetics, developmental biology), showing that they are neither individuals nor kinds of which traditional essentialism holds.

5. BIOLOGICAL KINDS AS HOMEOSTATIC PROPERTY CLUSTERS

The HPC view of natural kinds was introduced as part of an overarching realist view of science and ethics, a realism reinvigorated by developments in the theory of reference in the philosophy of language by Saul Kripke (1980) and Hilary Putnam (1975). Key arguments for anti-realist or anti-naturalist views in both of these domains, such as those that appealed to the incommensurability of scientific theories (e.g., Kuhn 1962) or to the indefinability of moral terms (e.g., Moore 1903) had relied on then dominant *descriptive theories of reference*, epitomized by Bertrand Russell's classic theory of descriptions, according to which names were equivalent to definite descriptions, and had their reference mediated via those descriptions. The causal theories of reference that Kripke and Putnam ushered in not only undermined those influential arguments but also constituted a toolkit for more constructive work for scientific realists. Richard Boyd was foremost among proponents of this reinvigorated form of scientific realism, using the toolkit in accounts of scientific precision (1973), metaphor in science (1979), and natural kinds (1988, 1991, 1999).

Boyd's work on natural kinds went largely uncited in the ongoing debates over the ontological status of species and biological kinds that persisted from about 1974 until the 1990s. Exceptions include Griffiths (1996, 1999) and Wilson (1996, 1999), which were extensions and modifications of Boyd's HPC view that also, until quite recently (e.g., Mallon 2003; Rieppel 2005a), went largely uncited. One reason for this may be that within the debates over the ontological status of biological kinds, the various versions of the HPC view were simply missed. Boyd's works were, for instance, in traditional analytical journals and more than one author (e.g., Kitcher 1987; Grene 1989; Crane 2004) has implied, if not explicitly charged, that most philosophers of biology did not consult these sources during the debates. Or perhaps this newer work on kinds, and its break from kind essentialism, was not made sufficiently clear. Whatever the case, it's worth highlighting and developing what we see as the most significant features of the HPC view of natural kinds.

Two key innovations of the HPC view mark the nature of its departure from traditional kind essentialism. Together they strike a balance between what we call *natural flexibility* and *explanatory integrity*, desiderata that often pull in opposite directions. A view of biological natural kinds must be naturally flexible in that it must allow one to make sense of biologists' embrace of intrinsic heterogeneity. And it must have explanatory integrity in that it depicts natural kinds as cohesive features of the world that allow for the regulation of explanatory and predictive success in the biological sciences. While the desideratum of natural flexibility pulls in the direction of pluralism, that of explanatory integrity pulls in the direction of realism about natural kinds. By striking a balance between these desiderata, the

HPC view, unlike the radical and conservative views it supplants, is a philosophical theory that avoids estranging itself from the very sciences it purports to characterize.

The first of these innovations is a metaphysical account of the living world's intrinsic heterogeneity, one that explicates the sense in which kind members vary by their very nature, rather than viewing variation as aberration from a norm. It consists in shifting, as biologists themselves do, ascriptions of individuative powers from properties per se, to clusters of properties. This is not the familiar view that a *strictly* delimited set of properties, rather than a single property, counts as necessary and sufficient for membership in a given kind. Rather, a *flexibly* delimited cluster of properties individuates a kind so that traditional notions of necessity and sufficiency give way to appropriately loosened ones. On one hand *no one* of the properties in the individuative cluster, nor any *particular subset* of them, is strictly necessary for kind membership. Necessity becomes more general. Each kind member necessarily instantiates *some* sub-set of the properties that typically cluster together. On the other hand not *just* one particular subset of properties in an individuative cluster is sufficient for kind membership. Sufficiency becomes more varied. Kind members can instantiate different particular subsets of clustered properties and yet still be said to instantiate the same cluster. This loosening of necessity and sufficiency allows members of a kind to *vary* with respect to the particular subset of typical properties they instantiate while yet being members of *a* kind by virtue of instantiating *these* subsets.

Crucially, not just any subset of properties will do. Taxonomic practice in biology suggests that properties count as typical of an individuative cluster because they are what we will call *causally basic*. They are properties of an individual from which many other theoretically interesting properties of that individual causally flow. Biologists count such properties as causally basic when their explanatory and predictive power cannot be straightforwardly reduced to further properties. We have said that practice in biology implies that relational properties can be causally basic in this way: biological individuals often are as they are and behave as they do because of the relations in which they stand. For example, many of an organism's properties will causally depend largely on the genealogical and reproductive relations in which it stands. Finches may tend to have beaks of a certain size and shape because of selective regimes their ancestors faced in the deep past, and because of the gene flow that distributed the traits that were selected for under those regimes. We will return to relational individuation in our worked examples (section 7). Here, we complete our point about causally basic properties by noting that the properties that causally flow from these more basic properties often appear to cluster as well, but are what we will call *surface* or diagnostic properties. The clustering and causal powers of such surface properties largely owe to the causal powers of the causally basic properties.

The second innovation of the HPC view further explicates how kinds for which there are no necessary and sufficient conditions in the traditional sense can nonetheless have real and explanatory integrity that allows them to serve as ground for biological explanation and prediction. This innovation shifts attention downward to the mechanisms underlying individuative clusters: properties in individuative property clusters tend to go together by virtue of underlying causal mechanisms and constraints, rather than our conventions or "language games". The underlying mechanisms and constraints tend to lead to the *coinstantiation of* the properties that are part of an individuative cluster. As a result, clusters naturally display an imperfect but homeostatic integrity of the sort demanded by exception-prone yet robust biological generalizations.

Consider how this second innovation helps dissolve a more pointed formulation of the worry about which particular (non-necessary) subsets of properties count as sufficient for membership in a single kind. Suppose that kind K's individuative property cluster, C, consists in ten individuative or essential properties: a, b, c, d, e, f, g, h, i and j. Members of K typically have these properties, but only typically. In principle individual I_1 may have the subset of properties $S_1 = \{a, c, e, g\}$; and individual I_2 may have the subset $S_2 = \{b, d, f, h\}$. On the HPC view, I_1 and I_2 could be instances of K despite there being no subset of properties that they share. But why, then, should one think that S_1 and S_2 *do* both belong to C, and so I_1 and I_2 to K? Surely, the objection continues, it is more plausible to think that S_1 and S_2 form clusters marking distinct kinds, with I_1 belonging to one corresponding kind, and I_2 to another. This is an objection to the HPC basis for *lumping*. One could pose a related objection to the HPC basis for *splitting*. Surely, it might be thought, there may be an individual I_3 that does not belong to K, even though I_3 possesses the subset of properties $\{g, h, i, j\}$. What reason could a HPC theorist have for precluding such an individual from the very same kind that I_1 and I_2 belong to, K? A seemingly natural answer—that I_3 shares with each of I_1 and I_2 just one of the ten properties in which C consists—does not seem available, since we've just seen that failing to share *any* of these ten properties at all does not preclude sharing kind membership. Here the HPC account delivers silence when probed about how to split off kinds from one another.

