The mind of the species problem

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The species problem is the long-standing failure of biologists to agree on how we should identify species and how we should define the word 'species'. The innumerable attacks on the problem have turned the often-repeated question 'what are species?' into a philosophical conundrum. Today, the preferred form of attack is the well-crafted argument, and debaters seem to have stopped inquiring about what new information is needed to solve the problem. However, our knowledge is not complete and we have overlooked something. The species problem can be overcome if we understand our own role, as conflicted investigators, in causing the problem.

Have enough words been said and written on the subject of what species are? How many evolutionary biologists sometimes wish that not one more word, in speech or text, be spent on explaining species? How many biologists feel that they have a pretty good understanding of what species are? Among those who do, how many could convince a large, diverse group of scientists that they are correct?

At this last and most essential task, many great scientists have tried and failed. Darwin, Mayr, Simpson and others have taught us about species, but none has been broadly convincing on the basic questions of what the word 'species' means or how we should identify species. For its entire brief history, the field of evolutionary biology has simply lacked a consensus on these two related questions. Indeed, there was broader consensus before Darwin. Given the once widespread acceptance of an essentialist view of species, perhaps Linnaeus was our most capable and persuasive species pundit[1], although he was wrong, of course. Darwin killed species essentialism, but in so doing, he fostered rather than settled questions about what species really are. Since then, the species problem has beseeched us like the mythical sirens. Again and again, we pose and seek an answer to the question 'what are species?'. Other allegories seem apropos as well[2]: consider that the species problem is like a sword, thrust by Darwin into the stone, and left for us to yank upon with determination and futility. The often dreamed of magic is a compelling definition of 'species' that fits our understanding of the causes of biological diversity and that leads us to identify species accurately and agreeably.

The focus on definitions

A recent listing found two dozen different definitions of 'species' (i.e. species concepts, Box 1), most of which were invented within the past few decades[3]; and, since then, new ones have continued to appear[4]. I was also seduced by the 'what are species?' question, and once devoted much time to puzzling over definitions. The result was an apparently unpublishable 'species' manifesto. Although it attracts some readers on the Internet, it has so far failed to inspire the groundswell of consensus that I once felt it deserved.

A striking commonality of these numerous definitions is that, with few exceptions, they are clearly not to be interpreted as the different meanings of a set of homonyms, but rather as competitors for the single best meaning. There seems to be something about the perceived extensions and the intensions (the ideas in the minds) that are shared between these many definitions. This commonality can also be appreciated whenever two or more evolutionary biologists use the word 'species' in scientific conversations. This happens frequently, usually with a seamless exchange of ideas. Despite many different notions of 'species', and uncertainty and disagreement over them, the word almost always gets passed back and forth with tacit understanding. This apparent consensus thrives until that awkward moment when someone asks another what he or she means by 'species', at which point the consensus and the shared thread of understanding can evaporate. It is as if on one hand we know just what 'species' means, and on the other hand, we have no idea what it means.

I cannot think of any other word that garners as much lexicographical attention as 'species'. Certainly evolutionary biology is full of difficult ideas, and words such as 'adaptation' and 'fitness' often deserve and receive a lot of attention[5]. But those discussions are broadly conceptual and do not focus on definitions *per se*, the way that 'species' debates do. Of course, many words resemble 'species' in having fuzzy extensions (i.e. wide-ranging, sometimes vague referents) and some are the subject of debates over definitions. For example, the definition of 'drought' can matter greatly for public policy[6,7], and the meaning of 'disease' generates both philosophical and practical debates[8]. But neither of these examples, nor any others that I can think of, resemble 'species' in being the subject of so much attention that is both broadly theoretical and so narrowly focused on achieving the best single definition.

