Chapter 2

The Species Problem: A Conceptual Problem?

Richard A. Richards

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1. Introduction

There have long been multiple ways of conceiving *species* that divide up biodiversity in different and inconsistent ways. This "species problem" goes back at least to Aristotle, who used the Greek term *eidos* (translated as the Latin *species*) in at least three different ways. [1] Two thousand years later, Darwin confronted the species problem, listing some of the different ways species were conceived.

> How various are the ideas, that enter into the minds of naturalists when speaking of species. With some, resemblance is the reigning idea & descent goes for little; with others descent is the infallible criterion; with others resemblance goes for almost nothing, & Creation is everything; with other sterility in crossed forms is an unfailing test, whilst with others it is regarded of no value. [2]

And one hundred years after Darwin, Ernst Mayr worried about this same problem in a book he edited, titled *The Species Problem*.

> 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. [3]

More recently, the species problem seems to have gotten worse. In 1997, Richard Mayden identified at least twenty-two species concepts currently in use. [4]

This multiplicity of species concepts is a genuine problem in that different ways of conceiving species divide biodiversity in different and inconsistent ways, and no single species concept is adequate. What counts as a species under one concept may not count as a species under another. So whether a group of organisms counts as a species depends on which species concept is used. 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 consequences of using different species concepts are often striking. Species counts, one way of measuring biodiversity, depend on which concept is used. The replacement of other concepts with the *phylogenetic species concept*, for instance, has multiplied 15 amphibian species into 140. [5] A recent survey of taxonomic research [6] 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, there was a 50% decrease in mollusc species. Overall, there was an increase of 48.7% when a *phylogenetic species concept* replaced other concepts.

Given that this there is so far no consensus on species concepts, these differences in species counts suggest that the conventional grouping of organisms into species may be arbitrary and reflects only the subjective point of view assumed, as Joel Cracraft suggests (emphasis added):

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*. [7]

This problem is magnified by the fact that which concept is used often depends on seemingly arbitrary facts, such as which organism is studied, as 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. [7]

But even among those who study the same organisms, there is disagreement about which species concept is best. Those who are committed to the method of taxonomy sometimes 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 consensus. [8]

This is clearly problematic for the understanding and preserving biodiversity, as Claridge, Dawah and Wilson recognize in their introduction to a recent collection of articles on species concepts:

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. [9]

Moreover, if the application of endangered species legislation is affected by species counts, then the consequences of the species problem spreads beyond biology and into public policy. [1] There are clearly costs if the adoption of a particular species concept results in increased species counts. The authors of the survey quoted above, have estimated the costs of the proliferation of species taxa, based on the fact that the adoption of the *phylogenetic species concept* results in increased species counts that reduce the geographic range of species, and that in turn 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. [6]

These additional costs might be justified *if* the increased species counts represented an objective improvement in the measure of biodiversity. But the additional costs are hard to justify if they are merely a consequence of some arbitrary choice of species concepts.

There are theoretical concerns here as well. If species are the fundamental units of evolution and classification, as is typically assumed, surely we need a satisfactory, unambiguous way to determine what counts as the fundamental units in these ways. [1] We need to have a good idea, for instance, about what counts as a species in order to identify and study speciation events. After all, only if a new species has been formed can there be speciation. And as long as species are the fundamental, basal units of classification, as is usually assumed, we need to know unambiguously what counts as a species to generate an unambiguous classification.

We might make progress on this long-standing species problem by thinking about scientific problems in general. Some scientific problems are empirical in the sense that they are solved by the addition of new empirical data or information. For example, we might solve a problem of disease by the observation of some bacterial or viral pathogen. As is well known, this is happening with a variety of cancers. On the other hand, some scientific problems are largely conceptual in the sense that they are solved not so much by the addition of new em-

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pirical information, but through some conceptual innovation, change or clarification. For example, problems related to planetary motion were solved by Johannes Kepler through the use of a new orbital concept based on elliptical rather than circular motion. And around the turn of the twentieth century, Wilhelm Johannsen coined the terms 'gene,' 'genotype,' and 'phenotype' to introduce new and useful concepts to the many problems in the study of heredity. [10] Sometimes old concepts get modified, as we see in relativistic physics with its new ways of conceiving *mass*, *space* and *time*. In each of these latter cases, progress was made through thinking about the concepts used, *not just* through the addition of new empirical information.

