

Revisiting the conceptual basis of species

Marc Ereshefsky

What is the proper definition of ‘species’? Biologists widely disagree on the answer. Hey (2001) writes that there are twenty-four definitions of ‘species’ in contemporary biology. Whether that number is correct or not is not important. What is important and cannot be denied is that there is widespread disagreement among biologists concerning what constitutes a species. This problem, the species problem, is far from new. It was present in Darwin’s time. We will turn to Darwin’s approach to the species problem shortly. But first let us explore the nature of that problem in contemporary biology.

The standard approach to the species problem suggests that though we have not yet found the correct definition of ‘species,’ we should keep trying and in due course, we will discover that definition. A different approach, the one offered here, suggests that after hundreds of years of failing to find the correct definition of ‘species,’ we have good reason to think there is no species category in nature. That is, extensive empirical investigations and biological theorizing have shown that there is no single correct theory of species waiting to be discovered. To demonstrate why this is a reasonable approach to the species problem, consider the current debate over ‘species.’

There are at least a dozen general species concepts – concepts whose proponents argue are concepts that apply to all of life. Prominent general species concepts fall into three major groups. There is the Biological Species Concept (Mayr 1970) and related interbreeding concepts. There is the Ecological Species Concept (van Valen 1976) and related ecological concepts. And then there are a variety of Phylogenetic Species Concepts (Baum and Donoghue 1995), which all assume that species are a type of monophyletic lineage. The important thing to notice about this variety of general species concepts is that they pick out different types of lineages in the world. The Biological Species Concept picks out groups of interbreeding organisms, the Ecological Concept identifies lineages of organisms that occupy the same niches, and the Phylogenetic Concepts focus on basal monophyletic lineages. Furthermore, what constitutes a species

on one concept may not be a species according to another concept. Asexual organisms do not form species according to the Biological Species Concept, but they do form species using the Ecological and Phylogenetic Concepts. Similarly, some taxa recognized by the Biological Species Concept are not species according to the Phylogenetic Concepts because those taxa are paraphyletic (de Queiroz and Donoghue 1988.). The point thus far is that the different general species concepts (Biological, Phylogenetic, and Ecological) pick out different types of lineages.

A similar phenomenon occurs among the species concepts used by protistologists. Traditionally the Morphological Species Concept has been the concept of choice for identifying protist species (Alverson 2008). However, in the last twenty years phylogenetic approaches using molecular data have become the preferred method (Finlay 2004, 600). In addition to these two approaches are applications of the Biological Species Concept (Vanormelingen et al. 2008) and Cohan's (2002) Ecological Species Concept. As with the general species concepts, protist species concepts pick out different types of lineages. Many, perhaps most, protists spend much of their lives as asexual organisms. So many protist lineages are not species according to the Biological Species Concepts. Nevertheless, those lineages constitute species on either the Morphological, Phylogenetic, or Ecological Concepts. The Phylogenetic and Ecological Species Concepts recognize protist species that the Biological Species Concept misses. Furthermore, there are disagreements among the Morphological, Phylogenetic, and Ecological Concepts concerning which lineages constitute species. Phylogenetic classifications based on such house-keeping genes as 16S rRNA miss ecologically distinct groups of organisms (Finlay 2004). And morphological analyses often miss ecologically identified species of green algae (Nanney 1999).

Stepping back from these details, we see that protist species concepts pick out different types of lineages of organisms. Some lineages are organisms that form interbreeding populations. Other lineages consist of organisms that share and exploit common ecological zones. Still others are monophyletic lineages based on molecular or morphological data. Does the diversity of types of lineages picked out by different species concepts show that we have not yet found the right definition of ‘species’ but nevertheless we should keep trying? As suggested above, a different conclusion can be

drawn. The organic world consists of different types of lineages that we happen to call ‘species.’ Those lineages are equally real and biologically important. The problem is not that we have so far failed to find the correct definition of ‘species.’ The problem is that in that search we have found that there are many different types of basal lineages in the world. What we thought was one type of taxon, species, is actually a multitude of different types of taxa.

How should these considerations affect our continuing search for the correct definition of ‘species’? Before answering that question let us introduce an important distinction – the distinction between the species category and species taxa. Species taxa are individual species, such as *Homo sapiens* and *Canis familiaris*. The species category is a more inclusive entity. It is the category that contains all species taxa. The existence of different types of lineages called ‘species’ (interbreeding, phylogenetic, and ecological lineages) should cause us to doubt the existence of the species category in nature. Why? If a putative scientific category is thought to exist in nature, independent of us, then it should satisfy certain criteria (Ereshefsky 2010). For example, there should be some feature that most entities in that category share. Furthermore, that feature should distinguish the entities in that category from entities in other categories. Returning to the different types of lineages highlighted by protist species concepts: is there some biological feature that most of the lineages called ‘species’ share that generally distinguishes them from genera and varieties? Consider some candidate features. Are most protist species interbreeding species? No. Are most monophyletic? Arguably yes, but then that does not distinguish them from other types of taxa such as genera. If there is no feature in most taxa we call ‘species’ that distinguishes them from other types of taxa, then we have reason to doubt the existence of the species category. Moreover, if we have good reason to doubt that the species category is a natural one, then we should stop trying to find the correct definition of ‘species.’

