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Species Concepts

Jody Hey

Introduction

In a general and nontechnical sense, species are kinds of organisms. But for naturalists, from at least the early days of the age of the Enlightenment (late 1600s) up to the present day, there has been uncertainty and debate about just what species are and how best to identify them. Questions about species are central to some of the oldest and most-discussed philosophical topics on the nature of kinds of things (i.e., categories or universals). Perhaps surprisingly, the advent of the theory of evolution in the mid-19th century only accelerated debates and discussion about species and did little to resolve some of the basic disputes, even as scientists came to understand how new species arose. The 20th and 21st centuries have seen extraordinary growth in scientific research on species diversity, as well as increasing conservation efforts to avoid species extinction in the face of habitat loss and other anthropogenic forces of environmental change. All of the research on speciation, and species discovery, and on conservation takes place amid ongoing discussions about how best to identify species.

General Overviews

Because of a large philosophical element, the literature on species concepts is unusually diverse for a biological topic. A great many sources, including those from biologists, are concerned with topics such as the role of definitions, operational versus conceptual ideas, and the reality of taxonomic groups. Because of the diversity of opinions held by biologists on questions about species, the only broad reviews on the topic are edited volumes. Mayr 1957 is the first edited volume to attempt to address the species problem in some breadth, both philosophically and in application. Slobodchikoff 1976 and Ereshefsky 1992 are useful edited volumes that contain a number of the important philosophical papers on the subject (some papers are in both volumes). Otte and Endler 1989; Claridge, et al. 1997; and Howard and Berlocher 1998 are edited volumes of original articles, written mostly from biological perspectives rather than philosophical ones, on basic questions about species in general and on questions that arise in particular empirical contexts. Wilson 1999 is a volume of original philosophical articles, some of which have gone on to be widely cited, and Wilkins 2009 is a compendium of terms and concepts, useful for parsing the philosophical literature.

Claridge, M. F., H. A. Dawah, and M. R. Wilson, eds. 1997. *Species: The units of biodiversity*. Systematics Association Special Volume 54. London: Chapman & Hall.

An edited volume with several very useful papers. The focus is largely on the practical aspects of species identification, rather than on philosophy or on the processes of speciation. Many articles address the practical issues that arise for species identification, in particular large taxonomic groups.

Ereshefsky, M., ed. 1992. *The units of evolution: Essays on the nature of species*. Cambridge, MA: MIT Press.

An anthology of reprints of major, mostly philosophical, papers.

Howard, D. J., and S. H. Berlocher, eds. 1998. *Endless forms: Species and speciation*. New York: Oxford Univ. Press.

A volume of original papers covering diverse topics related to species and speciation.

Mayr, E., ed. 1957. *The species problem: A symposium presented at the Atlanta meeting of the American Association for the Advancement of Science, December 28–29, 1955*. AAAS Publication 50. Washington, DC: American Association for the Advancement of Science.

A volume of original papers, with the first and last by Ernst Mayr promoting the biological species concept.

Otte, D., and J. A. Endler, eds. 1989. *Speciation and its consequences*. Sunderland, MA: Sinauer.

Although an edited volume with a broad scope, this book has a number of papers that became widely cited. The first section, with classic articles by Alan Templeton, Joel Cracraft, and Gareth Nelson, concerns species concepts directly, with the remainder of the book dwelling more on the speciation process.

Slobodchikoff, C. N., ed. 1976. *Concepts of species*. Benchmark Papers in Systematic and Evolutionary Biology 3. Stroudsburg, PA: Dowden, Hutchinson & Ross.

An anthology of reprints of major papers, many of them philosophical in nature.

Wilkins, J. S. 2009. *Defining species: A sourcebook from Antiquity to today*. American University Studies V203. New York: Peter Lang.

A terse encyclopedia covering the history of scientists and ideas relevant to questions about species.

Wilson, R. A., ed. 1999. *Species: New interdisciplinary essays*. Bradford Book. Cambridge, MA: MIT Press.

A volume of original, mostly philosophical papers on the nature of species and the species problem.

Aristotle, Taxonomy, and Essentialism

The terms "species" and "genus" and their nested relationship (i.e., multiple species within a genus) come from Aristotle, who used them not just for living things but for many grouping problems as part of a general logical system of classification. Aristotle also said that each species has an essence that distinguishes it from other species. Ereshefsky 2001 and Mayr 1982 cover the history of how biologists came to use these terms as part of a nested (i.e., hierarchical) taxonomic system of classification, with the term "species" referring to the basal or bottommost taxonomic rank (in some contexts, even lower ranks such as subspecies are used). Cain 1958 tells the story of how the pioneering systematist Carolus Linnaeus adapted Aristotle's system to biology, including Aristotle's idea of essences. Mayr 1959, Hull 1965, and Mayr 1982 describe how Charles Darwin's theory of evolution radically undermined essentialist ideas and replaced those ideas with a new outlook in which species do not have essences, and in which the variation among individuals is the raw material for the evolution of species. Hull 1965, drawing extensively from Ernst Mayr's work, describes from a philosophical perspective the harmful impact of Aristotle's essentialism on taxonomy. Winsor 2006 is highly critical of Mayr's reading of history and of the story that biologists before Darwin were essentialist and were overly influenced by Aristotle and Plato.

