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The species problem

THE SPECIES IDEA

Species are kinds of living things. This way of thinking about life seems to go back at least to Plato and Aristotle, who used the term *eidos* that meant in one sense, the appearance or form of a thing. For the naturalists who came after, species were also the relatively distinct groupings of individual organisms that were more or less similar in appearance and behavior, and that sometimes interbred. Since the development of a hierarchical taxonomy by Linnaeus in the eighteenth century, those organisms that had been grouped into species taxa were then grouped into more inclusive categories – genera, orders, classes, and ultimately kingdoms. Because species are the most basic groupings of organisms in this hierarchy, they are now usually regarded as the fundamental units of biodiversity. But for contemporary biologists steeped in evolutionary theory, species are much more. Darwinian evolution tells us that species are the things that are "born" in speciation from other species, change over time, produce new species, and ultimately "die" in extinction. Species are therefore also the fundamental units of evolution.

The idea of species has played a similarly significant role in philosophy. Philosophers have followed the tradition of Plato and Aristotle, as they understand it, and have treated those groups of organisms we identify as species as *natural kinds* with *essences*. In doing so, they have treated biological species as equivalent to chemical elements such as hydrogen and oxygen, and molecular kinds, such as water, that are made up of these elements. Biological species have in this way fit into a philosophical way of thinking known as *metaphysics*, which studies the basic, fundamental things and processes that exist. On this traditional essentialist approach, biological species, like hydrogen, oxygen and water, are the fundamental and eternal kinds of things we find in nature. And when we divide nature into species, elements and molecular kinds, we are, in the oft-paraphrased words of Plato, "cutting nature at its joints." But Darwinian evolution has seemed by many to challenge this idea that species are natural kinds with essences. Most obviously, evolution implies that species can no longer be regarded as eternal and unchanging. If so, then how do *species* fit into our philosophical understanding of the world?

The philosophical significance of this idea of *species* extends into our understanding of human nature. In the essentialist tradition, humans have a nature because they belong to the species-kind *human*. In more modern terms, humans are the way they are by virtue of being members of the species *Homo sapiens*. The idea of human nature is therefore dependent on our ideas of what it means to be a member of a species. In the past this might have meant an understanding based on the essence of being human. But with the Darwinian challenge to this traditional picture, we also get a challenge to traditional ways of thinking about human nature. If evolution forces us to rethink the nature of species, perhaps we must also rethink the nature of human nature.

SPECIES GROUPINGS

The biological and philosophical significance we place on this idea of species is particularly striking given the difficulties we have in consistently placing organisms into species in *microtaxonomy*. Here, the main tasks are first, dividing and grouping of organisms into species; second, providing criteria for species membership. On both tasks there is substantial and pervasive disagreement among biological systematists. Given any single group of individual organisms, systematists will often disagree about the number of species represented and the criteria used in making that determination. Some of these disparities in counts are highly striking. Counts of lichen species worldwide, for instance, range from around 13,000 to 30,000 (Purvis 1997: 111). Researchers have also counted from one to ten species in the fish genus *Metriaclima*, 101 to 240 species in Mexican birds, and 9000 versus 20,000 bird species worldwide. Jody Hey cites three reasons for these disparities in species counts: count creep, lumper/splitter tendencies, and the use of different species definitions:

> Consider the case of *Metriaclima*, a genus of 10 species of fish in Lake Malawi, Africa, that was devised to replace a single species

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> *Pseudotropheus zebra*, on the basis of additional collections … The first revision was a case of count creep, pure and simple – a closer look with more samples begat more species. But then another look, by others who were using the very same data … led to the conclusion that the new genus actually contains only two species … Nor are lumper/splitter debates limited to obscure organisms that are difficult to collect. Consider birds, which are probably the most observationally accessible animals on the planet … Conventional classifications place the number of species worldwide at around 9,000. But some ornithologists feel that the correct count, based on a proper reevaluation of all existing collections, would end up being closer to 20,000 … In fact, a count of endemic Mexican bird species went so far as to employ two different definitions of species; one returned a count of 101 species while the other returned a count of 249 species. (Hey 2001: 20)

Disparities due to count creep result from the fact that, when we look at more specimens, we simply see more differences and tend to postulate more species. Disparities due to lumper/splitter tendencies are a consequence of the subjective tendencies of individual researchers: some systematists are simply more prone to split groups of organisms into more species taxa than are other systematists.