Questions like these are good ones to ask. Yet they require empirical rather than a priori answers. To answer them, we require knowledge not simply about numbers of properties shared but about the underlying mechanisms and constraints that make the cluster a *cluster* (not just a set) of properties. Properties typical of individuative clusters *actually* go together in virtue of underlying mechanisms and constraints that lead to their coinstantiation in a *variety* of ways. The dependency relations between the properties are many and complex, so whether absences of certain of these relations in any one individual are sufficient to disqualify that individual as a member of a kind will depend on careful examinations of the case in relation to others: how much causal and hence explanatory integrity remains when certain properties are missing in comparison with others? This further depends in part on the dependency relations that are affected by the absence: is the absence of the property or set of properties associated with the absence of other dependency relations? Because of the variety in these dependency relations, not all property absences are equal, and judgments about them will depend largely on empirical details and deliberation on those details, rather than on a priori considerations from the armchair.

To illustrate this general point, consider species and the properties *being able to interbreed with conspecifics* (other species members), and *having a certain genotype,* both of which we have good reason to think are in the property cluster by which we define species. These two properties are causally interwoven in various ways. Interbreeding among conspecifics tends to spread common genes with which atypical or invasive genes are incompatible. This underlying mechanism of invasive gene suppression tends to lead to conspecifics having similar genotypes. Interbreeding also tends to spread similar genotypes through a distinct mechanism, where it is new but adaptive genes that are spread, rather than old but common ones that suppress gene pool modification. Both of these underlying mechanisms suggest there are ways in which genotype similarity depends on conspecifics' abilities to interbreed. In the reverse direction of dependency, genotypes are one important part of behavioural mating patterns and thereby lead to the very ability to interbreed. The structure of genetic material can also help determine whether the sharing of genetic material through reproduction will result in viable and fertile offspring. Given these diverse dependency relations between the property of being able to interbreed and the property of having a certain shared genotype, whether an organism's lacking either property disqualifies it from membership in a given kind depends on how many other causally basic properties organisms tend to lack as a result of such absence. It also depends on which underlying mechanisms fail to obtain, since one mechanism may have more impact on a cluster's individuative power than that of another. Given the complexity and resulting variation here and across cases, we suspect that there is no substantive, general answer that can be given to the question of which properties are strictly sufficient for membership in the kind species. We take this to be an argument for the HPC view's loosening of necessity and sufficiency, rather than problem for the view.

Stressing the import of the mechanisms underlying the individuative clusters raises a further question: are the underlying mechanisms also individuative? To answer it, we return to the notion of causally basic properties, properties whose explanatory and predictive powers are not straightforwardly reducible. Certainly mechanisms can satisfy this condition, but by reference to mechanisms that *underlie* clusters we have meant to refer to just those mechanisms that tend to lead to the coinstantiation of the essential properties but to which the explanatory and predictive power of those properties cannot be straightforwardly reduced. Reduction may be blocked because the coinstantiation mechanisms are multiply realizable (better: implementable), or for other standard non-reductivist reasons. Biologists appeal to these sorts of reasons (in their own ways) when stopping at a certain set of properties and claiming it is individuative of a kind. We remain open, however, to the incorporation of some underlying mechanisms into an individuative cluster. Cluster constituents may have to be adjusted when scientific progress does happen to consist in reduction. In such cases, reference to what were once underlying mechanisms may be incorporated into the HPC kind-term definition as part of the general, dynamic modification of that definition over time in response to further empirical detail, reflection, technological innovation, and so forth.

6. SPECIAL FEATURES OF THE HPC VIEW OF NATURAL KINDS

With the HPC view's two key innovations now plain, highlighting five special features that spring from these innovations will help clarify the view's often overlooked resources. Each of these features is desirable in any adequate account of natural kinds, and the HPC view is uniquely placed, we think, to naturally satisfy all of them.

Relational properties, homeostasis, and variability. On the HPC view, the individuative capacities of relational properties are not just given ad-hoc recognition. Recognition of these capacities is a *feature* of the HPC view because in many cases they are part of an inference to the best explanation of how a kind retains its integrity despite variability among intrinsic properties of kind members. A dark moth's property of *being fitter than peppered moths* is a relational property, one realized in part by the colours of other moths and by the selective pressure (say, soot-darkened habitat) with respect to which it makes sense to talk of fitness. The reliable instantiation of this relational property among dark moths—and thus the environmental context that in part realizes those instances—helps explain why those moths form a natural kind, a group of moths whose members are being selected for, despite variation among those moths' dark colourations and other intrinsic properties. More generally, reliably instantiated relational properties within property clusters help explain how the homeostatic nature of property clustering can be imperfect and yet stable enough to serve the individuative natural ground it does.

Variability, integration, and pluralism. Amongst those who reject the traditional forms of essentialism, pluralism has been a popular option. While compatible with at least some forms of pluralism, the HPC view provides for a more integrative response to the failure of traditional essentialism. Suppose that three forests very similar in theoretically interesting ways nonetheless do not share any set of properties that we could call necessary for membership in an overarching forest kind to which they belong. A typical pluralist response would be to stop trying to subsume these things under one putative kind and instead recognize three distinct and more fine-grained kinds, in this case three kinds of forest to which certain trees belong. In contrast, by rejecting the "necessity" of shared necessary properties for kind membership, the HPC view allows that the theoretically interesting similarities among the three forests may be sufficient to count each as an instance of a broader, more integrated forest kind. Since pluralism about natural kinds is often fuelled by continued investment in traditional notions of necessity and sufficiency, one virtue of the HPC view is that the integrationist alternatives it allows abandon this restrictive view of natural kinds.

Vague and borderline cases. The HPC view's embrace of the variability among instances of kind members, and associated deference to empirical solutions in hard cases of kind individuation, also readily accommodates (indeed, anticipates) vague and borderline cases of natural kinds *and* kind membership. It will sometimes be unclear what properties are the essential properties that typically compose an individuative cluster and mark a natural kind off from a nominal kind. These cases will often reflect temporary or even permanent epistemic limitations, but sometimes they will simply reflect intense intrinsic heterogeneity. Even when consensus is achieved regarding the properties *typical* of kind members, it may still be unclear if a *particular individual* has a sufficient subset of the typical properties to count as a kind member. This is just because the cluster properties are merely typical. Unclarities about particular individuals will sometimes reflect actual indeterminacy that stems from intrinsic heterogeneity. But when a membership problem isn't indeterminate but just hard, the HPC view will favour empirical resolution. The relevant tools at scientists' disposal in these situations are those to which naturalistic scientific realists frequently appeal, such as the epistemic guidance gleaned from explanatory, inductive, and predictive success.