Cain, A. J. 1958. Logic and memory in Linnaeus's system of taxonomy. *Proceedings of the Linnean Society of London* 169.1–2:

144–163.

A significant paper that makes the case that Linnaeus's commitment to Aristotelian logic included a commitment to species essentialism.

Ereshefsky, M. 2001. *The poverty of the Linnaean hierarchy: A philosophical study of biological taxonomy*. Cambridge Studies in Philosophy and Biology. Cambridge, UK: Cambridge Univ. Press.

A useful review and interesting critique of the history of how we classify organisms.

Hull, D. L. 1965. The effect of essentialism on taxonomy—two thousand years of stasis (I). *British Journal for the Philosophy of Science* 15.60: 314–326.

A widely cited paper that articulates the thesis that the Aristotelian view of species is essentialist and counterproductive.

Mayr, E. 1959. Darwin and the evolutionary theory in biology. In *Evolution and anthropology: A centennial appraisal*. Edited by B. J. Meggars, 1–10. Washington, DC: Anthropological Society of Washington.

This contains the earliest full articulation of Mayr's thesis that Darwin's theory of evolution by natural selection invoked a major change in biologists (and others), from viewing species as fixed types with essences to viewing species as lacking essences and within which variation is the raw material for evolutionary change.

Mayr, E. 1976. Typological versus population thinking. In *Evolution and the diversity of life: Selected essays*. By E. Mayr, 26–29. Cambridge, MA: Belknap.

A more complete and easier-to-find articulation of the ideas laid out in Mayr 1959.

Mayr, E. 1982. *The growth of biological thought: Diversity, evolution, and inheritance*. Cambridge, MA: Belknap.

A philosophical and historical treatise on how biologists came to understand species, and on the impact of Darwin's theory of evolution by natural selection on the way that scientists come to understand organisms and species. This book places Mayr's earlier thesis, that the theory of evolution triggered a change in biologists' view of species away from essentialism and toward an understanding of the role of variation, into a broad historical overview.

Winsor, M. P. 2006. The creation of the essentialism story: An exercise in metahistory. *History and Philosophy of the Life Sciences* 28.2: 149–174.

An important paper for understanding Mayr's claims regarding the history of essentialism. Winsor and others have argued that Mayr overstates the case that biologists before Darwin were essentialist.

The Origins of a Focus on Reproductive Barriers

In partial contrast to the idea that an individual species exists as a kind of thing, with a unique essence, there stands the observable phenomenon that organisms usually reproduce with others of the same kind and bear offspring of the same kind. As the ancient idea that living things arose spontaneously from nonliving things was replaced with a recognition that all organisms have parents that they resemble, early naturalists began to describe a conception of species that depended on reproduction—ideas that were later incorporated into the biological species concept. Most famous among these were John Ray, Georges Cuvier, and Comte de Buffon. Nordenskiöld 1928 is a useful history, and Lovejoy 1959 covers Buffon. Wilkins 2009 offers a broad philosophical history of ideas about species, and Mayr 1982, cited under Aristotle, Taxonomy, and Essentialism, focuses on the history of what came to be called the biological species concept.

Lovejoy, A. O. 1959. Buffon and the problem of species. In *Forerunners of Darwin: 1745–1859*. Edited by B. Glass, O. Temkin, and W. L. Strauss Jr., 84–113. Baltimore: Johns Hopkins Univ. Press.

A very useful telling of Buffon's complex views on species.

Nordenskiöld, E. 1928. *The history of biology: A survey*. Translated by Leonard Bucknall Eyre. New York: Tudor.

A comprehensive history that was translated from the original Swedish by Eyre. This book, originally published in three volumes in 1920–1924 (*Biologins historia*, Stockholm: Björck & Börjesson), has been reissued multiple times in English, most recently in 1988.

Wilkins, J. S. 2009. *Species: A history of the idea*. Species and Systematics 1. Berkeley: Univ. of California Press.

A thorough philosophical and historical telling of the history of the concept of species. Although idiosyncratic, with the author's own views laying fairly heavily on some aspects, the book is insightful and comprehensive.

Darwin's Conception of Species

Darwin 1859 is the seminal book on the theory of evolution by natural selection. Charles Darwin described a model in which one species gradually splits into two, and because he viewed this as a gradual process he argued that two similar forms could not be objectively identified as separate species as opposed to mere varieties of the same species. However, Darwin also avoided writing about both the fundamental nature of species and the means by which species should be identified. Beatty 1985 suggests that this was part of a strategy on Darwin's part to facilitate the acceptance of his arguments. Darwin's seeming deliberate avoidance of the issue has meant that until recently he has stood largely outside most discussion on species concepts. Ernst Mayr often wrote (e.g., see Mayr 1982, cited under Aristotle, Taxonomy, and Essentialism) that Darwin was wrong in viewing species as not objectively distinguishable from varieties and also wrong about how speciation happens (Mayr insisted that one species must split into separate populations before new species can emerge). More recently, Mallet 2008 and Reznick and Ricklefs 2009 describe a reemergence of acceptance of Darwin's speciation model, on the basis of new discoveries of the way new species arise without geographic barriers (i.e., sympatric speciation).