Consider the parallels between the motives and the species concepts of two of our most practiced 'species' definers. Ernst Mayr has been tweaking the Biological Species Concept for decades[1,9,10]. Joel Cracraft has been doing exactly the same thing with a version of the Phylogenetic Species Concept[11–13]. Both scientists are exceptional evolutionary biologists and ornithologists. Both argue that species are real and distinct entities in nature and that we need a succinct species concept that sums up the way in which they exist, and they both argue that we need a species concept that helps investigators to identify such things[10,12–14]. In short, they both want to understand real species and to be able to identify them, and both perceive a crucial role for a pithy definition. Despite these similarities, they are led to dissimilar definitions, and neither finds much utility in the other's concept. Of course, their concepts have some compatibility with each other and with evolutionary

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http://tree.trends.com 0169–5347/01/$ – see front matter PII: S0169-5347(01)02145-0

Box 1. Species concepts[a]

- Agamospecies Concept
- Biological Species Concept*
- Cladistic Species Concept
- Cohesion Species Concept*
- Composite Species Concept
- Ecological Species Concept*
- Evolutionary Significant Unit*
- Evolutionary Species Concept*
- Genealogical Concordance Concept
- Genetic Species Concept*
- Genotypic Cluster Concept
- Hennigian Species Concept*
- Internodal Species Concept
- Morphological Species Concept
- Non-dimensional Species Concept
- Phenetic Species Concept
- Phylogenetic Species Concept (Diagnosable Version)*
- Phylogenetic Species Concept (Monophyly Version)
- Phylogenetic Species Concept (Diagnosable and Monophyly Version)
- Polythetic Species Concept
- Recognition Species Concept*
- Reproductive Competition Concept*
- Successional Species Concept
- Taxonomic Species Concept

Reference

a 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

*Concepts that make reference to biological processes (e.g. reproduction and competition) that occur among organisms within species (and less so between species) and that contribute to a shared process of evolution within species.

theory[15], but, for those needing the single best definition, that is beside the point.

It is best to be plain about these and other similar efforts to find a definition that dispels the species problem. Descriptive definitions are not great containers of knowledge and they are not great tools for arbitrating the natural world. Individually, descriptive definitions are but small bundles of information or theory, and if they seem to be of any great aid in arbitration, it is because they are backed up by a far larger fund of knowledge. In short, if you have got the knowledge then the definitions are the easy part and fall readily into place. If your knowledge is incorrect or incomplete, no amount of wordplay will set it right. Those who have tried to puzzle out the species problem by focusing on definitions are missing something, and that something is bigger and more important than any definition.

But how could our knowledge, upon which the species debates have been built, be missing something? Do not evolutionary biologists know of genetics, fossils, geography and the vast organismal diversity that exists on our planet? Does not every evolutionary biologist know, from theory and mountains of evidence, that evolution gives rise to organismal groups, within which individuals are similar and closely related, and between which divergence can and does accrue? But, despite these intellectual riches, we must recognize that our knowledge of species has not been sufficient to resolve the species problem. Our obdurate debates[16] and our misplaced ambitions for 'species' definitions are a slap in the face – they forcefully remind us that there are some things that we just do not know about or understand sufficiently to describe them adequately[17].

The awkward juxtaposition of apparent ignorance and seemingly complete knowledge can also be seen in one of our most common modes of explanation. Consider the now traditional method in which the nature of species and the meaning of 'species' are addressed first by summing up the inadequate state of affairs, followed by an exertion of pure reason. There are dozens, if not hundreds, of elegant articles that employ this approach. These articles are permeated with the presumption that new argument, and not new information, will settle the question. Species pundits do not ask 'what new information do we need?'. By taking this approach, we are not acting like scientists. We are acting like some philosophers, particularly Aristotle, who addressed and supposedly solved questions of the natural world by giving words to intuited essences; that is, by making up definitions[18].

An untapped source of information

Fortunately, we can learn rather a lot from our unscientific behavior. Not only do we see in it a sure sign that we lack information about the species problem, but we also find a place in which to look for that information. That place is within ourselves, in the ways that our minds handle questions about species. To be clear, I am saying that one source of new information and insight, to which we should turn if we are to solve the species problem, is our own behavior. Note that several authors have concluded that we demand too much of species concepts and that some of our demands are inherently contradictory[2,19–22]. It is but a short step (and a great leap) to cast such arguments in terms of the question: what is it about our minds and our motives that mislead us?

