Opinion TRENDS in Ecology and Evolution Vol.xxx No.x

Full text provided by www.sciencedirect.com
SCIENCE DIRECT®

On the failure of modern species concepts

Jody Hey

Department of Genetics, Rutgers University, 604 Allison Rd, Piscataway, NJ 08854–8082, USA

The modern age of species concepts began in 1942, when Ernst Mayr gave concept names to several different approaches to species identification. A long list of species concepts then followed, as well as a complex literature on their merits, motivations and uses. Some of these complexities arose as a consequence of the semantic shift that Mayr introduced, in which procedures for identifying species were elevated to concepts. Much of the debate in recent decades over concepts, and over pluralism versus monism, can be seen as an unnecessary consequence of treating species identification criteria as if they were more fundamental concepts. Recently, biologists have begun to recognize both the shortcomings of a lexicon of multiple species concepts and a common evolutionary idea that underlies them.

Ernst Mayr and the origins of the species-concept debate

Concepts are ideas that are typically neither very broad nor overly specific. In the rough hierarchy of referential scope, concepts tend to fall somewhere below theories and somewhere above definitions. Thus, we have an all-embracing theory of evolution, within which occur more modest concepts, such as the concept of fitness. A general concept can, in turn, be defined more specifically, and in different ways at different times, depending on the context. This is particularly true of concepts that, similar to fitness, are often ambiguous.

This little taxonomy of kinds of ideas does not have strict rules, and it would not deserve any particular notice were it not for a famous instance in which it was broken. The concept at the center of this event was that of species. In 1942, Ernst Mayr introduced a new use of 'concept' in regard to species by elevating several different approaches to species identification to the level of concept [1]. By delineating multiple concepts of species, Mayr helped to trigger a new age of species-problem debate, one that now includes a complex lexicon of over 20 different 'concepts' of species [2].

Mayr's book was certainly a watershed in the history of the species problem. But might the semantic shift in the usage of 'concept' with regard to species have become the source for some of the ensuing confusion in the debates on species identification? This article connects the history of the shifting usage of 'concept' to the problematic debates on pluralism and monism, and to a recent, increasingly attended line of argument in which criteria for detecting species are disentangled from a basic common concept of species.

Corresponding author: Hey, J. (hey@biology.rutgers.edu).

The history of 'concept' in regard to species

Debates over the meaning of the word 'species' were already common before Darwin, although they became even more so afterward. For example, Darwin wrote about the difficulties associated with species definitions [3]: 'Nor shall I here discuss the various definitions which have been given of the term species. No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species.'

The discovery that species evolve and give rise to new species radicalized the ages-old conundrum. Biologists of Darwin's time were familiar with taxonomic puzzles over whether one was dealing with varieties or species. But with the realization that varieties gradually become species, it seemed for many that the game was up – that species designations did not simply appear to be arbitrary, but were in fact truly arbitrary. The heightened concern over the objectivity of basic taxonomic distinctions is found in several articles that address the limitations of the concept of species. These authors were not considering various definitions of species, but whether the very idea of species was useful [4–8]. These authors' usage of 'concept of species' and 'species concept' is directed at a seemingly univocal word, a word presumed to have just one meaning. Unlike today where 'species concept' usually appears in a context of multiple competing articulations of the meaning of 'species', the 19th and early 20th century use of 'concept' had little of the modern profusion.

This once common usage is represented in Dobzhansky's *A Critique of the Species Concept in Biology* [9]. Quoting from the first lines: 'The species concept is one of the oldest and most fundamental in biology. And yet it is almost universally conceded that no satisfactory definition of what constitutes a species has ever been proposed.'

Here Dobzhansky is treating the concept of species as something larger than any particular definition of the term. In this use, there is no multiplicity of species concepts, rather just a debate about what constitutes a species.

It was Mayr's *Systematics and the Origin of Species* [1] that invoked the modern era. In chapter five, Mayr wrote of how species concepts have changed over time, of the limitations of traditional concepts, and of the need for a new species concept (Box 1). Of course, there had been previous lists of species definitions [8,10]. But previous authors addressed the multiplicity of definitions within a framework of a single concept, assuming that the different definitions were all pointing at the same inscrutable reality.