There is a general insight to be gained in thinking about scientific problems in this way. From at least Plato and Aristotle on, it has been recognized that knowledge of the world is based on the application of language, ideas or concepts to the world. Consequently, successful inquiry depends in part on getting our language, ideas or concepts right. This can be relatively straightforward, as in Kepler's application of the ellipse to planetary motion, or in the invention of the concepts of *quark, atom, electron, element, compound, gene, protein, homology, enzyme, genotype, population, species, ecosystem, neuron,* etc. Or less straightforwardly, progress may be found in the relation between concepts. How is the idea of an *electron* related to the idea of an *atom*? And how is the concept of a *species* related to that of a *population*? It may also be that getting concepts right involves something less concrete and more abstract. Scientific progress might be predicated partly on getting clear about *scientific law, evidence, explanation, theory, testing, observation* and so on. And at an even more abstract level, scientific progress might result from thinking more clearly about the nature of various concepts, and how they are related. For instance, how is *observation* related to *evidence* and *theory*? And what is the relation between *scientific law* and *scientific explanation*?

So is the species problem empirical, conceptual or both? If empirical it will be solved by more empirical data or information. Present trends suggest that the problem is not exclusively empirical. The last century has made great progress in the empirical investigation of biodiversity and evolution, but the species problem seems to instead be getting worse! We now have more jointly inconsistent and individually inadequate concepts than ever. It is my contention here that the species problem is at least partly conceptual, and it is solved at an abstract level: the nature and relation of various species concepts. The solution is not merely a matter of introducing a new species concept, or modifying an existing concept. Rather it is to be found in an understanding how the various species concepts are related within a framework, how each concept works individually, and how this all has resulted in the species problem.

I shall argue that the species problem is solved first, by understanding the division of labor within the conceptual framework. Some species concepts are theoretical and are concerned with the nature of species things. Others are operational, telling us how to identify and individuate species things. Here I follow the lead of Richard Mayden and Kevin de Queiroz, but go a step further and argue that these operational concepts are better conceived as *correspondence rules*. The second component of the solution is based on an understanding of the structure of theoretical species concepts. I will argue that the primary, theoretical species concept has a structure - a definitional core and a descriptive periphery - and once we see how this conceptual structure works, we can understand why there has been an enduring species problem and how to solve it. Finally, I will conclude with a few thoughts about scientific concepts and how they get used within the social, "demic" structure of science. Part of understanding the species problem is to be found in how researchers and theorists in different fields, with different interests, engage the species concept.

2. The conceptual framework

The recent history of the species problem is not promising. Along with the increase in our understanding of biodiversity and the evolutionary processes that produced it has come a proliferation of species concepts. Richard Mayden [4] has identified and individuated over twenty species concepts currently in use. Some species concepts he identifies are based on similarity. The *morphological species concept* asserts that "species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means." The *phenetic species concept* is based on overall similarity and phenetic clustering. Some species concepts are based on molecular similarity, such as the *genotypic cluster concept* and the *genealogical concordance concept*. Other concepts are based on evolutionary processes. The *biological species concept*, advocated by Ernst Mayr, and Hugh Paterson's *recognition species concept* are based on sexual reproduction. But since not all organisms reproduce sexually, the *agamospecies concept* was proposed to serve as an umbrella concept for all taxa that are uniparental and asexual. Some process concepts are based on ecology, such as the *ecological species concept*, which identifies species with unique adaptive zones. Historical species concepts treat species as historical entities, extended in time. Here we find the *evolutionary species concept*; the *successional species concept*; the *paleospecies concept*; and the *chronospecies concept*, that each conceives of species as segments of a changing lineage. The *cladistic species concept*, the *composite species concept*, the *internodal species concept*, and the *phylogenetic species concept* are all based on the idea that speciation events can serve to demarcate the beginnings and endings of species lineages.