But often disagreements about species counts are due to the fact that different researchers use different ways of defining and conceiving species. One researcher might, for instance, use morphological or genetic similarity to group into species, while another might use interbreeding, and yet another might appeal to history or phylogeny. In other words, one person might use a species concept based on morphological or genetic similarity, while another might use a concept based on interbreeding or phylogeny. The differences in species counts due to the use of different concepts are often striking. The turn to a *phylogenetic species concept*, for instance, has multiplied fifteen amphibian species into 140 (MacLauren and Sterelney 2008: 28). A recent survey of taxonomic research quantifies the effects of a shift to this particular species concept from other concepts, finding a 300% increase in fungus species, a 259% increase in lichen species, a 146% increase in plant species, a 137% increase among reptile species, an 88% increase among bird species, an 87% increase among mammals, and a 77% increase among arthropods. Running counter to this trend, however, there was a 50% decrease in mollusc species (Agapow et al. 2004:168). Overall, there was an increase of 48.7% when a *phylogenetic species concept* replaced other concepts. (Agapow et al. 2004:164).

THE SPECIES PROBLEM

This use of different species concepts is more troubling than the other sources of disparity in species counts. Count creep and lumper/splitter differences are surely significant problems in the analysis of biodiversity, but they do not challenge two basic assumptions behind the view that species are the fundamental units of biodiversity and evolution: first, species are real; second, there is a single kind of species thing. If species really exist and there is some single kind of species thing, then we can potentially resolve the disagreements that arise from both the observation of new specimens and different tendencies to split or group. We can in principle, for instance, identify what makes a new specimen a genuine instance of a new species, whether through genetic analysis, observation of interbreeding or some other criterion. And we can establish that some researchers, whether splitter or lumper, really are getting the classification more right than others, by reference to whatever factors are important, be they morphological, genetic, or reproductive. But if the differences in grouping are due to the use of conflicting species concepts, then it is hard to see how we can come to agree on species groupings just on the basis of more information about biodiversity and evolution. If we are using different species concepts and criteria for what counts as a species, new information is unlikely to result in agreement because we disagree about what is even relevant! Someone who uses a reproductive criterion will not treat newly discovered similarities and differences as relevant, whereas they will be relevant to someone who uses a morphological concept.

What has happened recently reinforces this pessimism. The more we learn about biodiversity and all its complexity, the worse the problem seems to become. Instead of resolving differences in the use of species concepts, new information seems to have resulted in the multiplication of species concepts. On at least one count, there are now over twenty species concepts in circulation based on morphological or genotypic similarity, mate recognition systems, ecological niche, phylogenetic history and more (Mayden 1997). This may come as a surprise to those of us who learned the *biological species concept* in our introductory biology classes, that species are groups of interbreeding or potentially interbreeding organisms. It takes only a moment to realize, however, that this concept applies only to sexually reproducing organisms and we would need at least one other species concept for the many asexual organisms we find throughout the plant and animal kingdoms. The biological species concept is clearly inadequate if we are looking at asexually reproducing organisms.

As this limitation of the biological species concept suggests, sometimes the choice of species concept seems to depend on little more than which organisms one studies. Joel Cracraft explains:

> There has been something of a historical relationship between an adopted species concept and the taxonomic group being studied … Thus, for many decades now, ornithologists, mammalogists, and specialists from a few other disciplines have generally adopted a Biological Species Concept; most invertebrate zoologists, on the other hand, including the vast majority of systematists, have largely been indifferent to the Biological Species Concept in their day-to-day work and instead have tended to apply species status to patterns of discrete variation. Botanists have been somewhere in the middle, although most have not used a Biological Species Concept. (Cracraft 2000: 4–5)

But even among those who study the same organisms, there is disagreement about which species concept is best. Those who are committed to a method of taxonomy known as "cladistics" tend to use different concepts than those who have adopted the more traditional "evolutionary systematics." And even those who regard themselves as cladists find little agreement. In a recent volume, five different cladistic species concepts were proposed and developed, seemingly without any resolution (Wheeler and Meier 2000).

The bottom line is that there is pervasive disagreement about the nature of species; and this has led to disagreement about how we should divide and group organisms into species. Additional observation and research offers little promise. The more we learn the worse the conflict seems to become. This then is *the species problem*: there are multiple, inconsistent ways to divide biodiversity into species on the basis of multiple, conflicting species concepts, without any obvious way of resolving the conflict. No single species concept seems adequate.

SIGNIFICANCE OF THE SPECIES PROBLEM

While the problem seems to be getting worse, worries about it are not new. In 1957, Ernst Mayr was already lamenting its persistence:

> Few biological problems have remained as consistently challenging through the past two centuries as the species problem. Time after time

> attempts were made to cut the Gordian knot and declare the species problem solved either by asserting dogmatically that species did not exist or by defining, equally dogmatically, the precise characteristics of species. Alas, these pseudosolutions were obviously unsatisfactory. One might ask: "Why not simply ignore the species problem?" This also has been tried, but the consequences were confusion and chaos. The species is a biological phenomenon that cannot be ignored. Whatever else the species might be, there is no question that it is one of the primary levels of integration in the many branches of biology, as in systematics (including that of microorganisms), genetics, and ecology, but also in physiology and in the study of behavior. Every living organism is a member of a species, and the attributes of these organisms can often best be interpreted in terms of this relationship (Mayr 1957a: iii).