Mayr's device of elevating and multiplying the use of 'concept' with regard to species, and of attaching general

www.sciencedirect.com 0169-5347/$ – see front matter © 2006 Elsevier Ltd. All rights reserved. doi:10.1016/j.tree.2006.05.011

Box 1. Mayr's changing categorization of species concepts

Before Mayr's 1942 book, some authors had referred to different conceptions of species [53,54]. But Mayr went further in expanding the 'concept' usage by explicitly giving names to alternative perspectives on species. Furthermore, these identifiers were not authors' names. Although he described Linnaeus' idea of species, Mayr did not recognize a Linnaean species concept as others did [53,54]. Instead, he created named concepts using general descriptors including practical, morphological, genetic, sterility and biological [1]. In later publications, Mayr replaced his original categorization of five concepts with different categorizations on two separate occasions [39,55].

In 1957, Mayr acknowledged that alternative listings were possible and he identified two levels of species concepts: primary concepts, which were more theoretical and conceptual; and secondary concepts, which were more practical or applicable. Three concepts were listed as primary, namely typological, nondimensional, and multidimensional. By 'nondimensional', Mayr was referring to species in one location, and particularly to the occurrence of multiple species that remain separate when they are sympatric. By 'multidimensional', Mayr was referring to a view of species as groups of interbreeding (actually or potentially) populations. It is in the discussion of secondary concepts (also called 'species definitions') that follows, where Mayr discussed the biological species concepts and included his particular definition of a species: 'groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups' [17]. The discussion on concepts from 1957 is reiterated in nearly all its main points in the classic work *Animal Species and Evolution* [18].

Another substantial change in Mayr's taxonomy of concepts appeared later in 1969 [56]. In this paper, the two-level hierarchy of concepts from 1957 was completely gone. Instead, there were just three concepts: the typological (as before), the nominalistic (that species are just human constructs), and the biological. Importantly, the biological concept now takes the place, not just of a definition, but rather of a broad concept that includes both the nondimensional (reproductively isolated) and the multidimensional (interbreeding) concepts that were discussed in 1957 and 1963 [55].

It is these three species concepts that were presented in Mayr's history *The Growth of Biological Thought* [15]. It is also clear in 1969, as well as in 1982 and thereafter [57], that the biological species concept is a definition for Mayr, one that both says what a species is and that specifies the criteria for identifying species. The distinction that Mayr articulated in the late 1950s and early 1960s between concepts and criteria was gone by 1969 and thereafter.

descriptors to 'species concept', inspired new generations of concept inventors. After 1942, biologists were no longer limited to debating or devising definitions that had to fall under a single overarching concept of species, and it became respectable to go beyond defining 'species' and to give a definition its own name, its own 'concept' appellation. Simpson responded to Mayr and argued for a general species concept that was focused more directly on evolution than was Mayr's biological species concept [11,12]. Later Wiley identified Simpson's definition of species as the 'evolutionary species concept' [13], although Simpson himself appears to have avoided that phrase [14]. By the 1970s and into the 1980s, the list of concepts was expanding rapidly [2].

The diversity of modern species concepts

Mayr's purpose for delineating multiple species concepts was to emphasize the different kinds of methods and criteria used for species identification. Mayr's equating of species concepts with criteria for identification is clear in 1942, and especially in his writings after 1969 [15,16]. Interestingly, for several years in between, Mayr identified two levels of concepts: a primary theoretical level and a secondary level of definitions (that included the biological species concept) [17,18] (Box 1).

Although many authors embraced a multiplicity of concepts by devising and naming new concepts, not all have been as focused on criteria as was Mayr. The result is that the current long list of concepts spans a wide variety of inspirations, histories and purposes [2,19,20]. Indeed, it is now generally necessary when addressing general questions on species concepts to first attempt a classification of them on the basis of various properties [2,19,21–24]. At one extreme are concepts that are intended only to identify a particular subset of species with certain properties. At a different extreme are those concepts that clearly are intended to pertain to all species. Among these are approaches in which species are treated as kinds (i.e. categories or classes) of organisms. Mayr gave concept names to these (e.g. the practical species concept and the morphological species concept), but they are not theoretical and are not derived from genetical or evolutionary understanding. Similarly all embracing, although in a very different way, are those concepts that treat species as real entities and that summarize the fundamental nature of their existence, but that do not specifically articulate identification criteria. The evolutionary concept is one of these [2,12,24]. Then there are many concepts that span a spectrum of being partly about what a species is, or why it exists, and partly about how best to identify them (i.e. a criterion) [24].

Species pluralism: real or apparent?