Beatty, J. 1985. Speaking of species: Darwin's strategy. In *The Darwinian heritage: Including proceedings of the Charles Darwin Centenary Conference, Florence Center for the History and Philosophy of Science, June 1982*. Edited by D. Kohn, 265–281. Princeton, NJ: Princeton Univ. Press.

Makes the case that Darwin avoided defining the term "species" as a way to make it easier for his readers to use their own ideas on species and not to get distracted by definitions of tricky subjects.

Darwin, C. 1859. *On the origin of species by means of natural selection, or, The preservation of favored races in the struggle for life*. London: John Murray.

The classic original book on the theory of evolution by natural selection. Darwin envisioned the book as an abstract, perhaps to be followed by a longer volume, so it is written in a fairly accessible style and with few citations to other's work. The complete work can be freely accessed online.

Mallet, J. 2008. Mayr's view of Darwin: Was Darwin wrong about speciation? *Biological Journal of the Linnean Society* 95.1:

3–16.

Refutes Mayr’s arguments about Darwin’s view of species, both on historical grounds and also in light of recent evidence supporting Darwin’s model of the speciation process.

Reznick, D. N., and R. E. Ricklefs. 2009. Darwin’s bridge between microevolution and macroevolution. *Nature* 457.7231: 837–842.

A nice review that shows how research since the late 20th century on the speciation process supports models, such as Darwin’s, in which diverging populations are not completely isolated from one another.

The Changing View of Species Leading Up to the Modern Synthesis

With respect to species, Darwin focused on how natural selection could pull one species in two different directions to create two species. This idea led to a debate in the late 19th century on the role that gene exchange within species plays in retarding the splitting of one species into two, and eventually it led to the concept that a species is a reproductive and evolving entity. Jordan 1896 and Poulton 1903–1904 provide early articulations of what came to be the 20th-century view of species promoted by Ernst Mayr. Later, as the genetic theory of inheritance was joined with Darwin’s theory of evolution in the early 20th century, Dobzhansky 1937 lay out an accessible general portrait of how barriers to reproduction could arise and how new species emerged. Published a few years later, Mayr 1942 explicitly invokes reproduction within species (and lack thereof between) both as the fundamental aspect of what a species is and the criterion by which biologists should use to identify species. From the botanical side, Lotsy 1925 and Stebbins 1950 use the idea that species consist of reproductive communities.

Dobzhansky, T. 1937. *Genetics and the origin of species*. Columbia Biological Series 11. New York: Columbia Univ. Press.

A landmark work that enjoins the theories of genetics and evolution to describe how new species arise. Reprinted as recently as 1982.

Jordan, K. 1896. On mechanical selection and other problems. *Novitates Zoologicae* 3:426–525.

The first article to clearly focus on the evolution of reproductive barriers as the key to the formation of new species. This paper was one of Mayr’s favorites.

Lotsy, J. P. 1925. Species or linneon. *Genetica* 7.5–6: 487–506.

Another early paper that writes of species, this time from a botanical perspective, as a reproductive entity, what the author called a syngameon.

Mayr, E. 1942. *Systematics and the origin of species, from the viewpoint of a zoologist*. New York: Columbia Univ. Press.

In this classic book, Mayr states that there exist multiple species concepts, including “practical,” “morphological,” “genetic,” and “sterility.” He discusses their shortcomings and argues in favor of a “new concept” that he called the biological species definition. In later works this became known as the biological species concept. Republished as recently as 1999 (Cambridge, MA: Harvard Univ. Press).

Poulton, E. B. 1903–1904. What is a species? *Transactions of the Entomological Society of London* 51:lxxvii–cxvi.

Perhaps the first paper to describe a species as a reproductive and evolutionary unit, a kind of evolving entity. This is an idea that became commonplace in the 20th century and played a key role in the philosophy of species.

Stebbins, G. L. 1950. *Variation and evolution in plants*. Columbia Biological Series 16. New York: Columbia Univ. Press.

A classic volume on plant evolution, supporting the use of reproductive barriers as a species criterion.

