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Continuing After Species: An Afterword

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Abstract

This afterword to *Species and Beyond* provides some reflections on species, with special attention to what I think the most significant developments have been in the thinking of biologists and philosophers working on species over the past 25 years, as well as some bad jokes.

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As the current volume attests, biologists who play philosopher, as well as philosophers who play biologist, continue after species. For the most part, they do so in the shadow of "the species problem", poking a stick at it while making some interesting observations about species taxa in one or more globs of biospace. Shamelessly refusing to leave the comfort of the armchair for now, I would hazard the guess that philosophers and biologists alike who have responded to the species problem for the past 50 years with more than a poke have done so in three opposed ways: mostly offering solutions to the species problem (Hausdorf 2011; Richards 2010), occasionally declaring that a solution is impossible (Hull 1997; Reydon 2005), and elsewhere arguing that there is in fact no problem to be solved (Pavlinov 2013).

[†] This paper is dedicated to the memory of Dick Boyd and his infectious enthusiasm for scientific realism, naturalism, and natural kinds over the past 50 years. I am grateful to Dick for modelling how to think systematically and deeply about species, amongst other things. Thanks to John Wilkins for the invitation to write these reflections, and to John and to Frank Zachos for reading and commenting on an earlier draft.

The tendency to adopt one of these responses hasn't shown signs of decline in recent years, with all three tendencies clearly manifest in the current volume. Before saying something about "the species problem" beyond the "It's solved!", "It can't be solved!", and "It's not a problem!" responses to it, some initial stock-taking on the concept of species itself.

At least ideologically, as a card-carrying enthusiast for naturalistic philosophy of science, I remain attracted to utilising the latest technical modes of empirically-informed philosophical methodology, despite my confessed bodily affection for the laziness of the armchair, a professional hazard for all (but not only) philosophers. I was somewhat disappointed, however, with Siri's refusal to answer my simple query "Are species real?". Undaunted and ever-resourceful, I went directly to my methodological next stop: a Google Scholar search for "species". While not as common as either "cells" or "organisms"—and even less so once we add the singulars "cell" and "organism"—nonetheless "species" delivers well over 6 million hits on Google Scholar. GS hits for the terms cell(s), gene(s), and species occur in roughly a 3:2:1 ratio, shifting roughly to 3:1:2 for searches since 2020. (Interestingly, "gene(s)" shows roughly the same usage level and trajectory as "organism(s)".)

One thing that can be safely concluded is that talk about species has a robust academic history, one that shows little signs of dissipating to become merely history. In addition, with over 500 million hits on Google itself, and with roughly the same ratio of hits to "cell(s)" there as it has on Google Scholar, "species" prima facie earns its keep in more vernacular contexts. The tendency to make use of or appeal to the concept of species has been and remains strong across academic and non-academic contexts.

One reason for the robustness to the concept of species within both common sense and scientific thinking is a *clumpiness* to biological nature at the level of populations that is hard to ignore. As Kim Sterelny has put it in his under-appreciated "Species as Ecological Mosaics":

> The mechanisms of evolution have produced on Earth an astounding variety of life forms. Together with adaptive design, the evolution of that diversity is the central

> explanatory target of evolutionary biology. Though great, however, the diversity of life on Earth is limited in important ways. Diversity is bunched or clumped. … Life's mechanisms have produced *phenomenological species*: recognizable, reidentifiable clusters of organisms. This fact makes possible the production of bird and butterfly field guides, identification keys for invertebrates and regional floras, and the like. (Sterelny 1999, p.119).

Population-level clumpiness is typically conceptualised as cohesiveness, and *species cohesion* is a primary phenomenon to be explained (for example, by "gene flow"; see Barker and Wilson 2010). As Sterelny goes on to note, the reality of phenomenological species is the beginning, rather than the end, of reflection on the nature of species and their relationships to the mechanisms of evolution and the diversity of life forms (see also Minelli, this volume). For some, the existence of phenomenological species serves as a foundation for not only realism about species *taxa* but also about the species *category*, even if this proves to be a form of pluralistic or promiscuous realism (Dupre 1981, 1999; see also Wilson 1996, Barker, this volume). For others, attempting to make more of the concept of species beyond phenomenological species is to invite potential confusions of various kinds. They accordingly opt for a deflationary understanding of species, whereby species are little more than phenomenological species, if that (Ereshefsky 1992a, 1999; see also Mishler 1999, Wilkins, this volume).