As suggested here, part of the significance of the species problem is its implications for biological practice and theory. Biologists today see similar significance. Joel Cracraft acknowledges the species problem, then explains its significance to theory and practice:

> The primary reason for being concerned about species definitions is that they frequently lead us to divide nature in very different ways. If we accept the assumption of most systematists and evolutionists that species are real things in nature, and if the sets of species specified by different concepts do not overlap, then it is reasonable to conclude that real entities of the world are being confused. It becomes a fundamental scientific issue when one cannot even count the basic units of biological diversity. Individuating nature "correctly" is central to comparative biology and to teasing apart pattern and process, cause and effect. Thus, time-honored questions in evolutionary biology – from describing patterns of geographic variation and modes of speciation, to mapping character states or ecological change through time, to biogeographic analysis and the genetics of speciation, or to virtually any comparison one might make – will depend for their answer on how a biologist looks at species (Cracraft 2000: 6).

If Mayr and Cracraft are right, there is much at stake here for those who work in the biological sciences. Work in multiple areas depends on how species are grouped, and the principles used for grouping. The species problem still looms large in evolutionary biology.

There is practical significance as well. Many problems are generated by our inability to group organisms unambiguously into species. First and most obviously, the application of endangered species legislation seems to presuppose our ability to group organisms into species on the basis of a satisfactory grouping principle and species concept. Claridge, Dawah and Wilson recognize this in their introduction to a recent collection of articles on species:

> The prolonged wrangle among scientists and philosophers over the nature of species has recently taken on added and wider significance. The belated recognition of the importance of biological diversity to the survival of mankind and the sustainable use of our natural resources makes it a matter of very general and urgent concern. Species are normally the units of biodiversity and conservation … so it is important that we should know what we mean by them. One major concern has been with estimating the total number of species of living organisms that currently inhabit the earth … In addition, many authors have attempted to determine the relative contributions of different groups of organisms to the totality of living biodiversity … Unless we have some agreed criteria for species such discussions are of only limited value (Claridge, Dawah and Wilson 1997: 2).

The pessimism of these biologists is reinforced by the conflicting accounts of species we get in one official interpretation of the *Endangered Species Act* of 1973 (ESA) sponsored by the US Department of Interior and published by the National Academy of Science. Michael Clegg, the Chair of the *Committee on Scientific Issues in the Endangered Species Act*, tells us in the introduction that "Species are objective entities that are easily recognized. Their health and needs can be assessed and sound scientific management plans can be implemented" (National Research Council 1995: ix). We then learn that the *Endangered Species Act* seems to assume some version of the *biological species concept*.

> Species of organisms are fundamental objects of attention in all societies, and different cultures have extensive literature on the history of species concepts. The Endangered Species Act defines species to include "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." In the act, the term *species* is used in a legal sense to refer to any of these entities. In addressing its use in the ESA, one must remember, however, that species has vernacular, legal and biological meanings (National Research Council 1995: 5).

But it should be obvious that this way of conceiving species is highly problematic. First, and paradoxically, *species* now get understood in terms of *subspecies* – which is itself not obviously definable except relative to *species*. Second, the assumption of interbreeding seems to rule out non-sexually reproducing organisms. Third, not only must we worry about biological species concepts, but also the vernacular and legal concepts. Species concepts continue to multiply now on the basis of how non-biologists in different cultures think – and how legal scholars think! In spite of these further complications, Clegg remains optimistic:

> Many societies have notions of kinds of organisms, usually organisms that are large and conspicuous or of economic importance. The term *species* can be applied to many of these kinds and can be accurate as a scientific and vernacular term, because the characteristics used to differentiate species can be the same in both cases. Largely for this reason, the question of what a species is has not been a major source of controversy in the implementation of the Endangered Species Act (National Research Council 1995: 5).

But then he goes on to recognize the difficulties in identifying subspecies – which count as species in the assumed definition above:

> Greater difficulties have arisen in deciding about populations or groups of organisms that are genetically, morphologically, or behaviorally distinct, but not distinct enough to merit the rank of species – i.e., subspecies, varieties, and distinct population segments (National Research Council 1995: 5).