An effect of the vigorous debate on species is the often-repeated claim that there can be no single species concept, and that some kind of pluralistic view of species should be adopted. Some proposals for pluralism are philosophical in nature and attempt to accommodate different metaphysical aspects of species [25,26]. More typically, proposals for pluralism are motivated by the fact that particular criteria for identifying species are not applicable in all situations and the observation that multiple concepts can give conflicting results when they are applied [27–30]. Certainly, biologists are pluralistic if we really do have different basic conceptions of species (different ideas on fundamental aspects of species existence). But, what if much of the species concept debate is actually over criteria for identifying species, and is not so much a debate over basic theoretical ideas on the causes and existence of species? If the debate were recognized as being mostly about criteria, perhaps calls for pluralism would not seem so radical or interesting.

The appeal of pluralist proposals is that they seem to offer a way out of the long-running debate over the best concept. But, in some key ways, the apparent simplicity is illusory. Even if one commits to pluralism, there are still many ways to be philosophically pluralistic about species [31,32], and it seems as if embracing pluralism can entail a slippery slope of ironic debate over which pluralism is best [33]. Related to this concern is that a seemingly simple proposal for a pluralism that retains just some of the many species concepts immediately leads to the difficult question of which specific concepts are valid enough to retain [33]. In short, species-concept pluralism can be seductive, but it might not actually help to settle anything.

Returning to a common concept of species

One piece of evidence suggesting that we do share a common concept of species is that biologists discuss species regularly without explicit reference to species concepts, and that disagreement over 'species' does not necessarily arise unless a discussant explicitly brings up the subject of species concepts. In this literal linguistic sense, we appear to share a species concept [34,35]. Perhaps more to the point: are there any participants in species debates who actually think that species do not arise by evolution, or who disagree with the general idea that organisms within a species share an evolutionary history with each other more so than they do with organisms in other species? If not, then it is fair to say that biologists do indeed share some basic ideas about species and that we are not species pluralists with regard to some fundamentals. These notions are far from being useful criteria for identification, and thus might be taken for granted, but they are not trivial.

In recent years, there has grown a thread of argument that claims that many of our species concepts share underlying ideas on the nature of species [2,14,24,36–38]. More specifically, the case has been made that many species concepts state or imply something close to Simpson's articulation of an evolutionary species [12]. Mayden's [2] review of species concepts concluded that Simpson's general definition of species is consistent with the other concepts and that, unlike the others, it is not operational (i.e. not about criteria). Much the same point was made by Miller [38]. Similarly, de Queiroz [24] reviewed species concepts and concluded that the differences among them did not reflect differences in an underlying conception of species. Rather, the differences tend to involve those features that are most explicitly operational, what de Queiroz identifies as 'contingent properties' that are shared by many (but not all) species [39]. Thus, for example, reproductive isolation [1], systems of shared mate or gamete recognition [40], and monophyly [41] are all treated as necessary properties of species by particular species concepts. However, under a more basic view of species, each of these can be viewed as not necessary, but rather contingent upon history and circumstances. The underlying concept, which de Queiroz calls the 'general lineage concept' (as in Mayden's interpretation), is essentially Simpson's concept of species. A similar conclusion, albeit from a different approach, is that we share a common conception of species as evolutionary groups [37]. Members of an evolutionary group share an evolutionary history as well as sharing in processes of genetic drift and adaptation. In effect, an evolutionary group is the contemporaneous tip of an evolutionary lineage. None of these ideas were proposed as new species concepts, but rather as articulations of a common conception of species that is widely shared, including by those who actively debate the profusion of more narrow criterion-based 'concepts'.

Other evidence that biologists are stepping back from the debate over multiple concepts comes from papers that address species identification and delineation, but do so while avoiding discussion of the multiple species concepts. For example, some recent surveys of methods for identifying species boundaries avoid particular species concepts [42,43]. de Queiroz's point that a common concept of species can be seen when we set aside questions on operational criteria has also been accepted in several recent papers on species delineation and on the nature of species [44–47].