The details of each of these species concepts are not important for purposes here. What is important is that first, with increased empirical understanding, species concepts seem to be proliferating; second, these concepts are inconsistent, carving nature in different and inconsistent ways; third, no single concept is adequate, applying across biodiversity. The *biological species concept*, for instance, applies only to sexually reproducing organisms, and therefore cannot be used to group asexual organisms. Fourth, the species problem does not seem to be solved by additional empirical information. This suggests that the problem is not exclusively empirical, and requires a conceptual solution.

Mayden recognizes this. After outlining all these species concepts, he argues that there are really two main kinds of species concepts: *primary theoretical concepts* tell us what kinds of things species taxa are; *secondary operational concepts* tell us how to identify and individuate species taxa. This approach is hierarchical because the operational concepts depend on the

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theoretical concepts. Operational concepts do not tell us what species are, but *given a particular theoretical concept*, how to identify and individuate them. [4] Operational and theoretical concepts are therefore not competing but supplementary ways of thinking about species. It is therefore possible to use different operational concepts, without dividing biodiversity up in inconsistent ways – if a single theoretical concept is used.

This hierarchical thinking about species may have the potential to solve the species problem, but only if there is a single, adequate theoretical concept. Mayden argues that there is such a concept, based on the fundamental idea of a lineage: the *evolutionary species concept (ESC).* Mayden [4] gives three statements of this concept. The first from G. G. Simpson asserts that a species is "a lineage (an ancestral-descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." The second statement, from Edward Wiley, identifies species as "a single lineage of ancestor-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." The third formulation, from Wiley and Mayden, is that a species is "an entity composed of organisms which maintains its identity from other such entities through time and over space, and which has its own independent evolutionary fate and historical tendencies." According to Mayden, the *ESC* is theoretically significant and universal. It can apply across biodiversity. [4]

The *Evolutionary Species Concept* is not obviously operational. One cannot just observe lineages of the relevant kind in nature. The *ESC* therefore requires other operational, species concepts:

While the ESC is the most appropriate primary concept, it requires bridging concepts permitting us to recognize entities compatible with its intentions. To implement fully the ESC we must supplement it with more operational, accessory notions of biological diversity – secondary concepts. Secondary concepts include most of the other species concepts. While these concepts are varied in their operational nature, they are demonstrably less applicable than the ESC because of their dictatorial restrictions on the types of diversity that can be recognized, or even evolve. [4]

Secondary operational concepts are those that can be readily applied to biodiversity, and are indicative of species lineages. Species concepts based on morphological or genetic similarity, for instance, can help identify lineages, since organisms within a single lineage will generally share some morphological and genetic traits. Concepts based on processes such as reproductive isolation and cohesion, mate recognition systems and ecological niches, can also be used to identify lineages since these are processes that operate in the formation and persistence of lineages.

Kevin de Queiroz has proposed a similarly hierarchical way to think about species concepts. According to de Queiroz, there are the *species concepts* proper that give the necessary properties of species and provide theoretical definitions. Then there are *species criteria* that give contingent properties and are “standards for judging whether an entity qualifies as a species.” [11] Many of the species concepts in use are to be understood as species criteria rather than species concepts proper.

> The species criteria adopted by contemporary biologists are diverse and exhibit complex relationships to one another (i.e. they are not necessarily mutually exclusive). Some of the better-known criteria are: potential inter-breeding or its converse, intrinsic reproductive isolation... common fertilization or specific mate recognition systems... occupation of a unique niche or adaptive zone... potential for phenotypic cohesion... monophyly as evidenced by fixed apomorphies... or the exclusivity of genic coalescence... qualitative... or quantitative... Because the entities satisfying these various criteria do not exhibit exact correspondence, authors who adopt different species criteria also recognize different species taxa. [11]