Notice also that the interbreeding criterion of the species definition does not appear in this passage. Rather, it appeals to morphological, genetic and behavior distinctness. It is difficult to make sense of this account of species given what the report later has to say about the history of species concepts:

> [B]iologists with different perspectives and problems in mind have different ideas about what a species is and what role it should play in particular areas of science. Some systematic biologists have declared that there is no single unit that can be called species, and, for example, that the concept of species used in classifying mosses might be quite different from that used for classifying species of birds with respect to population and genetic structure (National Research Council 1995: 51).

The authors then ask: "Why should the term *species* be so problematic? Why, after centuries of investigations, are systematic biologists unable to simply and easily tell us which groups of organisms are species and which are not?" (National Research Council 1995: 51–52). While the authors then give an answer – "speciation is a gradual process" – it should be obvious that there is more to a satisfactory answer. As already acknowledged, different species concepts are in use. Given all these complications, Clegg's optimism that "species are objective entities that are easily recognized" seems hardly warranted. As important as it may be to preserve biodiversity, doing so is clearly more complicated than Clegg acknowledges.

In actual application of the Endangered Species Act we find just the sorts of complications we might expect. On a morphological species concept, or one involving geographic isolation, we might classify the red wolf of the southeastern US as a separate species from the wolves of eastern Canada. But on other criteria, such as potential interbreeding, we might classify them together, as is implied by science journalist Carl Zimmer in a recent article in *Scientific American*:

> Wolves in the southeastern U.S. are considered a separate species, the red wolf (*Canis rufus*). This wolf has been the subject of an enormous project to save it from extinction, with a captive breeding effort and a program to reintroduce it to the wild. But the Canadian scientists argue that the red wolf is really just an isolated southern population of *C. lycaon*. If that is true, then the government has not in fact been saving species from extinction. Thousands of animals belonging to the same species are still thriving in Canada (Zimmer 2008: 73).

To complicate things further, it appears that coyotes have in fact successfully interbred with *C. lycaon*, and both groups contain DNA of the other group. On an interbreeding concept, both groups of wolves are members of a species also containing coyotes (Zimmer 2008: 72).

The differences in species counts and application of endangered species concepts have real consequences beyond the preservation of biodiversity. The turn to the *phylogenetic species concept* that multiplied species counts so dramatically, also has a cost. The authors of the survey quoted above have estimated the cost of the proliferation of species taxa, based on the fact that increased species counts will reduce the geographic range of species, that will then make more species protected.

> Any increase in the number of endangered species requires a corresponding increase in resources and money devoted toward conserving those species. For example, it has been estimated that the complete recovery of any of the species listed by the U.S. Endangered Species Act will require about $2.76 million … Thus, recovering all species listed currently would cost around $4.6 billion. With widespread adoption of the PSC [*phylogenetic species concept*], this already formidable amount could increase to $7.6 billion, or the entire annual budget for the administering agency (U.S. Fisheries and Wildlife Services) for the next 120 years (Agapow *et al*. 2004: 169).

And as these authors then indicate, this estimate of an additional $3 billion in cost might well be conservative.

There are other practical reasons to worry about our ways of grouping organisms into species. We might, for instance, worry about the preservation of biodiversity independent of any legislative demands. Measurements of biodiversity often employ the concept of *species richness* to measure biodiversity (MacLauren and Sterelny 2008: 3). Species richness is straightforwardly dependent on species counts (higher species counts means greater species richness), so if our species counts are problematic so will be our assessments of biodiversity. The management of food sources and natural resources also often requires we know something about particular species as Joel Cracraft argues:

> The importance of species concepts is not restricted to the seemingly arcane world of systematics and evolutionary biology. They are central to solving real-world practical problems that affect people's lives and well-being. … Consider, for example, cases in which species concepts might have important consequences: (1) a group of nematodes that attack crops, or act as vectors for plant viruses, where failure to individuate species correctly might mean that food supplies are at risk. … (2) a group of exotic beetles that attack timber resources, where failure to individuate species correctly might mean that their place of origin could be misidentified and thus potential biological control agents overlooked (Cracraft 2000: 6–7).

Similarly, human disease vectors may well be associated with particular species (Cracraft 2000: 7). It is well known, for instance, that malaria infects humans by contact with just a few of the species of mosquito in the genus *Anopheles*. Other species do not present a risk. If so, we may need to get our species grouping right to prevent the spread of this disease. There are many other instances where species determinations have similar practical import, but the main message here should already be clear: There is a lot at stake in getting our species groupings right and that depends on getting our species concepts right.

REALISM AND PLURALISM

Lurking behind the species problem are two philosophical worries. On the first *realism* worry, we might – given the proliferation of species concepts – doubt that species are real things in nature. Cracraft expresses this worry.