The Biological Species Concept

Mayr 1942, cited under the Changing View of Species Leading Up to the Modern Synthesis, is the original source for the formally named biological species concept (BSC). After this and throughout his long life, Ernst Mayr (b. 1904–d. 2005) was a forceful advocate for the idea that species should be defined in reproductive terms. Although he altered the precise wording of the definition on several occasions, nothing that came later was inconsistent with the 1942 definition: “Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.” Importantly, Mayr saw the BSC not just as a definition of what a species is, but also the guiding idea behind species discovery and identification. In effect, Mayr saw the BSC as the answer to both the “What” question (i.e., “what is a species?”) and the “How” question (i.e., “how should species be identified”). The BSC is often cited as a guiding principle in the identification of genes that contribute to reproductive barriers between species. Coyne and Orr 2004 thoroughly covers how the BSC is useful when trying to reconstruct, from an evolutionary genetic perspective, how two species came into being. However, as an answer to “how should species be identified?,” the BSC has seen limited use. Sokal and Crovello 1970 provides a thorough critique on operational grounds, that it is generally not feasible to use the presence or absence of reproductive barriers (as articulated in the BSC) as criteria for taxonomy. Avise and Ball 1990 (cited under the BSC versus the PSC) argues that while reproductive barriers are difficult to identify, such barriers will tend to cause different genes and traits to show concordant patterns of divergence, and that it is this concordance of divergence that is the hallmark of the early stages of species formation. On the botanical side, Stebbins 1950, cited under the Changing View of Species Leading Up to the Modern Synthesis, uses the BSC extensively; however, the BSC has had a mixed following among botanists, for reasons well covered in Grant 1957. The author of Raven 1976 was quite skeptical that the BSC could be applied meaningfully and consistently across plants.

Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sunderland, MA: Sinauer.

A thorough overview on the genetics of speciation, focusing strongly on the evolutionary origins of reproductive isolation.

Grant, V. 1957. The plant species in theory and practice. In *The species problem: A symposium presented at the Atlanta meeting of the American Association for the Advancement of Science, December 28–29, 1955*. Edited by E. Mayr, 39–80. AAAS Publication 50. Washington, DC: American Association for the Advancement of Science.

A thorough discussion of the issues that arise when applying the BSC to plants, with emphasis on the many intermediate cases due to several causes, including frequent hybridization between forms and high rates of variation in degrees of outcrossing.

Raven, P. H. 1976. Systematics and plant population biology. *Systematic Botany* 1.3: 284–316.

Argues against the BSC for plants. States that it is naive to suppose that the BSC could be used to objectively identify biological units that would have some equivalence across different contexts (i.e., species in one situation means the same thing it does in another).

Sokal, R. R., and T. J. Crovello. 1970. The biological species concept: A critical evaluation. *American Naturalist* 104.936:

127–153.

A widely cited early critique of the operational features of the BSC. Some of the key criticisms are described as providing support for a phenetic view of species, in which overall similarity or distance is the relevant quantity.

The Phylogenetic Species Concept

A number of authors have drawn on the idea of an evolutionary tree in order to develop species concepts. Fægri 1937 states that species should be considered to be evolutionary lineages and that this constitutes a phylogenetic species concept. However, this idea of a lineage, which was also introduced to the discussion later in Simpson 1951, cited under the Evolutionary Species Concept, eventually became known as the evolutionary species concept. Later, the author of Rosen 1979 suggested that species should be identified on the basis of derived traits that are uniquely shared. On an evolutionary tree, the unique defining traits for a particular species can be envisioned as changes that occur on the branch leading only to that species. Within a cladistics approach to phylogeny, the ideal is to have taxonomic groups be monophyletic, such that a taxon contains all, and only, the descendants of a particular common ancestor. Donoghue 1985 argues that the criterion of monophyly should be extended to species, and the author identifies this as the phylogenetic species concept (PSC). The emphasis on monophyly, not just for more-inclusive taxa (e.g., genera, classes, etc.) but also for species, has the nice feature of putting species discovery on the same basis as the cladistics approach to the discovery of phylogenetic history. However, for sexual organisms, there is a boundary of sorts between branching phylogenetic relationships among species and the reticulate relationships between sexual organisms of the same species. Hennig 1966, a treatise that led to the founding of cladistics, discusses this feature of species at length, and it is the key point of the critique in Wheeler and Nixon 1990 on the use of monophyly for species identification. A related but distinct idea, also called the phylogenetic species concept, is that species are the smallest diagnosable groups of organisms. In this view, articulated in Nelson and Platnick 1981, Cracraft 1983, Cracraft 1989, and Nixon and Wheeler 1990, there is no criterion of monophyly but rather a criterion of diagnosis, on the basis of some unique combination of shared characters that distinguish species. Other useful papers are Baum and Donoghue 1995, which presents a different take on different kinds of phylogenetic species concepts, McKitrick and Zink 1988, which dissects the benefits and limitations of a phylogenetic species concept, and Davis and Nixon 1992, which is noteworthy for describing a method for applying a phylogenetic species concept that does not require monophyly.

Baum, D. A., and M. J. Donoghue. 1995. Choosing among alternative "phylogenetic" species concepts. *Systematic Botany* 20.4: 560–573.

A synthetic piece that finds a divide between concepts that are history based and those that are character based, and argues that one's preference depends on how one views the goal of systematics.

Cracraft, J. 1983. Species concepts and speciation analysis. *Current Ornithology* 1:159–187.

This article identifies a version of the PSC by focusing on diagnosability rather than on monophyly or shared derived characters: "a species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (p. 170).

Cracraft, J. 1989. Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In *Speciation and its consequences*. Edited by D. Otte and J. A. Endler, 28–59. Sunderland, MA: Sinauer.

Here the author provides an update to his version of the PSC: a species ". . . is an irreducible (basal) cluster of organisms, diagnosably distinct from such clusters, and within which there is a parental pattern of ancestry and descent" (pp. 34–35).