Surface and basic properties. By making explicit scientists' often implicit distinction between surface and basic properties, the HPC view articulates the way in which empirical considerations guide taxonomic decisions. Any kind membership(s) that an individual *actually* enjoys is (are) *determined* by its basic properties. Our *definitions* do not always successfully track these determining properties. Especially in novel areas of enquiry, definitions often appeal mostly to mere surface properties, in part because, as we've noted, these also tend to cluster as a result of their dependence on clustering basic properties. The derivative clustering of surface properties ensures they have epistemic value: such patterned causal dependence on basic properties makes them especially sensitive diagnostic tools that allow epistemic failures and successes to guide our kind term definitions past these surface properties, to the basic ones. The kinds that our definitions pick out are more natural to the extent that they appeal to more basic, rather than surface, properties.

Naturalism and the epistemic regulation of "natural kind". The HPC view carries a commitment to a thoroughgoing naturalism, according to which philosophical reflection on science is continuous with and epistemically regulated by ongoing scientific practice. Such naturalism seems especially crucial in philosophy of biology where, for instance, the conceptual needs and implications of evolutionary theory, the molecular revolution, and more recently the increased attention to microbial biology, are still being worked out. We have argued that our view of biological natural kinds as HPC kinds is truer to the naturalism needed than are the alternatives, especially in how it makes sense of explanatory and predictive practice in the biological sciences. Development of the HPC view is philosophical maturation in the right direction, maturation of the sort encouraged by Hilary Putnam in his lament that "[m]eta-science is today in its infancy: and terms like 'natural kind' and 'normal member' are…resisting speedy and definitive analysis…" (1970: 104).

7. THREE WORKED EXAMPLES

In presenting worked examples of HPC kinds, we begin with species because criticisms of the HPC view have centered on this case. This focus is unsurprising given the above-mentioned fact that the canonical rejection of traditional kind essentialism in biology has been based on species. But because we think the exclusive focus on species has impoverished debates about biological kinds, we also present detailed HPC accounts of genes and stem cells. Doing so cashes an important promissory note issued by the proposal that biological kinds are HPC kinds.

Species. Each species taxon (e.g., *Homo sapiens* or *Mus musculus*) is an HPC natural kind, with species members (merely) typically sharing several biologically real and scientifically important features. This accommodates the common point (e.g., Sober 1980; Okasha 2002) that, in accord with the intrinsic heterogeneity of biological kinds, there is no single phenotypic or genotypic property that could serve as the essence of a species taxon.

Certain features shared by conspecifics (species members) are sufficiently diagnostic to allow us to distinguish the species they form from others. In fact, species are and have been fairly reliably recognized in the history of biology by phenotypic properties, and nowadays there are very reliable genetic ways of diagnosing an organism's species membership. Such diagnostic surface features (morphological, physiological, developmental, behavioural) characteristic of a particular species cluster largely in virtue of causally basic features—properties, mechanisms, and so on—that promote species cohesion. One such feature is common ancestry from a founding population. Another is the ability of species members to interbreed. As noted above, the gene flow implemented by interbreeding both protects descendents from maladaptive genes, and propagates variation generated in one part of the species to the rest. Moreover, the same or similar ecological niche being occupied by species members leads to members facing similar ecological and evolutionary pressures. Species members also share similar genetic and developmental constraints, so that the same limits on generating phenotypic variation hold of different species members.

Which of these cohesion-promoting features (or combination thereof) is causally most relevant for keeping a species' surface features clustered is an empirical question and may vary from species to species. Features such as "being descended from population X" and "being able to interbreed with organisms from species Y" are characteristic of organisms in many species: they can be parts of the cluster that individuates a species. This shows that species are paradigm examples of the fact that biological kinds' causal capacities are often (in part) contextually determined. Any given species' individuative features are usually relational rather than intrinsic properties (Griffiths 1999; Okasha 2002) as the features that promote cohesion within a species are typically relational properties of conspecifics that form the causal or otherwise determinative basis for the clustering of intrinsic phenotypic properties of conspecifics.

In addition to claiming that each species *taxon* such as *Homo sapiens* (whose members are organisms) is an HPC kind, we also claim that the species *category* (whose members are species taxa) is an HPC kind. Species taxa are members of the species category in virtue of features that determine which groups of organisms are species. The following is a cluster of causally basic features that most *species* share:

- shared phenotypic and genetic properties across species members, some of which are unique to the species and not possessed by higher taxa
- species members are descended from a founding population
- gene flow among species members
- species members have the ability to interbreed with their conspecifics, but not with members of other species
- species members occupy the same ecological niche
- species members face similar selection pressures
- species members share similar developmental constraints
- species behave as a unit in evolution and independently of other species

This is a cluster of correlated features rather than features that all species share. For instance, asexual species' organisms cannot interbreed.

By claiming that the species category is an HPC kind we broach debate about species *concepts* with the above-mentioned integrationist resources of the HPC view (Wilson 1999, 2005). Biologists have proposed many different species concepts or definitions—Mayden (1997) lists 25 current species concepts—each of which uses a specifically explicated variant of one (or combination) of the features bulleted above. The perceived contrasts and incompatibilities between these concepts result, first, from the fact that some conditions (e.g., the ability to interbreed) are important for some species, whereas other conditions are used for other species (e.g., asexual species). Second, in one and the same species taxon several of the above features and mechanisms can obtain, and biologists may pragmatically favour one over the other, depending (say) on whether they are interested in classifying species by fossils and organism morphology, explaining species' ecological dynamics, studying population genetic behaviour, explaining species' distinct evolutionary fates, and so on. Philosophers have often endorsed such a pluralism about species concepts (Dupré 1993; Kitcher 1984). Indeed, Marc Ereshefsky (1992, 1998) argues that pluralism implies that the there is no species category and that we should abandon the term "species". On his radical "eliminative pluralism" there are instead three distinct categories (or natural kinds): "biospecies" (species taxa defined in terms of interbreeding), "phylospecies" (defined in terms of common descent), and "ecospecies" (ecological selection).

Ereshefsky is right that interbreeding, shared genealogy and niche-sharing are real features governing species cohesion (as reflected by the above list), and that across species sometimes one, sometimes another, feature may be effective to a higher degree than the others. However, Ereshefsky ignores that usually *several* such features apply to a species taxon at a time. Many of the features mentioned by Ereshefsky or the above list hold of most species; moreover, their clustering is not accidental. In fact, these features are usually causally interwoven, thereby creating the biological units recognized as species (Brigandt 2003). Pointing out that the species *category* is an HPC cluster kind shows that different so-called species concepts are commensurable. Each of them focuses on one aspect of what characterizes species and in doing so overlooks a broader, more integral kind, one individuated by a cluster of features whose metaphysical and explanatory integrity is captured by an HPC interpretation of the species category.