Once we are introspective in this way, we immediately obtain one clear answer to the question 'what are species?'. In our minds and in our language, species are categories. That is to say, the names for species and the usage of those names take an entirely conventional syntactical role that is taken by all categories. Just as 'planet' is the name of a category, and appears as a predicate in sentences (e.g. 'The Earth is a planet.'), so 'polar bear' is also a category and a frequent predicate in sentences. Whatever else they are, categories are things in the mind and in our language, and they are used for organizing our thoughts and language about organismal diversity.

Taxa

Of course, 'species are categories' is just a starting point, but it is one that helps us to tap into a large tradition of inquiry on the connections between categories in the mind and things in the real world[17,23–26]. Categories are motivated by recurrent observations about the world[27]. Humans are great observers of patterns of repetition, and we devise our categories as a response. These so-called 'natural kinds' are in our heads, but they are also out there in the world, in some way. For example, frozen wispy crystals of water sometimes fall to earth in great numbers and we identify them as snowflakes. The 'snowflake' category exists in our minds, but in some sense it is also a feature of the world outside ourselves, a world that is disposed to repeatedly generate individual falling wispy crystals of water. Each of the species that we identify is a category, but it is also a natural kind that exists as a pattern of recurrence in the world. We call these natural kinds 'taxa' and, whatever else they are, there is no escaping the fact that we identify them first on the basis of recurrent patterns that we find in nature.

What does it take to make such a species taxon? One answer is that it does not take much: given a simple observation of a few organisms that seem similar to one another, and different from others, and a biologist is off and thinking about devising a new taxon. Another answer is that it varies tremendously with the observer. Not surprisingly, biologists cannot agree on how distinct a seemingly new pattern must be to motivate a new named category. These lumper/splitter debates go round and round, much as they have for hundreds of years. Consider the situation with birds, which for people are probably the most observable animals on the planet. Conventional classifications place the number of bird species worldwide at around 9000. But some feel that a proper evaluation would yield a count closer to 20 000 (Refs 28,29).

So now we have one answer to 'what are species?'. They are categories and, more particularly, they are named natural kinds of organisms: taxa. We also know what causes them, and that they are the result of two processes: (1) the evolutionary processes that have caused biological diversity; and (2) the human mental apparatus that recognizes and gives names to patterns of recurrence.

Evolutionary groups

For many biologists, however, species taxa are entirely inadequate for many of the purposes for which we use 'species'. These biologists are interested in the causes of species, not our mental contributions to taxa, but rather the evolutionary processes that create patterns of biodiversity. Of the many concepts listed by Mayden[3], many either strongly imply or explicitly state that a species is a group of related organisms, one that is enjoined by evolutionary processes that go on within it, and that is separate from other groups because of the absence of shared evolutionary processes with those other groups (Box 1). It is these theoretical ideas of evolving groups that descend fairly directly from Darwin's teachings, and they mark a drastic departure from purely categorical or taxonomic ideas of species. But be sure to note the vagueness of these commonplace ideas of evolutionary groups. As much as they are backed by strong theory, any attempt to translate this theory into strict criteria for the unequivocal identification of evolutionary groups requires much work (and if the history of the species problem is any indication, is bound to fail).

Fundamental conflicts

Now let us compare and contrast the idea of a species taxon with the idea of a species as an evolutionary group. To begin with, these two meanings of 'species' refer to things that are fundamentally and ontologically dissimilar. To the extent that instances of either of them exist, they do so in very different ways. An evolutionary group is an entity, somewhat discrete in space and time, and capable of changing and being acted upon[30–34]. It does not matter that its parts (individual organisms) can move around with respect to one another, and it does not matter that it is not entirely distinct and separate from other such entities. Evolutionary groups share these properties with all sorts of other entities, and the arguments about their ontology (the way they exist) are fairly simple, at least compared with those for categories and taxa[32]. Whether natural kinds exist is an often-debated question, but even if they do, it is an altogether different sort of existence than for individual entities[35–37].