Davis, J. I., and K. C. Nixon. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. *Systematic*

***Biology* 41.4: 421–435.**

This highly cited paper describes the method of population aggregation analysis for species diagnosis under the PSC as articulated in Cracraft 1983.

Donoghue, M. J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. *The Bryologist* 88.3: 172–181.

This article presents a clear articulation of the idea that monophyly should be extended to include species and that species monophyly should be the basis of the phylogenetic species concept. However, earlier, the term “phylogenetic species concept” is used in Cracraft 1983 for a related but not-identical idea.

Fægri, K. 1937. Some fundamental problems of taxonomy and phylogenetics. *Botanical Review* 3.8: 400–423.

A prescient but largely overlooked article on species concepts in plants. Several years before Mayr 1942 (cited under the Changing View of Species Leading Up to the Modern Synthesis), Fægri made the point that biologists actually have multiple different species concepts. This also appears to be the first paper to use “phylogenetic species concept” in reference to the idea that a species is an evolutionary lineage (i.e., what would later come to be called the evolutionary species concept).

Hennig, W. 1966. *Phylogenetic systematics*. Urbana: Univ. of Illinois Press.

An English translation of a volume published in German (*Grundzüge einer Theorie der phylogenetischen Systematik*) in 1950 (Berlin: Deutscher Zentralverlag). Newer printings appeared in 1979 and 1999. Hennig argued that only shared derived traits could be used for the basis of phylogenetic reconstruction. This is the basis of a general method that came to be called “maximum parsimony,” as well as the founding principle of the field of cladistics.

McKitrick, M. C., and R. M. Zink. 1988. Species concepts in ornithology. *The Condor* 90.1: 1–14.

Discusses the PSC in Cracraft 1983, with the addition of a criterion of monophyly. A useful reference for the limitations of using a species criterion that may in application focus on traits that are relatively unimportant in speciation.

Nelson, G., and N. Platnick. 1981. *Systematics and biogeography: Cladistics and vicariance*. New York: Columbia Univ. Press.

An important book on cladistics and systematics. The authors adopt a concept under which “. . . species are simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters” (p. 12). This is quite similar to the definitions that appeared later as versions of the PSC, particularly that in Cracraft 1983.

Nixon, K. C., and Q. D. Wheeler. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6.3: 211–223.

This paper is often cited together with those of Cracraft on the PSC. They define a species as “. . . the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)” (p. 218).

Rosen, D. E. 1979. Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative biogeography. *Bulletin of the American Museum of Natural History* 162:267–376.

This lengthy monograph is widely cited for including an articulation of the idea that species identification should be made on the basis of shared derived traits, an idea that later came to be called the phylogenetic species concept in Donoghue 1985.

Wheeler, Q. D., and K. C. Nixon. 1990. Another way of *looking at* the species problem: A reply to de Queiroz and Donoghue. *Cladistics* 6.1: 77–81.

This paper provides an important critique of the use of monophyly as a species criterion.

The BSC versus the PSC

Although both the biological species concept (BSC) and the phylogenetic species concept (PSC) are consistent with evolutionary theory, as discussed in Avise and Ball 1990, there has been a great deal of debate over which concept is the better or more useful. Wheeler and Meier 2000 provides a series of articles that explicitly debate the pros and cons of the BSC as well as two versions of the PSC. Zink and McKitrick 1995 dissects the merits and problems of both concepts, with a focus on birds, and concludes in favor of the PSC. Ernst Mayr wrote many articles in support of the BSC, but probably the one that most directly pits the BSC versus the PSC is Mayr 1996. Agapow, et al. 2004 reviews how, when both the PSC and BSC are used, the PSC typically yields higher counts of species than are found using other methods.

Agapow, P.-M., O. R. P. Bininda-Emonds, K. A. Crandall, et al. 2004. The impact of species concept on biodiversity studies. *Quarterly Review of Biology* 79.2: 161–179.

As the debate between proponents of different species concepts heated up, Agapow and colleagues undertook a thorough literature review to assess the impact that using different guiding concepts had on the numbers of species reported. The main point is that phylogenetic species concepts typically return more species than does the biological species concept. The article is comprehensive, and it is a useful guide on many practical aspects of applying species concepts.

Avise, J. C., and R. M. J. Ball. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. In *Oxford surveys in evolutionary biology*. Vol. 7. Edited by D. Futuyma and J. Antonovics, 45–67. Oxford: Oxford Univ. Press.

This paper argues that the BSC and PSC each emphasize important parts of the divergence process and that some criticisms by one camp or another overlook important common connections. The paper emphasizes the role that barriers to reproduction play in creating phylogenetic concordance among genes and traits.

Mayr, E. 1996. What is a species, and what is not? *Philosophy of Science* 63.2: 262–277.

Revisits the nature of biological species and discusses the problems with a PSC, in particular its failure to articulate what a species is, in contrast to how to identify them (at which he also finds the PSC wanting).

Wheeler, Q. D., and R. Meier, eds. 2000. *Species concepts and phylogenetic theory: A debate*. New York: Columbia Univ. Press.