Genes. Genes are another HPC kind. This view is natural in light of recent disputes about whether there is one or two or three gene concepts—or no scientifically useful gene concept at all (Beurton et al. 2000; Griffiths and Stotz 2007; Moss 2003; Stotz and Griffiths 2004; Waters 2000). These debates stem precisely from the fact that genes form a quite heterogeneous kind, one heterogeneous enough that different scientists have come to use and define the term "gene" in different ways. This heterogeneity offers support for a HPC view of genes. A brief overview of these debates and the empirical developments that they reflect buttress this conclusion.

In the 1970s it was assumed that a unique structural definition of genes was possible, characterizing a gene as an *open reading frame*: a stretch of DNA bounded by a start and stop codon and preceded by a promoter sequence. Such a DNA sequence was assumed to be transcribed into RNA as an intermediate and then translated to a functional protein as the final product, so that there is a one-one relation between genetic elements and gene products. Yet it became clear that gene structure and function is incredibly more complicated in non-bacterial eukaryotes (see Stotz forthcoming). To mention just some of the complexities, the relation between genetic elements and gene products is actually *many-many*. A DNA segment can give rise to an RNA transcript, where only some chunks of it are selected and fused to be translated to the protein product. In different cells of an organism or in one cell at different points in time, different parts of the RNA can be selected, leading to one DNA element (one gene?) producing many protein products with distinct amino acid sequences. Which parts are selected is determined by other cellular entities, so that the actual protein product for which a gene codes is also dependent on factors *external* to this gene. Several non-contiguous DNA elements (one gene or several genes?) can be independently transcribed to RNAs, which are then fused together to yield a single protein product.

Due to this many-many relation between DNA elements and gene products, it is unclear which DNA elements (and their mereological sums) count as a gene, as a mere part of a gene, or as a collection of several genes. As a result, different scientists may use different criteria for individuating genes and use the term "gene" in different ways. This is aggravated by the fact that the relation from DNA elements to RNA products is largely one-one, but the relation between DNA elements and protein products is many-many. Nowadays it is clear that both RNAs (originally assumed to be mere intermediates) and enzyme-forming proteins fulfill important cellular functions (Mattick 2003). Researchers focusing on RNAs or rather on proteins as the molecular gene products of interest are likely to individuate different DNA elements as independent genes.

A gene's expression (regulation) is determined by its adjacent regulatory DNA sequences and on non-genetic substances that bind to the regulatory regions, thereby accounting for the fact that an individual's different cells and tissues express different genes even though they all share the same genes. Consequently, certain structural hallmarks of stretches of DNA are only defeasible criteria as to whether the DNA stretch produces a functional product (resulting in problems for using computerized algorithms that find genes based on an organism's newly sequenced genome). A DNA sequence that codes for a product in one organism may not do so in another species, due to differences in genetic regions external to the gene that impact the gene's expression. (Such a DNA element that looks structurally like a gene but does not code for a product is called a "pseudogene".) As a result, the central causal power of a gene—coding for a product—is an extrinsic property of a gene. Some scientists consider the enhancers and silencers regulating a gene to be part of the gene (due to their impact on the gene's function), while others use "gene" to refer only to the coding region.

The properties making up the cluster individuating the kind "gene" include the following (cf. Wilson 2005: 126):

- reliably replicated across cell divisions and inherited across generations

- consists of DNA
- part of a chromosome
- encompasses a coding region bounded by a start and stop codon, subdivided in coding exons and non-coding introns
- preceded by a promoter
- regulated by enhancers and silencers
- codes for a functional RNA
- codes for a functional protein
- undergoes mutation
- undergoes recombination
- generates heritable variation across generations
- tied to a phenotypic effect, which it produces in certain genetic and organismal contexts

Genes possess most of the above properties, but there are exceptions, as genes form a structurally diverse kind. Most genes are stretches of DNA, but in retroviruses they are made of RNA. In eukaryotes genes are organized in chromosomes, but prokaryotes do not have chromosomes. Most genes code for a protein via RNA as an intermediate product, but for some genes RNA is the final functional product. Many genes are a single open reading frame (transcription unit), but sometimes a gene consists in several non-contiguous open reading frames, possibly located on different chromosomes. While most independent transcription units have separate promoters (preceding each such gene and controlling its expression), a transcription unit need not have a promoter of its own. One gene can have many phenotypic effects; and as the effect of a gene is strongly contingent on its genetic, organismal, and environmental context, an individual gene need not have a unique and well-defined morphological or physiological phenotypic impact.

Despite being a heterogeneous kind, genes are of central causal significance (the kind possesses explanatory integrity), as each gene codes for the production of a functional product (be it RNA or protein), which in turn fulfills molecular functions. The way in which gene expression is regulated (when it is expressed and in which cells it is expressed) is an essential part of explaining an organism's development and physiology. Some of the above properties characteristic of genes are intrinsic properties of genes (referring to their internal structure), others are extrinsic properties (specifying a gene's causal dispositions in a certain context or referring to non-genetic elements influencing the behaviour of genes). The underlying mechanisms and constraints that in part account for the homeostatic clustering of properties in the above list consist in complex cellular and organismal processes that underlie genes' abilities, as structural molecular entities, to produce direct and indirect causal effects (within a cell, within an organism, across generations). Among the individuative properties there are many important causal-explanatory relations, which further account for their correlations. For instance, the structure of genes as open reading frames, together with their having structural elements such as promoters, enhancers, and silencers, explains how they produce RNA and, in appropriate contexts, protein products. The molecular mechanism of DNA replication explains how mutations and recombinations can occur and (given the phenotypic effect of genes) lead to heritable phenotypic variation across generations.

Stem cells. Stem cells are morphologically-structurally undifferentiated cells with two basic characteristics. First, they can divide and self-renew themselves for an extended period of time, by dividing into two stem cells or one stem cell and a more differentiated cell, called a progenitor cell (in turn giving rise to particular differentiated cell types). In contrast, committed progenitor cells and differentiated cells can divide only a limited number of times and division results in (more) differentiated cells. Second, stem cells can give rise to various differentiated cell types. When this happens and which differentiated cell type is produced is dependent on the stem cells' *microenvironment*, i.e., chemicals secreted by other cells or physical contact with the extracellular matrix and neighbouring cells. There are different subkinds of stem cells. Embryonic stem cells are *pluripotent*, i.e., they can beget most cell types (in higher animals any cell type derived from the three germ layers). So-called "adult" stem cells are tissue-specific, such as neural, liver, bone marrow, skin, epithelial, or blood stem cells. Tissue-specific stem cells are *multipotent*, they can give rise to a limited class of cell types. For example, blood stem cells produce all types of blood cells (red blood cells, B and T lymphocytes, neutrophils, macrophages, platelets, etc), whereas neural stem cells can produce neurons, astrocytes, and oligodendrocytes as the brain's major cell types. Because of their abilities of self-renewal and generation of many cell types, stem cells play a central role in the development of animals and in the regeneration of tissues during both normal cell turnover and response to tissue damage. Consequently, research on both embryonic and adult stem cells is a focal area of biomedical research.