Lessons on the method of multiple concepts

Perhaps the long-running debate over the best species concept is dying. If so, it comes without the oft-hoped for widespread recognition of a common protocol for species identifications. In this light, it is useful to appreciate that some of our most persistent questions on how best to identify species were present long before Mayr's book, and that the fundamental form of those questions has not changed greatly. There were different species definitions in discussion and use before the publication of Darwin's book in 1859, as well as between 1859 and 1942 [8,10]; they were not called 'concepts', but otherwise the debates are familiar. For example, Mayr's elevation of protocols and criteria to the level of concepts did little to alleviate a long-standing tension between the use of shared organismal traits to identify species versus the use of shared reproduction. The modern version of this debate lies between various versions of the phylogenetic species concept and Mayr's biological species concept [48]. But the debate over whether shared traits or shared reproduction form the ideal basis for species identification was going on before 1942 and indeed before Darwin [49], with at least some biologists of earlier times recognizing the general inadequacy of all existing definitions of either stripe. For example, Nicholson [10] states: 'On a closer examination, however, it will be found that these two leading ideas in the definition of species – external resemblance and community of descent – are both defective and liable to break down if rigidly applied.' In this passage, Nicholson appears to have recognized a fundamental failing of criterion-based definitions of 'species', which is that species definitions cannot solve the difficulty of species identification. Definitions cannot be forced to serve the arbitration of entities that are truly ambiguous. The fact is that species are hard to identify for a variety of reasons related to the various ways that they can be truly indistinct [50–52], and no criterion that presumes to delineate natural boundaries can overcome this. It seems possible that this lesson is beginning to sink in. Perhaps our fifty-plus years of argument over multiple species concepts has been a necessary prerequisite for this realization.

As scientists we should not confuse our criteria for detecting species with our theoretical understanding of the way species exist [24]. Detection protocols are not concepts. This point would be child's play if we were talking about electrons or disease agents, but because real species are so difficult to study, and because our best understanding of them includes their often being truly indistinct, we have had trouble separating the detection criteria from our more basic ideas on the existence of species.

Acknowledgements

I thank J. Wilkins, M. P. Winsor, R. Harrison, J. Mallet and K. de Queiroz, as well as A. Templeton and two anonymous reviewers for helpful comments and critique.