What of "the species problem", a focus for much of the ongoing philosophical discussion of species? The species problem is really a cluster of problems. That cluster both stems from and fuels at least four kinds of ongoing discussions in the philosophical deep end of the biological pool. These discussions arise from and involve:

1. the diverse characterisations that have been given of species by biologists over the past 100 years;

2. questions about the standing of species as a distinctive rank in the Linnaean hierarchy that has remained the dominant scheme of taxonomic classification of populations of organisms since it established itself as such over 250 years ago;
3. debates over the ontological status of species, such as whether species are natural kinds, individuals, processes, feedback systems, or even, as John Locke might have put it, creatures of the understanding;
4. emerging technologies for species delimitation (such as coalescent models) and the corresponding issue of species discordance.

If we continue to locate species as one of the Big Four concepts applied in describing and explaining the world of living things—gene, cell, organism, and species—perhaps the confluence of the preceding four dimensions partially explains why there is a species problem but no corresponding gene, cell, or organism problems.

The other part to such an explanation, however, is surely historical, concerning two distinct spotlights thrown on species in the history of biological thought. First, species were cast on stage by the title of Darwin's *On the Origin of Species by Means of Natural Selection* (1859). Darwin's own reflections on and hesitations about species continue to attract scrutiny and discussion, even in recent years (de Queiroz 2011; Mallett 2010, 2013; Stamos 2003). Second, the term "biological species concept" was both introduced and promoted by the ornithologist Ernst Mayr (Mayr 1942) and others (Wright 1940; Dobzhansky 1950) as labelling a settled view of the nature of species. That view, according to which species are reproductively isolated populations stabilized by gene flow resulting from interbreeding, emerged from the so-called Modern Synthesis of the 1930-40s that integrated the theory of natural selection and genetics, or to put it more crudely, Darwin and Mendel.

In the introduction to my collection of essays *Species: New Interdisciplinary Essays* (MIT Press, 1999), I noted that "the last decade has seen something of a publication boom on the topic" (Wilson 1999a, p.ix), going on to chiefly cite collections with dominant contributions from biologists: "Otte and Endler 1989; Ereshefsky 1992b; Paterson 1994; Lambert and Spence 1995; Claridge, Dawah, and Wilson 1997; Wheeler and Meier 1999 [sic]; Howard and Berlocher 1998" (p.ix). Much of that publication boom was in response to the growing recognition of the breakdown of whatever consensus there was around Mayr's "biological species concept", and how that did (and didn't) affect the continuation of thinking about processes of speciation and the goals of conservation and the preservation of biological diversity.

One editorial directive given to me in the invitation to write this Afterword was to reflect especially on the development of discussions of species and the species problem over the past 25 years. The trading zone between philosophers of biology and biologists of a greater variety of stripes has expanded, even if the bulk of recent work on core topics, such as speciation and phylogenetic constraints on taxonomy, continues to operate on the territory of biologists beyond that zone. Both the expanded trading zone and the tendencies to live beyond it can be seen in *Species: New Interdisciplinary* Essays, particularly in two essays it contains that develop ideas which have been especially influential during this time, the first more so amongst biologists, the second more so amongst philosophers.

Kevin de Queiroz's "The General Lineage Concept of Species and the Defining Properties of the Species Category" provided one of his earliest and most extended discussions of the general lineage concept of species, while Richard Boyd's "Homeostasis, Species, and Higher Taxa" remains the most discussed paper on the homeostatic property cluster view of natural kinds that has an application to species. Each of these views might be best thought of as providing an overarching framework for thinking about species, one completed by further biological details that might well vary from context to context.

De Queiroz's (1998, 1999) general lineage conception of species (later, *metapopulation lineage* conception, de Queiroz 2005, 2007), has come to be viewed by many as the successor to Mayr's biological species concept, being the closest thing we have to an adequate, monistic conception of species. For de Queiroz, species are "segments of population-level lineages" (de

Queiroz 1999:53), with different extant species conceptions providing different criteria for the segmentation, and "populations" covering both sexual and asexually reproducing organisms. While its generality in subsuming more specific views of the nature of species is no doubt one source of its appeal for biologists, philosophers are more likely to view *segments of population-level lineages* as taking us little way to identifying what species are. In the morass of biological entities, many things—from nuclear families to multi-Order clades—are such segments: a parent and its offspring form a segment of a population-level lineage; a pair of these form a metapopulational lineage segment. Since the ancestor-descendant relationship holds of many biological entities, segments of population-level lineages are ubiquitous in the living world, as are metapopulations. The heavy lifting, conceptually speaking, lies elsewhere in delineating species as a particular type of metapopulational lineage.