Despite these two general and biologically crucial characteristics, stem cells form a heterogeneous kind and the term "stem cell" is used and defined in different ways by different scientists (Shostak 2006; Slack 2000). There are different kinds of stem cells, such as embryonic stem cells and different types of tissue-specific adult stem cells that differ (apart from their origin, location, and capacity as to which differentiated cells they can produce) in their internal features, including the genes they express and the proteins and sugars their cell surfaces exhibit. Even within one such type of tissue-specific stem cell there is heterogeneity (Blau et al. 2001). Across different animal groups such as mice and humans, stem cell morphology and behaviour shows some differences (Robert 2004). Hydra epithelial cells are able to both carry out differentiated functions and serve as stem cells (van der Kooy and Weiss 2000). Researchers have of course tried to discover internal-molecular features that are characteristic of all stem cells, i.e., what defines "stemness" as Ramalho-Santos et al. (2002) put it. Several studies point to large sets of genes that show higher expression in stem cells than some differentiated cell types. However, the gene sets of three such studies have only a single gene in common (Vogel 2003), making it unclear whether there is a complex molecular signature common to all stem cells.

There is substantial evidence that a cell's being and remaining a stem cell is partially determined by its cellular microenvironment (Watt and Hogan 2000). Furthermore, studies have shown that several types of adult stem cells can be induced by experimentally created environments to produce cell types that they do not usually produce, e.g., neural stem cells can give rise to skeletal muscle (Blau et al. 2001). Such findings about plasticity and transdifferentiation have generated excitement among biomedical researchers, as they make room for the possibility that not only embryonic, but also adult stem cells can give rise to any desired cell type under appropriate conditions. Based on these findings, Blau et al. (2001) suggest that a stem cell is not a particular entity (a certain cell being either a stem cell or non-stem cell), but a cellular function or disposition that a cell can possess under certain microenvironmental conditions—a function that comes in degrees and may change with a cell's location and microenvironment. There are many cell divisions—from a stem cell, to a multipotent progenitor, a committed progenitor, up to a fully differentiated cell—and the characteristic abilities of stem cells (self-renewal and production of many cell types) gradually decline along such a division and differentiation pathway. This explains both why stem cells are an internally heterogeneous kind and why they form a kind with vague boundaries separating them from non-stem cells.

In light of these preliminary facts, the properties making up the cluster individuating the kind "stem cell" include the following:

- morphologically undifferentiated
- ability of self-renewal (cell division with at least one daughter cell of the same type) over an extended period of time
- ability to give rise to various differentiated cell types (pluripotency, or at least multipotency)
- developmentally derived from certain cells or tissues
- located in specific parts of tissues
- particular complex profile of gene expression and presence of transcription factors
- found in certain cellular-molecular microenvironment ('niche'), which influences the stem cell's behaviour
- low rate of cell division

In spite of these properties being typically correlated and shared by most stems cells (but not by more differentiated cells), there are exceptions, so that the above describes a genuine HPC kind. For instance, while most stem cells are not visibly differentiated, stem cells of the basal epidermal layer show morphological differentiation (Slack 2000), and some neural stem cells have some functions of differentiated astrocytes (van der Kooy and Weiss 2000). Most tissue-specific stem cells become active and divide only in cases of tissue damage, so that stem cells typically have a low rate of cell division. This distinguishes them from progenitor cells producing fully differentiated cells, but not from differentiated cells that rarely divide or cannot divide at all. Adult stem cells are often defined in terms of the tissue or organ in which they reside (e.g., neural stem cells) and often occupy a location within this tissue distinct from the place where differentiated cells can be found. However, hematopoietic stem cells circulate freely in the blood. Given that tissue specific stem cells can—at least under experimental conditions—be induced to show the capacities of stem cells from other tissue types, it is presently unclear whether tissue origin and location or instead multi/pluripotency is more defining of stem cells.

It is also currently unknown which combination of genetic and molecular features of cells' interior environments and microenvironments are shared by most stem cells, and which are characteristic of only certain kinds of stem cells in a way that would suggest some features of "stemness" are multiply realized. It is the burden of future research to show which molecular features are part of the kind's individuate cluster (properties a, b, c, … in section 5), which are only diagnostic surface properties, and which are underlying mechanisms and constraints that partially account for the clustering of the individuative properties. Certain proteins and sugars on the cell surface are probably merely diagnostic for certain kinds of stem cells in specific organisms, and produced by the causally more fundamental gene activity inside the cell; if so, they are surface properties associated with the HPC kind "stem cell", rather than constituents of the individuate cluster. The underlying mechanisms and constraints that partially account for the clustering of the properties and capacities typical of stem cells include those that implement processes taking place inside stem cells and in particular their cellular microenvironments (stem cell niches). Some of the above listed properties characteristic of stem cells are intrinsic properties. But others are extrinsic or relational properties, including the most crucial ones (ability of self-renewal and multipotency), that are substantially determined by factors external to individual stem cells, such as their microenvironment, stem cell niche, and interaction and competition among stem cells.

Having broadened the philosophical discussion beyond the case of species, we close by returning to that case, exploiting the preceding discussion in order to remove some of the misunderstandings that underlie species-focused critiques of the HPC view.

8. MISSING THE MARK: SOME RECENT OBJECTIONS

Some authors have claimed that the HPC view suffers from problems that afflict traditional essentialism about species. Arnold Kluge, for example, has said that "whatever is 'homeostatic' cannot, by definition, evolve" (2003:234), in effect claiming that the HPC view is, like traditional kind essentialism about species, incompatible with the evolution of species over time. This objection, however, rests on a misunderstanding of the types of features that constitute individuative clusters.

Individuative features can be mechanisms that are not only compatible with evolution, but promote it. Indeed, we saw in the previous section that one typical individuative feature of many species is the ability of their members to interbreed, an ability that leads to intraspecific gene flow. Of course, neither interbreeding nor gene-flow entail that a certain genotypic or phenotypic trait is shared by all species members and does not change. But gene flow can and often does propagate change generated in one population to other parts of that population. Such individuative features of species promote the species' evolution, but also promote phenotypic unity among species members, which conforms to the desideratum that an appropriate notion of a natural kind ought to yield kinds with natural integrity. Even a speciation event does not break the operation of mechanisms such as interbreeding and gene flow. Interbreeding is first possible within the members of a founder species, and then within each of the two descendant species. Contrary to Kluge's worry, the features that individuate species as HPC kinds actually *explain* why species are units of evolution by accounting for the fact that *if* genotypic or phenotypic change takes place, the species changes as a whole (responds as a unit to change).