It is important to note what is not being suggested here. Though we might have reason to doubt that there is a real species category in nature, that does not imply that the lineages we call ‘species’ do not exist. When a biologist identifies a lineage of organisms that share a unique ecological role and calls it a ‘species’ that biologist is highlighting a real lineage in nature. The same goes for the biologist that uses the Biological Species

Concept. We have good reason to think that each of these lineages exist, if the empirical and theoretical work is done properly. But calling them ‘species’ does not imply that there is a real category that all lineages called ‘species’ belong to. Calling them ‘species’ just implies that within a particular classification those lineages are the least inclusive taxonomic units according to one set of biological parameters. Stepping back, then, the suggested approach to the species problem offered here has three parts. First, we have good reason to think there is no species category in nature. Second, and consequently, we should stop looking for the correct definition of ‘species.’ Third, none of this implies that the taxa we call ‘species’ do not exist. The classification of basal taxonomic units can continue as usual.

The suggestion that there is no species category in nature yet we can continue to doing taxonomy as usual is not new. Some writers (Ghiselin 1969; Beatty 1992; Hodge 1987; Ereshefsky 2011) suggest that Darwin was sceptical of the species category, nevertheless he did not doubt the existence of those taxa biologists called ‘species.’ Interpreting what Darwin thought about the species problem is not easy, and there is a far bit of disagreement among scholars (Mallet 2010). The interpretation of Darwin followed here suggests that Darwin doubted the existence of the species category because he doubted the existence of the distinction between species and varieties. According to that interpretation, Darwin thought the exercise of ranking taxa was futile. There are taxa, and they form a branching pattern that constitutes the Tree of Life. But whether a particular branch is a species or a genus or a variety, according to Darwin, is an arbitrary decision. Nevertheless, Darwin believed that a classification based on the branching pattern of nature could be objective. That is, he thought that the taxa we call ‘species,’ ‘genera,’ etc. exist, and their relations are objective. But for Darwin, the assignment of the Linnaean ranks, including the rank of species, does not correspond to anything in nature. Such designations indicate the level of inclusiveness of a taxon within a classification. A taxon called a ‘species’ is less inclusive than something called a ‘genus.’ But that is the extent to which the Linnaean ranks, including the species rank, capture anything objective.

Some recent sceptics of the species category suggest that the word ‘species’ should be banished from biology (Mishler 1999; Fisher 2006). Darwin did not take such an

approach to the word ‘species.’ According to some Darwin scholars (Ghiselin 1969; Beatty 1992), Darwin doubted the existence of the species category but he did not suggest that we should stop using the word. In fact, Darwin wrote that “I mean by species, those collections of individuals, which have commonly been so designated by naturalists” (1975, 98; also see 1859[1964]). In other words, Darwin did not think there was a correct theoretical definition of species, such as the Biological Species Concept or some other species concept. He thought that ‘species’ merely refers to those taxa competent naturalists call ‘species.’

There are good theoretical and pragmatic reasons to follow Darwin’s approach to the species problem in contemporary biology. Darwin doubted the existence of the species category because he doubted the difference between the ranks of variety, species, and genus. We have reason to doubt the existence of the species category because that category is at best a heterogeneous class of non-comparable lineages. There are lineages of interbreeding organisms, lineages of organisms that live in distinct ecological zones, and various different types of monophyletic lineages. The species problem persists not because we have failed to find the correct type of lineage, but we have found too many.

But that raises practical questions. If the word ‘species’ is ambiguous because it refers to different types of taxa, does it not lose its effectiveness as a tool for communication? Some biologists think that is the case and suggest banishing the word from biology (Mishler 1999, Fisher 2006). However, purging the word ‘species’ from biology is an impractical suggestion. ‘Species’ is well entrenched in biology and elsewhere. Students are taught the term from their earliest encounters in biology. Field guides and taxonomic monographs use the word ‘species.’ And the term is found in our governments’ laws. From a practical standpoint, it would be very hard to eliminate the word ‘species.’

Furthermore, there is no compelling reason to get rid of the word ‘species.’ If we are careful in how we use the word, the ambiguity of ‘species’ is not a pressing problem. Many terms in biology are ambiguous, nevertheless successful research is conducted. Consider the word ‘gene.’ It is ambiguous, yet genetics is a thriving discipline. When it comes to the word ‘species,’ there is a simple strategy that can help avoid confusion (Ereshefsky 2011). If the meaning of ‘species’ affects our understanding of a biological

study, then we should be explicit about which species concept is being used in that study. For example, if a biodiversity study counts species using the Biological Species Concept, then that should be stated. The same holds for a biodiversity study that uses a phylogenetic approach. That way when the two studies are compared, we will not wrongly think we are comparing the same type of lineage. This is a problem in biodiversity studies where species counts compare different types of species lineages (Marris 2007). In such situations, it is important to say which type of species concept is being used. In other biological studies, knowing which species concept is being used does not affect our understanding of those studies, so saying which species concept is being used is unnecessary. For example, if we merely want to indicate that one taxon is less inclusive than another taxon within a classification, we can simply refer to them as ‘species’ and ‘genus’ without stating which species concept is being used.

Given the above considerations, what is the take home message for protistologists concerning the species problem? Protistologists should, of course, continue their investigations of different types of protist lineages. The recommendation here is just that the pursuit of the correct definition of ‘species’ should be abandoned. We have tried to answer that question for hundreds of years without success. Along the way, there have been significant research achievements. One of those is that we have discovered that organisms form different types of biologically significant lineages. However, no single type of lineage has risen above the pack such that it and only it should be called ‘species.’ Moreover, there is no good reason to think we will find that uniquely correct definition of ‘species.’

At the end of the *Origin of Species*, Darwin expresses some relief in not having to continue looking for the correct definition of ‘species.’ He writes that it “will be of no slight relief” to “not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species” (1859[1964]). Darwin felt no need to give a definition of ‘species.’ Yet he obviously produced significant theoretical work and more than a few classifications. We too can conduct successful biological research without providing the definition of ‘species.’

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