As influential amongst philosophers of biology as the metapopulational lineage conception has been amongst biologists has been Boyd's homeostatic property cluster view of species and of natural kinds more generally (Boyd 1999; see also Griffiths 1999 and Wilson 1999a). The HPC view, originally developed in defending moral realism (Boyd 1988), has been articulated as part of a broader naturalistic form of scientific realism (Boyd 1991, 2010, 2019). For Boyd, species are phenomena that cohere due to a variety of homeostatic mechanisms, such as gene exchange, reproductive isolation, coadapted gene complexes, developmental constraints, and niche construction (e.g., Boyd 1999: 164-165), and these phenomena are mostly plausibly viewed as natural kinds (pp.167-169). Here the general idea has been to reconceptualise what natural kinds are, showing how thinking of species as such reconceptualised kinds both allows one to address many issues about species and to serve as a paradigm for other applications (see also Wilson, Barker, and Brigandt 2007; Wilson 2005: ch.3-6).

In commissioning and assembling the essays in *Species*, I took its subtitle, *New Interdisciplinary Essays*, not only to refer to the interface between biologists and philosophers but also to signal an invited expansion in the nature of the interdisciplinary contributions to the discussion. In addition to innovative and influential essays from evolutionary theorists (such as de Queiroz) and philosophers of biology (such as Boyd), the volume also included contributions from a pair of developmental psychologists (Keil and Richardson 1999), a cultural anthropologist (Atran 1999), and a ciliatologist specializing in eukaryotic protists (Nanney 1999).

Research since then on "folk biology" in both developmental psychology and cultural anthropology has blossomed, with perhaps its best-known application being in the sophistication of discussions of Indigenous classification and taxonomy of the living world (Ludwig and El-Hani 2020; Ludwig and Poliseli 2018; Ludwig and Weiskopf 2019). Yet this work has had only a limited impact on core discussions of species and the species problem amongst philosophers and biologists (see Kendig 2020 and Kendig, this volume, for exceptions).

By contrast, the corresponding discussions not so much of eukaryotic protists in particular but of the microbial world more generally have informed those discussions. In this regard, it is interesting to note that Wilkins devotes to microbial species roughly one-third of a chapter newly added to the second edition of his *Species: The Evolution of the Idea*, "The Development of the Philosophy of Species" (esp. pp.317-330; see also Wilkins 2006). Insights gained from this attention to the microbial world have informed more general views of the nature of species. For example, explorations of the significance of lateral or horizontal gene transfer, more prevalent in the microbial than in the macrobial world, have reinforced one idea fueling pluralistic views of the species category: that whatever "species" are in bacteria they are really something different in kind from species in plants and animals (O'Malley 2014: ch.2; see also Franklin 2007, Franklin-Hall 2010).

The microbial geneticist Ford Doolittle has developed perhaps the most sophisticated forms of this view over a number of years (e.g., Doolittle 2009, 2013, 2019; Doolittle and Zhazybayeva 2009; Novack and Doolittle 2020). Other and contrasting recent discussions have defended the application of Mayr's biological species concepts to bacteria by assimilating homologous recombination to interbreeding (Bobay and Ochman 2017, 2018), building on earlier work by Dykhuizen and Green (1991) on *Escherichia coli* and extending this assimilative exercise to encompass the *pangenome*, the complete set of genes in all strains of a given microbial species (Bobay 2020).

The associated development of metagenomics alongside techniques for large-scale sampling of genomic elements, both of which have been pioneered in the microbial world, forms part of this shift informing a species literature that has been skewed historically by an overwhelming focus on the macrobial world. The growth of computationally-driven delimitation methods, the most popular of which are multispecies coalescent models (Carstens et al. 2013), has been one important development in the species literature. Viewed as integrating population genetics with phylogenetic analysis in order to more accurately construct species trees, multispecies coalescent models now provide a large number of algorithmic species discovery procedures that have been taken to build on de Queiroz's general lineage conception of species (see Quinn, this volume; Smith and Carstens, this volume).