A related objection, put forward by Ereshefsky (2007b), is that the HPC view assumes that species and higher taxa need not be historical entities, whereas biologists define taxa at least partially by common ancestry from a specific founder population and thus historically. This assumption of the HPC view is not objectionable because nothing of consequence follows from it. The HPC view does not claim that species *must* be historical entities; no view of natural kinds should impose this modal constraint on our understanding of species. But this does not entail the claim, fallaciously deduced by Ereshefsky (2007b: 297), that the HPC view also does not *allow* that species are historical entities. The HPC view allows that species are historical entities even though it does not insist upon their being such. Indeed, our proposed list of individuative features of a species demonstrates that, on our view, species as HPC kinds are *in fact* historical entities. After all, shared genealogy is a typical individuative (and in turn defining) feature of most species. In this misunderstanding the HPC view of species Ereshefsky also misses a virtue of the HPC view more generally: because it does not impose untoward modal constraints on kinds, it permits various features to be included in the individuative clusters, as suggested by empirical findings.

Finally, Marc Ereshefsky and Mohan Matthen (2005) appeal to the existence of stable polymorphisms, i.e., variation among a species' members that is maintained by biological mechanisms, in objecting to the HPC view of species. In *sexual* polymorphism cases, male morphologies and behaviours differ significantly from those of females; in *developmental* polymorphism cases the phenotype of an individual may substantially change with its developmental stage (larva and adult); and in *seasonal* polymorphism cases the phenotype of an individual may change depending on its environment. Ereshefsky and Matthen claim that the HPC approach cannot accommodate such polymorphisms because it focuses on features that kind members *share*.

This strikes us as a bizarre objection, not least of all because the existence of such polymorphisms is explicitly recognized in many statements of the HPC view (e.g., Boyd 1999: 165; Wilson 1999: 200, 2005: 102-103; Rieppel 2005b: 470). More generally, in light of the embrace of the intrinsic heterogeneity of biological kinds, a feature highlighted by our earlier appeal to the *natural flexibility* of the HPC view, it is difficult to see how pointing to a particular form that such heterogeneity takes—its clustering into polymorphisms—could undermine that view. It may be that the distribution of a trait is such that a simple property is shared by all members; or it can be such that organisms that have (say) character A_1 also tend to have A_2, while other organisms have B_1 (instead of A_1) which is correlated with B_2. Thus the HPC view can cover sexual polymorphisms if A_1=male and B_1=female, and seasonal or developmental polymorphisms if A_i refers to a particular environment or life history stage. The properties shared by many species members are often indeed complex properties such as "if an individual is male, then it has property B", and the HPC account readily captures this phenomenon. Although Ereshefsky and Matthen label this "the mereological maneuver", we see nothing in what they say about this that makes this a problematic, implausible, or ad hoc view to adopt. (Indeed, it seems to us dead right, in light of the empirical practices in the biological sciences.)

The polymorphism objection errs in mistakenly assimilating the HPC view to phenetic views of species, which emphasize overall weighted phenotypic and/or genotypic similarity as the determinant of species taxa. What distinguishes the HPC view from pheneticism, however, is precisely its appeal to causally basic properties, underlying mechanisms, and external constraints, all of which equip the HPC view with the power to *explain much about* (rather than fail as a consequence of) the intrinsic heterogeneity of any particular biological natural kind, and how it clusters in the form of polymorphisms. The intrinsic variation here, and the polymorphic clumps within it, are to be explained in terms of variation and regularities in causally basic properties, underlying mechanisms, and external constraints. Ereshefsky and Matthen (2005) thus also err in claiming that the HPC view does not explain the variation within taxa such as polymorphisms, and this betrays their more general neglect of the suitability of the HPC view for capturing intrinsic heterogeneity.

Of course there is a limit to just how much typical variation and polymorphic clustering can be explained by these three features of the HPC view. But temper that concession by keeping in mind that an organism may be a member of several natural kinds, including trans- and subspecific kinds. In the case of sexual polymorphism, some properties of a certain gorilla may best be explained by her being a member of the kind "female gorilla" (subspecific), or by being a female (transpecific), rather than by her being a member of the kind "gorilla". Distinct generalizations may require distinct kind concepts, such as gorilla or male animal. Species taxa are a significant organizational feature of the biological world, but they are far from the only biological natural kind about which there are robust generalizations and which feature intrinsic heterogeneity.

9. CONCLUSION

Our chief, general aim in this paper is to make the case that the HPC view of natural kinds deserves the attention not only of philosophers of biology and biologists themselves, but other philosophers of science and metaphysicians. There remain many open issues surrounding just how the HPC view is to be developed and deployed in particular contexts—for example, how useful is it for thinking about social kinds, and how should one characterize cases where it would be counter-productive to appeal to the HPC view? By showing that some of the common objections to the HPC view rest on inadequate appreciation of the desirable features of the view, and by emphasizing the need for a *general* response to the failure of traditional kind essentialism in the biological sciences, rather than one that appears to apply only to species, we hope to have advanced discussion to a point where these can seem not simply open but live issues for anyone thinking about natural kinds in a biologically heterogeneous world.

REFERENCES

Atran, S., 1990, *Cognitive Foundations of Natural History: Towards an Anthropology of Science*. Cambridge: Cambridge University Press.

Amundson, R., 2005, *The Changing Role of the Embryo in Evolutionary Biology: Roots of Evo-Devo*. New York: Cambridge University Press.

Armstrong, D., 1980, "Identity Through Time," in P. van Inwagen (ed.), *Time and Cause*. Dordrecht: Reidel.

Ayers, M., 1999, *Locke, Volume II Ontology*. New York, NY: Routledge.

Barker, M.J., 2005, "Species of Biology: The Cohesion and Individuality of Biological Species." M.A. Thesis, University of Alberta.

Barker, M.J., in press, "The Empirical Inadequacy of Species Cohesion by Gene Flow", *Philosophy of Science*.

Barker, M.J. and R.A. Wilson, submitted, "Flowing Genes and Cohesive Species."

Beurton, P.J., R. Falk, and H.-J. Rheinberger (eds.), 2000, *The Concept of the Gene in Development and Evolution*. Cambridge: Cambridge University Press.

Blau, H.M., T.R. Brazelton, and J.M. Weimann, 2001, "The Evolving Concept of a Stem Cell: Entity or Function?" *Cell* 105: 829-841.

Boyd, R.N., 1973, "Realism, Underdetermination, and a Causal Theory of Evidence", *Noûs* 7:1-12.

Boyd, R.N., 1979, "Metaphor and Theory Change", in A. Ortony (ed.), *Metaphor and Thought*. New York: Cambridge University Press.