References

1 Mayr, E. (1942) *Systematics and the Origin of Species,* Columbia University Press
2 Mayden, R.L. (1997) A hierarchy of species concepts: the denouement in the saga of the species problem, In *Species: The Units of Biodiversity* (Claridge, M.F. et al. eds), pp. 381–424, Chapman & Hall
3 Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection,* Murray
4 Bailey, L.H. (1896) The philosophy of species-making. *Bot. Gaz.* 22, 454–462
5 Farlow, W.G. (1898) The conception of species as affected by recent investigations on fungi. *Am. Nat.* 32, 675–696
6 Trelease, W. (1900) Some twentieth century problems. *Science* 12, 48–62
7 Bessey, C.E. (1908) The taxonomic aspect of the species question. *Am. Nat.* 42, 218–224
8 Britton, N.L. (1908) The taxonomic aspect of the species question. *Am. Nat.* 42, 225–242
9 Dobzhansky, T. (1935) A critique of the species concept in biology. *Philos. Sci.* 2, 344–355
10 Nicholson, H.A. (1872) *A Manual of Zoology,* Appleton & Company
11 Simpson, G.G. (1951) The species concept. *Evolution* 5, 285–298
12 Simpson, G.G. (1961) *Principles of Animal Taxonomy,* Columbia University Press
13 Wiley, E.O. (1978) The evolutionary species concept reconsidered. *Syst. Zool.* 27, 17–26
14 de Queiroz, K. (1999) The general lineage concept of species and the defining properties of the species category, In *Species* (Wilson, R.A., ed.), pp. 49–89, MIT Press
15 Mayr, E. (1982) *The Growth of Biological Thought,* Harvard University Press
16 Mayr, E. (2000) The biological species concept, In *Species Concepts and Phylogenetic Theory: A Debate* (Wheeler, Q.D. and Meier, R., eds), pp. 16–29, Columbia University Press
17 Mayr, E. (1957) Species concepts and definitions, In *The Species Problem* (Mayr, E., ed.), pp. 1–22, American Association for the Advancement of Science
18 Mayr, E. (1963) *Animal Species and Evolution,* Belknap Press of Harvard University Press
19 Endler, J.A. (1989) Conceptual and other problems in speciation, In *Speciation and its Consequences* (Otte, D. and Endler, J.A., eds), pp. 625–648, Sinauer Associates
20 Hull, D.L. (1997) The ideal species concept – and why we cannot get it, In *Species: The Units of Biodiversity* (Claridge, M.F. et al. eds), pp. 357–380, Chapman & Hall
21 Baum, D.A. and Donoghue, M.J. (1995) Choosing among alternative 'phylogenetic' species concepts. *Syst. Bot.* 20, 560–573
22 Pigliucci, M. (2003) Species as family resemblance concepts: the (dis-)solution of the species problem? *BioEssays* 25, 596–602
23 Harrison, R.G. (1998) Linking evolutionary pattern and process: the relevance of species concepts for the study of speciation, In *Endless Forms: Species and Speciation* (Howard, D.J. and Berlocher, S.H., eds), pp. 19–31, Oxford University Press
24 de Queiroz, K. (1998) The general lineage concept of species: species criteria and the process of speciation, In *Endless Forms: Species and Speciation* (Howard, D.J. and Berlocher, S.H., eds), pp. 57–75, Oxford University Press
25 Kitcher, P. (1984) *Species. Philos. Sci.* 51, 308–333
26 Dupré, J. (1993) *The Disorder of Things: Metaphysical Foundations of the Disunity of Science,* Harvard University Press
27 Dupré, J. (1999) On the impossibility of a monistic account of species, In *Species* (Wilson, R.A., ed.), pp. 3–22, MIT Press
28 Mishler, B.D. and Donoghue, M.J. (1982) Species concepts: a case for pluralism. *Syst. Zool.* 31, 491–503
29 Ereshefsky, M. (1992) Eliminative pluralism. *Philos. Sci.* 59, 671–690
30 Rossello-Mora, R. (2003) Opinion: The species problem, can we achieve a universal concept? *Syst. Appl. Microbiol.* 26, 323–326
31 Reydon, T.A.C. (2004) Why does the species problem still persist? *BioEssays* 26, 300–305
32 Ereshefskey, M., ed. (1992) *The Units of Evolution: Essays on the Nature of Species*, MIT Press
33 Hull, D.L. (1999) On the plurality of species: questioning the party line, In *Species* (Wilson, R.A., ed.), pp. 23–48, MIT Press
34 Brigandt, I. (2003) Species pluralism does not imply species eliminativism. *Philos. Sci.* 70, 1305–1316
35 Hey, J. (2001) The mind of the species problem. *Trends Ecol. Evol.* 16, 326–329
36 Avise, J.C. and Wollenberg, K. (1997) Phylogenetics and the origin of species. *Proc. Natl. Acad. Sci. U.S.A.* 94, 7748–7755
37 Hey, J. (2001) *Genes Categories and Species,* Oxford University Press
38 Miller, W. (2001) The structure of species, outcomes of speciation and the 'species problem': ideas for paleobiology. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 176, 1–10
39 de Queiroz, K. (2005) Ernst Mayr and the modern concept of species. *Proc. Natl. Acad. Sci. U.S.A.* 102 (Suppl. 1), 6600–6607
40 Paterson, H.E.H. (1985) The recognition species concept, In *Species and Speciation* (Vrba, E.S., ed.), pp. 21–29, Transvaal Museum
41 Rosen, D.E. (1979) Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative biogeography. *Bull. Am. Mus. Nat. Hist.* 162, 267–376
42 Sites, J.W. and Marshall, J.C. (2003) Delimiting species: a Renaissance issue in systematic biology. *Trends Ecol. Evol.* 18, 462–470
43 Winston, J. (1999) *Describing Species,* Columbia University Press
44 Sites, J.W. and Marshall, J.C. (2004) Operational criteria for delimiting species. *Annu. Rev. Ecol. Evol. Syst.* 35, 199–227
45 Wiens, J.J. and Servedio, M.R. (2000) Species delimitation in systematics: inferring diagnostic differences between species. *Proc. R. Soc. B* 267, 631–636
46 Cohan, F.M. (2002) What are bacterial species? *Annu. Rev. Microbiol.* 56, 457–487
47 Fraser, D.J. and Bernatchez, L. (2001) Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Mol. Ecol.* 10, 2741–2752
48 Wheeler, Q.D. and Meier, R., eds) (2000) *Species Concepts and Phylogenetic Theory: A Debate*, Columbia University Press
49 Grant, V. (1994) Evolution of the species concept. *Biol. Zentbl.* 113, 401–415
50 Hey, J. *et al.* (2003) Understanding and confronting species uncertainty in biology and conservation. *Trends Ecol. Evol.* 18, 597–603
51 O'Hara, R.J. (1994) Evolutionary history and the species problem. *Am. Zool.* 34, 12–22
52 de Queiroz, K. (2005) Different species problems and their resolution. *BioEssays* 27, 1263–1269
53 Clausen, J. *et al.* (1939) The concept of species based on experiment. *Am. J. Bot.* 26, 103–106
[54] Poulton, E.B. (1904) What is a species? *Proc. Entomol. Soc. Lond.* 1903. lxxvii–cxvi.
55 Beurton, P.J. (2002) Ernst Mayr through time on the biological species concept – a conceptual analysis. *Theory Biosci.* 121, 81–98
56 Mayr, E. (1969) The biological meaning of species. *Biol. J. Linn. Soc.* 1, 311–320
57 Mayr, E. (1996) What is a species and what is not? *Philos. Sci.* 63, 262–277