In light of these developments it is easy to forget that, until the turn of the twenty-first century, microbes—bacteria and the eukaryotic protists, for example—were largely ignored in the species literature. Furthermore, attempts to shed that ignorance were often met with ridicule and hostility. Bacteria were typically simply bracketed out from the rest of the living world in discussions of species; in an informal interview, Ernst Mayr went so far as to call eukaryotic protists a "sort of garbage can group" (Mayr 2004). Microbial biologists, whether working on bacteria, eukaryotic protists, or other microbial organisms and clonelines, mostly just got on with the job of describing the diversity they found in the microbial world (Nanney 1999, Warren et al. 2016). They chiefly opted for phenetic views of microbial groups, including of those referred to by Linnaean binomials and so regarded as species.

Although both the labels "pheneticism" and "numerical taxonomy" (Sokal and Crovello 1970; Sneath and Sokal 1973) have made a quiet exit from discussions of species over the past 25 years, it is perhaps worth reflecting on the relationship between multispecies coalescent models and pheneticism. Both ultimately rely on computational strategies that require judgements of similarity, revealing a conventional dimension to taxonomic decisions, including with respect to species. The reliance of pheneticism about species on similarity judgments of this kind served as a red flag for those skeptical of either mind-dependent or theoretically neutral conceptions of species (e.g., Hull 1997, 1999; Mayden 1997). Whether the same holds true of multispecies coalescent models, or whether they are, by contrast, taken to manifest a kind of pluralistic realism about species (Nathan 2019a), remains to be seen.

This niche in the species literature promises to become further sophisticated by the continuing integration of focused discussions of genealogical discordance (Haber 2019, Velasco 2019). Here the lineages of component entities (such as genomes) diverge from those of which they are components (such as organisms and species). More general discussion of the phenomenon of discordance (Haber and Molter 2019) has already informed views of multispecies biofilms (Pedroso 2019) and broader evaluations of methodologies within phylogenetic reconstructions (Quinn 2019).

Both de Queiroz's metapopulational lineage conception of species and Boyd's homeostatic property cluster view of species have suggested ways to develop kinds of pluralistic realism about species. "Pluralism" because of the multiplicity of criteria for lineage segmentation (de Queiroz) and of homeostatic mechanisms (Boyd), and "realism" as acknowledgment that these criteria and mechanisms constitute the joints at which nature itself is carved. The attraction of an eliminativist view of species has proved strong for some who have weighted the pluralistic dimension to such views more heavily (Mishler and Donoghue 1982; Ereshefsky 1992a), leading to the idea that, as Mishler and Wilkins (2018: 1) have noted, "the species rank should disappear as part of a general move to rankless taxonomy (Ereshefsky 1999, Mishler 1999; Pleijel 1999)".

Barker (2019b) has recently argued that a dilemma facing Ereshefsky's (1992a) arguments for eliminative pluralism holds more generally for all extant forms of eliminative pluralism. Call the categories putatively replacing the species concept the *successor categories*. Barker's dilemma turns on the features and relationships shared by such successor categories. If these are shared across successor categories, then they are the basis for forming a superordinate category—such as species—thus undermining the *eliminativist* part of eliminativist pluralism. If these are not shared across successor categories, however, then this undermines the *pluralism* of the view, since without these each successor category inherits whatever doubts there are about the scientific interest of the species category (see Barker 2019b: 672-673).

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Given that this afterword began with some faux-data about "species", it seems appropriate that it end with a perhaps apocryphal story about philosophy. In the darkness before naturalistic light illuminated philosophy of biology as a new field within the philosophy of science just over 50 years ago, the end of philosophy was being predicted by many in the Anglo-American traditions dominated by "linguistic philosophy". What had been figured out was that philosophical problems were puzzles to be dissolved, matters simply of the language games we chose to play or not play. And all that was needed was a record of what philosophy was, a record to be created as the *Encyclopedia of Philosophy*.

Contained within the eight large volumes of the original *Encyclopedia* was barely a whiff of anything about the philosophy of biology, let alone about species, except insofar as Aristotle seemed to have had views about them. Wind forward to the contemporary online treasure-trove, the *Stanford Encyclopedia of Philosophy*, and things couldn't look more different. "Species" not only of course has its own substantive entry, but discussions of species can be found in articles on conservation biology, biodiversity, Darwinism, human nature, philosophy of macroevolution, and biological individuals. Rather than being records of a moribund past, these discussions are very much part of ongoing interchanges between philosophers and biologists, often drawing as much on articles in journals in the evolutionary, ecological, and other biological sciences as on those in *Philosophy of Science* or *Biology and Philosophy*. If they are a record of anything, they are a record of the healthy future that the species problem has for philosophers and biologists alike.

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