An edited exchange of views on different versions of the PSC and on the BSC. A useful reference for the different viewpoints, but also an example of how scientists with strong views can talk past one another.

Zink, R. M., and M. C. McKitrick. 1995. The debate over species concepts and its implications for ornithology. *The Auk* 112.3: 701–719.

A revisiting and updating of the issues addressed in their earlier paper (McKitrick and Zink 1988, cited under the Phylogenetic Species Concept), with a reasonable assessment of the pros and cons both of the PSC and the BSC. The authors conclude in favor of the PSC.

The Evolutionary Species Concept

Simpson 1951 presents a response to Ernst Mayr's articulation of the biological species concept and argues that a more basic idea of what a species is must include the time dimension. The key point was that biologists understand that at a fundamental level, species are evolutionary lineages that are evolving separately from other species. The idea was also developed to a lesser degree in Fægri 1937, cited under the Phylogenetic Species Concept. Wiley 1978 revisits the points made by George Simpson and identifies this idea as the evolutionary species concept. Mayden 1997 reviews twenty-four species concepts and finds that all are consistent with the evolutionary species concept. De Queiroz 1998 and, more recently, de Queiroz 2007 draw on the consistency that different species concepts have with the idea of species as evolutionary lineages, arguing for a general lineage concept that is based on evolutionary thinking and that can be seen to include other species concepts.

de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation: A conceptual unification and terminological recommendations. In *Endless forms: Species and speciation*. Edited by D. J. Howard and S. H. Berlocher, 57–75. New York: Oxford Univ. Press.

A modern classic that clearly shows how the discussion over species concepts tends to confuse the idea of what a species is with the criterion used for identifying species. The paper goes on to show that different species concepts are in common on the conceptual side with the evolutionary lineage concept, and that what distinguishes them is varying criteria.

de Queiroz, K. 2007. Species concepts and species delimitation. *Systematic Biology* 56.6: 879–886.

An updated overview of the thesis originally put forward in de Queiroz 1998.

Mayden, R. L. 1997. A hierarchy of species concepts: The denouement in the saga of the species problem. In *Species: The units of biodiversity*. Edited by M. F. Claridge, H. A. Dawah, and M. R. Wilson, 381–424. Systematics Association Special Volume 54. London: Chapman & Hall.

An encyclopedic review of virtually all formally named species concepts. This very useful paper also highlights the commonality that all species concepts have with the idea of species as evolutionary lineages.

Simpson, G. G. 1951. The species concept. *Evolution* 5.4: 285–298.

An interesting discussion of different species concepts, this important paper argues for a concept that includes the fundamental idea that species are evolutionary lineages.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 27.1: 17–26.

Reviews Simpson 1951 and names the evolutionary species concept.

Niche-Based Conceptions of Species

From ecology comes the idea that every species occupies a niche and that because of competitive exclusion, different species cannot occupy the identical niche. Van Valen 1976 extends this idea to questions on species and proposes that species consists of those organisms that share an ecological niche. Mayr 1982, cited under Aristotle, Taxonomy, and Essentialism, includes this idea in an update to the author's species definition under the biological species concept (BSC). For species that rarely or never exchange genes, such as with many prokaryotes, a niche-based species concept is developed in Cohan 2002, cited under the Challenge of Asexual Species. Templeton 1989 develops the cohesion species concept, which includes the ideas of genetic exchangeability (i.e., capacity for sexual reproduction) as well as demographic exchangeability. The latter occurs when members of a species share an ecological niche, and thus they are exchangeable in terms of playing the same role in the environment. In this view an asexual species may exhibit a turnover process among its members, with individual organisms replaced in the environment by descendants of others of the same species, even though they do not engage in sexual reproduction.

Templeton, A. R. 1989. The meaning of species and speciation: A genetic perspective. In *Speciation and its consequences*. Edited by D. Otte and J. A. Endler, 3–27. Sunderland, MA: Sinauer.

An important and insightful paper that outlines the cohesion species concept. As part of this idea, Templeton also articulates the idea that organisms within a species are not only genetically exchangeable, but also demographically exchangeable. The paper is noteworthy for connecting this latter, essentially ecological idea, to genetic ideas on species.

Van Valen, L. 1976. Ecological species, multispecies, and oaks. *Taxon* 25.2–3: 233–239.

The original reference for the ecological species concept.

The Challenge of Asexual Species

Prokaryotes do not engage in meiosis or sexual reproduction; however, to varying degrees a bacterium is able to take up DNA in rough proportion to how dissimilar it is from its own. Ravin 1963 uses this process as the basis of the genospecies concept, in which a prokaryote species includes those bacteria capable of incorporating one another's DNA. Rosselló-Mora and Amann 2001 reviews this and related ideas and considers how species concepts, designed primarily for eukaryotes, do not fit the world of asexual bacteria. Gevers, et al. 2005 provides a more recent review of these issues, incorporating insights from genome sequencing. Cohan 2002 argues that prokaryotes do form groups that are functional in ecological terms, and that the relevant grouping concept for many bacteria is that of ecotype, a group of bacteria that share an ecological niche and that share in selective sweeps. Doolittle and Papke 2006 argues, on the basis of genome sequence data as well as evolutionary theory, that there is no inherent tendency for evolution to give rise to distinct kinds of bacterial species.