Like Mayden, de Queiroz argues that there is single, primary species concept that is adequate – applying across biodiversity. This is, according to de Queiroz, the *general lineage concept*:

> Species are segments of population-level lineages. This definition describes a very general conceptualization of the species category in that it explains the basic nature of species without specifying either the causal processes responsible for their existence or the operational criteria used to recognize them in practice. It is this deliberate agnosticism with regard to causal processes and operational criteria that allows the concepts of species just described to encompass virtually all modern views on species, and for this reason, I have called it the general lineage concept of species. [11]

In a later paper, de Queiroz describes this general theoretical concept in terms of a “metapopulation lineage,” which he describes as “sets of connected subpopulations, maximally inclusive populations.” [12]

Mayden and de Queiroz are largely right about the conceptual framework and the potential solution to the species problem. There may be multiple, seemingly inconsistent ways of thinking about species, but these ways of thinking are not all equivalent. The *biological species concept* and the *evolutionary species concept*, for instance, are not competing ways to think about species. Rather they a complementary. The biological species concept, based on interbreeding, is valuable insofar as it indentifies the kind of lineages required by the evolutionary species concept. Nor need each concept be individually adequate, applying across biodiversity. The biological species concept, based on reproductive cohesion and isolation, need only apply to sexually reproducing organisms. The important insight here is that some

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ways of thinking are substantive (evolutionary species concept) and tell us what species things are, and some ways are operational (biological species concept), telling us how to identify and individuate species taxa. But it may be misleading to think about all these ways of thinking as "concepts."

This division of conceptual labor echoes a debate early in the twentieth century about how to define scientific concepts in physics, such as *length* and *mass*. The physicist P. W. Bridgman proposed that we should define these concepts in terms of the *operations* we use to measure them. *Mass*, for instance, would be defined in terms of the ways of measuring mass - the resistance to acceleration, or the operation of gravity. Bridgman's proposal that operations give definitions became known as "operationalism," and came to be seen as an answer to the philosophical problem of how to connect theoretical laws, that contain only non-observational terms, to observation. How can we connect laws about unobservable particles, for instance, to the empirical regularities we observe in nature? The philosopher of science Rudolf Carnap explained this problem:

> Our theoretical laws deal exclusively with the behavior of molecules, which cannot be seen. How, therefore, can we deduce from such laws a law about observable properties such as the pressure or temperature of a gas or properties of sound waves that pass through the gas? The theoretical laws contain only theoretical terms. What we seek are empirical laws containing observable terms. Obviously, such laws cannot be derived without having something else given in addition to the theoretical laws.... That something else that must be given is this: a set of rules connecting the theoretical terms with the observable terms. [13]

Carnap called these rules connecting theoretical and observable terms "correspondence rules." What is significant in Carnap's proposal is that these *correspondence rules* connecting theoretical concepts to observation are not really concepts in the usual theoretical sense. This is clear in Carnap's rejection of the view (disagreeing with Bridgman) that operational rules can provide definitions: "There is a temptation at times to think that the set of rules provides a means for defining theoretical terms, whereas just the opposite is really true". [13] Nor can correspondence rules function *as* definitions: "What we call these rules is, of course, only a terminological question; we should be cautious and not speak of them as definitions. They are not definitions in any strict sense." [13] Rather, the definitions give operational guidance, telling us what operations are relevant. What is important here is that those concepts that function operationally are different from those that function theoretically. In effect, they tell us how to observe a thing, not what sort of a thing it is.

We can apply Carnap's insight here to the species problem. As argued by Mayden and de Queiroz, some species concepts are theoretical. They tell us how to conceive species. They define species taxa and constitute the species category. But some species concepts are operational. They tell us how to identify and individuate the groups that are properly species *giv-*

en a particular theoretical concept. But these so-called operational concepts are really *rules* that help us to determine if a group of organisms satisfies the demands of the theoretical concept. The biological species concept is really a rule about how to identify and individuate the sexually reproducing lineages that constitutes species taxa. By using this terminology, referring to operational concepts as “correspondence rules,” Carnap thought we could avoid the general confusion of definitions and operations. He also thought this solved a problem in science, the tendency of philosophers to ask scientists for definitions of scientific concepts in familiar, non-theoretical terms.