Boyd, R.N., 1988, "How to be a Moral Realist," in G. Sayre-McCord (ed.), *Essays on Moral Realism*, Ithaca, NY: Cornell University Press.

Boyd, R.N., 1989, “What Realism Implies and What it Does Not”, *Dialectica* 43: 5-29.

Boyd, R.N., 1991, “Realism, Anti-foundationalism, and the Enthusiasm for Natural Kinds”, *Philosophical Studies* 61: 127-148.

Boyd, R.N., 1993, “Metaphor and Theory Change (second version)”, in A. Ortony (ed.), *Metaphor and Thought*. 2nd edition. New York: Cambridge University Press.

Boyd, R.N., 1999, “Homeostasis, Species, and Higher Taxa”, in R. A. Wilson (ed.), *Species: New Interdisciplinary Essays*. Cambridge, MA: MIT Press.

Brigandt, I., 2003, “Species Pluralism Does Not Imply Species Eliminativism”, *Philosophy of Science* 70: 1305-1316.

Brigandt, I., in press, “Natural Kinds in Evolution and Systematics: Metaphysical and Epistemological Considerations”, *Acta Biotheoretica*.

Camardi, G., 2001, “Richard Owen, Morphology, and Evolution”, *Journal of the History of Biology* 34: 481-515.

Craver, C., 2005, “Mechanisms and Natural Kinds”, Presented at the Biannual Meeting of the International Society for the History and Philosophy and Social Sciences of Biology (ISHPSSB), July 15th, 2005, Guelph, ON, Canada.

Crane, J., 2004, “On the Metaphysics of Species”, *Philosophy of Science* 71: 156-173.

Devitt, M., unpublished, “Resurrecting Biological Essentialism.”

Dupré, J., 1993, *The Disorder of Things: Metaphysical Foundation of the Disunity of Science*. Cambridge, MA: Harvard University Press.

Elsasser, W., 1965, *Atom and Organism*. Princeton: Princeton University Press.

Ereshefsky, M., 1992, “Eliminative Pluralism”, *Philosophy of Science* 59: 671-690.

Ereshefsky, M., 1998, “Species Pluralism and Anti-Realism”, *Philosophy of Science* 65: 103-120.

Ereshefsky, M., 2001, *The Poverty of the Linnaean Hierarchy: A Philosophical Study of Biological Taxonomy*. Cambridge: Cambridge University Press.

Ereshefsky, M., 2007a, "Species", in E.N. Zalta (ed.), *The Stanford Encyclopedia of Philosophy* (Summer 2007 Edition). http://plato.stanford.edu/archives/sum2007/entries/species/

Ereshefsky, M., 2007b, "Foundational Issues Concerning Taxa and Taxon Names", *Systematic Biology* 56: 295-301.

Ereshefsky, M. and M. Matthen, 2005, "Taxonomy, Polymorphism, and History: An Introduction to Population Structure Theory", *Philosophy of Science* 72: 1-21.

Ghiselin, M., 1974, "A Radical Solution to the Species Problem", *Systematic Zoology* 23: 536-544.

Grene, M., 1989, "Interaction and Evolution", in M. Ruse (ed.), *What the Philosophy of Biology Is: Essays Dedicated to David Hull*. Boston, MA: Kluwer Academic Publishers.

Griffiths, P.E., 1996, "Darwinism, Process Structuralism, and Natural Kinds", *Philosophy of Science* 63 (Proceedings): S1-S9.

Griffiths, P.E., 1997, *What Emotions Really Are: The Problem of Psychological Categories*. Chicago, IL: University of Chicago Press.

Griffiths, P.E., 1999, "Squaring the Circle: Natural Kinds with Historical Essences", in R.A. Wilson (ed.), *Species: New Interdisciplinary Essays*. Cambridge, MA: MIT Press.

Griffiths, P.E. and K. Stotz, 2007, "Gene", in D.L. Hull and M. Ruse (eds.), *The Cambridge Companion to the Philosophy of Biology*. Cambridge: Cambridge University Press.

Hull, D., 1965, "Effect of Essentialism on Taxonomy: Two Thousand Years of Stasis", *British Journal for the Philosophy of Science* 15: 314-326. Reprinted in M. Ereshefsky (ed.), *The Units of Evolution: Essays on the Nature of Species*. Cambridge, MA: MIT Press.

Hull, D., 1978, “A Matter of Individuality”, *Philosophy of Science* 45: 335-360. Reprinted in M. Ereshefsky (ed.), *The Units of Evolution: Essays on the Nature of Species*. Cambridge, MA: MIT Press.

Hull, D., 1999, “On the Plurality of Species: Questioning the Party Line,” in R. A. Wilson (ed.), *Species: New Interdisciplinary Essays*. Cambridge, MA: MIT Press.

Keller, R.A., R.N. Boyd and Q.D. Wheeler, 2003 “The Illogical Basis of Phylogenetic Nomenclature”, *The Botanical Review* 69: 93-110.

Kitcher, P., 1984, “Species”, *Philosophy of Science* 51: 308-333.

Kitcher, P., 1987, “Ghostly Whispers: Mayr, Ghiselin, and the “Philosophers” on the Ontological Status of Species”, *Biology & Philosophy* 2: 184-192.

Kluge, A.G., 2003, “On the Deduction of Species Relationships: A Précis”, *Cladistics* 19: 233-239.

Kornblith, H., 1993, *Inductive Inference and Its Natural Ground: An Essay in Naturalistic Epistemology*. Cambridge, MA: MIT Press.

Kripke, S., 1980, *Naming and Necessity*. Cambridge, MA: Harvard University Press.

Kuhn, T., 1962, *The Structure of Scientific Revolutions*. Chicago: University of Chicago Press.

Mallon, R., 2003, “Social Construction, Social Roles, and Stability”, in F.F. Schmitt (editor), *Socializing Metaphysics: The Nature of Social Reality*. Lanham, MD: Rowman and Littlefield.

Mayden, R.L., 1997, “A Hierarchy of Species Concepts: The Denouement in the Saga of the Species Problem”, in M.F. Claridge, H.A. Dawah and M.R. Wilson (eds.), *Species: The Units of Biodiversity*. London: Chapman & Hall.

Mayr, E. 1959a, "Darwin and the Evolutionary Theory in Biology", in *Evolution and Anthropology: A Centennial Appraisal*. Washington, DC: The Anthropological Society of Washington.

Mayr, E., 1959b, "Where are we?", in C. Wooldridge (ed.), *Genetics and Twentieth Century Darwinism* (Cold Spring Harbor Symposia on Quantitative Biology, Vol. 24). New York: The Biological Laboratory.

Mayr, E., 1976, *Evolution and the Diversity of Life: Selected Essays*. Cambridge, MA: The Belknap Press of Harvard University Press.