Cohan, F. M. 2002. What are bacterial species? *Annual Review of Microbiology* 56:457–487.

This influential review argues that genome sequence data support the idea that prokaryote diversity is structured in ecological terms, and that the relevant unit for considering diversity is the ecotype. Bacterial species, defined on the basis of divergence or detection assays, typically contain multiple ecotypes.

Doolittle, W. F., and R. T. Papke. 2006. Genomics and the bacterial species problem. *Genome Biology* 7.9: article no. 116.

Reviews the discoveries on species diversity that have come with genomic data. Conclude that neither data nor theory support the necessity of bacteria forming distinct groups and that we need not assume that bacterial species exist.

Gevers, D., F. M. Cohan, J. G. Lawrence, et al. 2005. Re-evaluating prokaryotic species. *Nature Reviews Microbiology* 3.9: 733–739.

A useful review of how genome sequencing has shaped our understanding of how diversity is structured among prokaryotes, and what this means for species concepts in prokaryotes.

Ravin, A. W. 1963. Experimental approaches to the study of bacterial phylogeny. *American Naturalist* 97.896: 307–318.

This is the article that briefly names and describes the genospecies concept. A genospecies includes those bacteria whose respective genotypes permit interbacterial genetic transfer and recombination.

Rosselló-Mora, R., and R. Amann. 2001. The species concept for prokaryotes. *FEMS Microbiology Reviews* 25.1: 39–67.

Reviews the species concepts from the bacterial perspective and finds that none of the concepts proposed for eukaryotes fit bacteria very well. The authors argue for a pragmatic approach that includes information both on similarity and evolutionary history.

The Meaning of "Concept" in Species Concept Debates

Dobzhansky 1935 is the last best example of an article that addresses the biological term "species" while treating it as a single concept. In this article, and virtually all its predecessors on questions about species, species parlance assumed a single, albeit ineffable, conception. This changed with Mayr 1942, cited under the Changing View of Species Leading Up to the Modern Synthesis, with the assertion that there were in fact different species concepts being deployed by investigators who identified species in different ways. This book changed the form of debates about species, and within a few decades over twenty more species concepts had been named. Ernst Mayr envisioned the biological species concept (BSC) both as a definition of the term "species" and a criterion for species discovery. De Queiroz 1998 and de Queiroz 2007, both cited under the Evolutionary Species Concept, argue compellingly that this dual aspect of the BSC, or any species concept that claims such a dual role, muddies the waters, and that it is necessary to distinguish the conceptual component of what a species is from the criterion used to identify species. Hey 2006 reviews Mayr's changing viewpoint on this very question of concept versus criterion and argues that much of the debate over species since Mayr 1942 has suffered for failure to note this distinction.

Dobzhansky, T. 1935. A critique of the species concept in biology. *Philosophy of Science* 2.3: 344–355.

A nice review of the difficulty of having a strict species criterion given a gradual evolutionary process. The paper is also noteworthy for its reference to "species concept" in the singular, as if there is just one. This usage gradually disappeared after Mayr 1942 (cited under the Changing View of Species Leading Up to the Modern Synthesis).

Hey, J. 2006. On the failure of modern species concepts. *Trends in Ecology & Evolution* 21.8: 447–450.

This critique of the debate over multiple species concepts begins with a review of Mayr's approach to identifying multiple concepts, and Hey supports the argument that different species concepts actually share an underlying view of how species exist but differ in their criterion. The paper also critiques proposals for species pluralism.

Pluralism

With multiple, diverse species concepts championed by different biologists, one current of the debate has been over whether biologists should accept a variety of concepts, with the appropriate concept tailored to its appropriate context. Mishler and Donoghue 1982 argues for a free and pragmatic pluralism in which different systematists develop species concepts as needed. Ereshefsky 1992 advocates a much more restrictive form of pluralism. Kitcher 1984, from the philosophical side, and Rosselló-Mora 2003, from a more directly biological perspective, argue that in practice, biologists work with different concepts of species. Hull 1999 provides a powerful critique of species pluralism.

Ereshefsky, M. 1992. Eliminative pluralism. *Philosophy of Science* 59.4: 671–690.

Argues for a restrictive pluralism of species concepts based on biologically motivated concepts that meet specific criteria.

Hull, D. L. 1999. On the plurality of species: Questioning the party line. In *Species: New interdisciplinary essays*. Edited by R. A. Wilson, 23–48. Bradford Book. Cambridge, MA: MIT Press.

This important and engaging paper addresses the difficulties of a pluralistic approach to species. The main problem is that there are many ways to be pluralistic, and trying to decide which is best just recapitulates the debate at a different level.

Kitcher, P. 1984. Species. *Philosophy of Science* 51.2: 308–333.

A philosophical take on species that argues that a species is best considered as a set of organisms and that in reality, biologists work with different conceptions of what species are.

Mishler, B. D., and M. J. Donoghue. 1982. Species concepts: A case for pluralism. *Systematic Zoology* 31.4: 491–503.