Another major difference between the two viewpoints is the role that distinction plays in their existence. We recognize and devise species taxa pretty much as a direct result of having perceived a seemingly distinct pattern of recurrence. We devise taxa because they usefully serve our drive to categorize things, and so their very existence (such as it is) goes hand-in-hand with their perceived degree of distinction. By contrast, evolutionary groups exist regardless of our recognition of them, and they might or might not be distinct. Note that as much as the word 'group' can be taken to convey distinction, in fact the world is full of things that exist and are not at all distinct. Some that we are familiar with are clouds, populations, and ecosystems. Since the early 20th century, evolutionary biologists have been well trained in the many ways that evolving groups of organisms might not be distinct. Genes can be and are exchanged at varying rates between such groups, and there are myriad ways that levels of gene exchange can be structured to create groups within groups[38].

Finally, consider our very different motivations towards the different usages of 'species'. Names of taxa are among children's very first words (not the technical jargon, of course, but words like 'dog' and 'bird') and adult biologists employ taxa in exactly the same manner: that is, as named categories. Consider too that all human societies have taxa that are part of taxonomic systems that share some remarkable similarities with each other and with those systems used by professional biologists[25,39]. Surely humans have been devising and using taxa ever since their ancestors evolved the capacity for language. If there is one thing at which our brains are adept, it is recognizing and devising different kinds of organisms. But the idea of species as evolutionary groups is in stark contrast to this categorical tradition that is imbedded within our minds. The tradition of thinking of species as evolutionary groups is only 140-years old, and it is knowledge that comes to a person late in life, at least compared with the knowledge of categories of organisms.

In short, we have two widely differing ways of appreciating biological diversity[17,21,33]. We have the ages-old instinct to categorize, and we have the modern tradition of scientific inquiry. Our instincts give us taxa, but our inquires have only recently led us to understand evolutionary groups. The taxa are relatively easy to find and invent, whereas the evolutionary groups are difficult to study, for they are often truly indistinct with fuzzy boundaries between groups, and the forces that conjoin them can be subtle. Research on a species, as an evolutionary group, requires study of the very processes of direct and indirect interaction among organisms, including reproduction and competition, that can cause those organisms to be a species.

The causes of the species problem

In addition to carrying conflicting ideas of species, we evolutionary biologists also try to do something else – we try to find a way to have the taxa be the same as the evolutionary groups. The two things are ontologically different, but they can correspond when all those organisms that we would place in a category also collectively and completely constitute an evolutionary group. The human species is probably our most accessible example of a species taxon that also corresponds well to an evolutionary group. In general, our taxa can serve as hypotheses of the organisms that constitute evolutionary groups. Evolutionary biologists are very familiar with this mode of thought. However, we will fail in our studies if we forget the reasons why the two sorts of things might have little correspondence with one another.

(1) The patterns that we observe are a function of our own capacity for perception and judgment. Furthermore, there is no reason why our senses should be as subtle as all of nature. When we devise taxa, we are not objective, and we must keep in mind that different human observers will find different taxa. It is also useful to imagine a thought experiment of the taxa that would be devised by an alien observer, by one who uses different senses and who operates on a different scale of observation.

(2) Real evolutionary groups need not be distinct, and can overlap or be nested within one another, whereas categories are created as a direct function of perceived distinction. Attempts to delimit evolutionary groups by the boundaries of the categories will cause some groups to be missed and others to be wrongly circumscribed.

(3) Most importantly, we must keep in mind that the evolutionary processes that caused the patterns that we recognize, and which we use to form taxa, are processes that acted long ago. As time passes, the wave front of evolutionary processes leaves behind strong patterns of similarity and differences among organisms. It is those patterns that we use for the taxa, but the place where evolutionary groups exist is at that wave front – they are caused by the evolutionary processes that are going on right now. The patterns of similarity that we recognize are the remnants of former evolutionary groups that might have long since shifted and splintered.

The species problem is caused by two conflicting motivations; the drive to devise and deploy categories, and the more modern wish to recognize and understand evolutionary groups[17]. As understandable as it might be that we try to equate these two, and as reasonable and correct as it might be to use taxa as starting hypotheses of evolutionary groups, the problem will endure as long as we continue to fail to recognize our taxa as inherently subjective, and as long as we keep searching for a magic bullet, a concept that somehow makes a taxon and an evolutionary group both one and the same.

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