Mayr, E., 1982, *The Growth of Biological Thought*. Cambridge, MA: Harvard University Press.

Mattick, J.S., 2003, "Challenging the Dogma: The Hidden Layer of Non-Protein-Coding RNAs in Complex Organisms", *BioEssays* 25: 930–939.

McOuat, G.R., 1996, "Species, Rules, and Meaning: The Politics of Language and the Ends of Definitions in 19th-Century Natural History", *Studies in the History and Philosophy of Science* 27: 473-519.

Müller-Wille, S., 1999, *Botanik und weltweiter Handel: Zur Begründung eines Natürlichen Systems der Pflanzen durch Carl von Linné (1707–1778)*. Berlin: Verlag für Wissenschaft und Bildung.

Müller-Wille, S., 2003, "Joining Lapland and the Topinambes in Flourishing Holland: Center and Periphery in Linnaea Botany", *Science in Context* 26: 461-488.

Moss, L., 2003, *What Genes Can't Do*. Cambridge, MA: MIT Press.

Moore, G.E., 1903, *Principia Ethica*. Cambridge: Cambridge University Press.

Okasha, S., 2002, "Darwinian Metaphysics: Species and the Question of Essentialism", *Synthese* 131: 191-213.

Putnam, H., 1970, "Is Semantics Possible?", in H. E. Kiefer and M. K. Munitz (eds.), *Language, Belief and Metaphysics*. Albany, NY: State University of New York Press.

Putnam, H., 1975, "The Meaning of 'Meaning'", reprinted in his *Mind, Language, and Reality*: Collected Papers, Volume 2. Cambridge: Cambridge University Press

Ramalho-Santos, M., S. Yoon, Y. Matsuzaki, R.C. Mulligan, and D.A. Melton, 2002, "'Stemness': Transcriptional Profiling of Embryonic and Adult Stem Cells", Science 298: 597-600.

Rieppel, O., 2005a, "Modules, Kinds, and Homology", *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 304B: 18–27.

Rieppel, O., 2005b, "Monophyly, Paraphyly, and Natural Kinds", *Biology and Philosophy* 20: 465–487.

Rieppel, O., 2006, "The PhyloCode: A Critical Discussion of Its Theoretical Foundation", *Cladistics* 22: 186–197.

Rieppel, O., 2007, "Species: Kinds of Individuals or Individuals of a Kind", *Cladistics* 23: 373–384.

Rieppel, O., in press a, "Origins, Taxa, Names and Meanings", *Cladistics*.

Rieppel, O., in press b, "Species as a Process", *Acta Biotheoretica*.

Rieppel, O. and M. Kearney, 2007, "The Poverty of Taxonomic Characters", *Biology and Philosophy* 22: 95–113.

Robert, J.S., 2004, "Model Systems in Stem Cell Biology", *BioEssays* 26: 1005-1012.

Rupke, N.A., 1993, "Richard Owen's Vertebrate Archetype", *Isis* 84: 231-251.

Scharf, S.T., 2007, "Identification Keys and the Natural Method: The Development of Text-Based Information Management Tools in Botany in the Long 18th Century". Doctoral Dissertation, University of Toronto.

Shoemaker, S., 1979, "Identity, Properties and Causality," in P. A. French, T. E. Uehling Jr., and H. K. Wettstein (eds.), *Midwest Studies in Philosophy, Volume 4, Studies in Metaphysics*. Minneapolis, MN: University of Minnesota Press.

Shostak, S., 2006, "(Re)defining Stem Cells", *BioEssays* 28: 301-308.

Slack, J. M. W., 2000, "Stem Cells in Epithelial Tissues", *Science* 287: 1431-1433.

Slote, M., 1979, "Causality and the Concept of a "Thing,"" in P. van Inwagen (ed.), *Time and Cause*. Dordrecht: Reidel.

Sober, E., 1980, "Evolution, Population Thinking, and Essentialism", *Philosophy of Science* 47(3): 350-383.

Stevens, P.F., 1984, "Metaphors and Typology in the Development of Botanical Systematics 1690-1960, or the Art of Putting New Wine in Old Bottles", *Taxon* 33: 169-211.

Stevens, P.F., 1994, *The Development of Biological Systematics: Antoine-Laurent de Jussieu, Nature, and the Natural System*. New York: Columbia University Press.

Stevens, P.F., 1997, "How to Interpret Botanical Classification—Suggestions from History", *BioScience* 47:243-250.

Stotz, K., forthcoming, "2001 and All That: A Tale of a Third Science", *Biology and Philosophy*.

Stotz, K. and P.E. Griffiths, 2004, "Genes: Philosophical Analyses Put to the Test," *History and Philosophy of the Life Sciences* 26: 5-28.

van der Kooy, D. and S. Weiss, 2000, "Why Stem Cells?" *Science* 287: 1439-1441.

Vogel, G., 2003, "'Stemness' Genes Still Elusive", *Science* 302: 371.

Waters, C.K., 2000, "Molecules Made Biological", *Revue Internationale de Philosophie* 4: 539-564.

Watt, F.M. and B.L.M. Hogan, 2000, "Out of Eden: Stem Cells and Their Niches," *Science* 287: 1427-1430.

Wilkins, J., 2004, "The Origins of Species Concepts: History, Characters, Modes, and Synapomorphies." Doctoral Dissertation, University of Melbourne.

Wilson, R.A., 1996, "Promiscuous Realism", *British Journal for the Philosophy of Science* 47: 303-316.

Wilson, R.A., 1999, "Realism, Essence, and Kind: Resuscitating Species Essentialism?" in R.A. Wilson (ed.), *Species: New Interdisciplinary Essays*. Cambridge, MA: MIT Press.

Wilson, R.A., 2005, Genes and the Agents of Life: The Individual in the Fragile Sciences: Biology. New York, NY: Cambridge University Press.

Wilson, R.A. 2007, "The Biological Notion of Individual", in E.N. Zalta (ed.), *The Stanford Encyclopedia of Philosophy* (Fall 2007 Edition). http://plato.stanford.edu/archives/fall2007/entries/biology-individual/

Winsor, M.P., 2003a, "Non-essentialist Methods in Pre-Darwinian Taxonomy", *Biology and Philosophy* 18: 387-400.

Winsor, M.P., 2003b, "Setting Up Milestones: Sneath on Adanson and Mayr on Darwin", in D.M. Williams and P.L. Forey (eds.), *Milestones in Systematics*. London: Taylor and Francis.

Winsor, M.P., 2006a, "Linnaeus's Biology Was Not Essentialist", *Annals of the Missouri Botanical Garden* 93:2-7.

Winsor, M.P., 2006b, "The Creation of the Essentialism Story: An Exercise in Metahistory", *History and Philosophy of the Life Sciences* 28: 149-174.