Argues that different species concepts cannot be resolved with one another and that systematists need to develop species concepts on a case-by-case basis.

Rosselló-Mora, R. 2003. Opinion: The species problem, can we achieve a universal concept? *Systematic and Applied Microbiology* 26.3: 323–326.

Argues for pluralism on pragmatic grounds.

Skepticism

Skepticism toward species in various ways has often been expressed, most famously in Darwin 1859, cited under Darwin's Conception of Species, which asserts that we cannot expect to be able to objectively distinguish species from varieties. Levin 1979 reiterates this point, particularly with regard to plants. Mishler 1999 and Pleijel and Rouse 2000 suggest on cladistics grounds, but essentially for similar reasons as others, that the species rank could not be uniquely identified and should be done away with. Nelson 1989 states that the species rank is no different from other taxonomic ranks and that in this sense, species do not exist in any way that is different from how other taxa exist.

Levin, D. A. 1979. The nature of plant species. *Science* 204.4391: 381–384.

Asserts that defined plant species are far too vague in various ways to be very useful.

Mishler, B. 1999. Getting rid of species? In *Species: New interdisciplinary essays*. Edited by R. Wilson, 307–315. Bradford Book. Cambridge, MA: MIT Press.

Suggests on cladistics grounds that all taxonomic ranks, including that of species, be done away with and that taxa simply be monophyletic groups.

Nelson, G. 1989. Species and taxa: Systematics and evolution. In *Speciation and its consequences*. Edited by D. Otte and J. A.

Endler, 60–81. Sunderland, MA: Sinauer.

Argues, very much against the grain of most species discussion, that the species rank is not unique and different from other taxonomic ranks.

Pleijel, F., and G. W. Rouse. 2000. Least-inclusive taxonomic unit: A new taxonomic concept for biology. *Proceedings of the Royal Society of London B: Biological Sciences* 267.1443: 627–630.

Makes the case that the species taxonomic rank does not fit well within the larger taxonomic framework, and that it should be replaced in this context with the idea of the least-inclusive taxonomic unit.

Philosophy and the Human Component

Debates among biologists about species have some direct connections to debates among philosophers about the nature of kinds of things (sometimes called "universals"). In philosophy, the idea that a kind or category actually exists as part of the real world has been called realism. The nominalist critique of realism rejected this viewpoint and claimed that only instances of kinds (e.g., individuals or entities) could actually exist. Questions about species fit into the realism/nominalism debate because biologists identify kinds of organisms (i.e., species) and they treat species as real things. In this context, Ghiselin 1974 argues that individual species are not kinds of things but are in fact entities in themselves that are created and enjoined by evolutionary processes. Hull 1976 addresses the philosophical side of Michael Ghiselen's idea, and Ghiselin 1997 develops the thesis more fully. Hey 2001a and Hey 2001b more fully identify two conflicting motivations on the part of biologists that underlie the persistent debate about species. On the one hand, biologists identify species and treat individual species as if they are indeed typical kinds of things, just as they identify kinds in other contexts. In doing this, biologists, like all people in many contexts, are classifying on the basis of recurrent patterns in nature. However, biologists also understand from the theory of evolution that evolution gives rise to evolving populations or organisms, and that because of shared evolutionary history the individuals within a population closely resemble one another and (if they are sexual) reproduce with one another. The difficulty is that the kinds of things that are identified on the basis of similarity (i.e., as most species are identified in practice) may not correspond to actual evolving populations. Much of the debate about species can be seen as an attempt to combine these two disparate ideas, of species as kinds of organisms and species as evolving populations.

Ghiselin, M. T. 1974. A radical solution to the species problem. *Systematic Zoology* 23.4: 536–544.

A classic paper in the philosophy of species. With regard to the difficulty that species appear to be classes (i.e., categories), and the nominalist critique that classes (including species, if species are indeed classes) are not real, this paper states firmly that species are not classes but are instead individuals, with all the associated reality that comes of being an individual, just as for individual organisms.

Ghiselin, M. T. 1997. *Metaphysics and the origin of species*. SUNY Series in Philosophy and Biology. Albany: State Univ. of New York Press.

For the philosophically inclined, this is a fuller and more complete articulation of the thesis put forward in Ghiselin 1974.

Hey, J. 2001a. *Genes, categories, and species: The evolutionary and cognitive causes of the species problem*. New York: Oxford Univ. Press.

This book develops the thesis that biologists have conflicting motivations toward species. On the one hand, they tend to classify organisms and to identify new species, on the basis of patterns of similarity and differences they observe. On the other hand, they understand evolution and want to have species be the role players in evolutionary theory.

Hey, J. 2001b. The mind of the species problem. *Trends in Ecology & Evolution* 16.7: 326–329.

A short, accessible telling of some of the main points in Hey 2001a.

Hull, D. L. 1976. Are species really individuals? *Systematic Zoology* 25.2: 174–191.

This oft-cited paper reviews the philosophical criteria of the state of being an individual, concluding that most biologists have treated species as if they are classes, not individuals, but that evolutionary theory justifies their treatment as individuals.

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