> They want the physicist to tell them just what he means by “electricity”, “magnetism”, “gravity”, “a molecule”. If the physicist explains them in theoretical terms, the philosopher may be disappointed. “That is not what I meant at all”, he will say. “I want you to tell me, in ordinary language, what those terms mean.” [13]

The problem here is that the scientist is being asked for something he or she cannot give – a definition in something other than theoretical terms. Each of these concepts has satisfactory definitions, but they are in terms of the theoretical framework. That is the proper source for definitions – telling us how to interpret these concepts – not the operations to measure or identify the things that satisfy them. Carnap concluded:

> The answer is that a physicist can describe the behavior of an electron only by stating theoretical laws, and these laws contain only theoretical terms. They described the field produced by an electron, the reaction of an electron to a field, and so on…. There is no way that a theoretical concept can be defined in terms of observables. We must, therefore, resign ourselves to the fact that definitions of the kind that can be supplied for observable terms cannot be formulated for theoretical terms. [13]

There are three things to note here about Carnap’s analysis. First is his emphasis on the role of theoretical frameworks in the interpretation of scientific concepts. Theoretical terms are to be understood in terms of the overarching theory. For a species concept the overarching theory is evolutionary theory. Second is the proposal that we think about operations as rules rather than concepts. What we might call operational *concepts*, are really *rules* for connecting theoretical concepts to observation. Third, there soon came to be a general consensus against operationalism in physics. That consensus continues today. There are obvious reasons for the rejection of operationalism. It seemed to lead to the multiplication of concepts of such basic things as *length.* [14] The operations to measure length at the scale of stars and galaxies are different than the operations to measure length at the scale of a football field or at the atomic level. The problem is that if we base concepts on operations, there seems to be a new concept for each distinct operation. With operationalism comes the proliferation of concepts like *length.* Similarly we should expect the proliferation of concepts like *mass, density* and *temperature, etc.* If there is more than one way to measure each, there will be multiple concepts. It is no wonder that operationalism was rejected in physics. It should similarly be rejected in evolutionary biology and with respect to the species problem.

If we adopt Carnap's approach, distinguishing theoretical definitions from operational "correspondence rules," and apply this approach to the species problem, the species problem largely dissolves. So, for instance, given a particular theoretical concept (either Mayden's *ESC* or de Queiroz's general lineage concept) some kinds of similarities will be indicative of the relevant kind of population lineage, and will therefore help identify and individuate species taxa. For those population lineages of sexually reproducing organisms, reproductive cohesion, reproductive isolation and mate recognition systems will be relevant to the identification and individuation of species taxa. And for non-sexually reproducing lineages, there will other correspondence rules. If so, then the species problem is largely a consequence of not discriminating between species concepts proper and the correspondence rules that help apply species concepts to the world.

Implicit in this division of conceptual labor are two distinct sets of evaluative criteria. Theoretical concepts best serve the needs of evolutionary theory and biosystematics if they are universal – apply across biodiversity. This is in effect, a unification requirement. A single concept will ideally *unify* phenomena – the apparently discrete groupings of organisms that we see across biodiversity and processes that produce these groupings. On the other hand, operational concepts, or better "correspondence rules," do not need to unify. Rather as different processes operate across biodiversity there is instead a proliferation of rules. We need different rules, for instance, for sexual and asexual organisms. The more we find out about evolutionary processes, the more rules we will discover to identify and individuate species things. Rather than unification, with correspondence rules/operational concepts there is proliferation. The more the merrier!

There are good reasons to think that Mayden and de Queiroz have the broad outlines of a primary theoretical concept right as well - even though there may be differences in each of the three formulations Mayden provides of the ESC and de Queiroz's general lineage concept. A primary theoretical concept must be theoretically significant and consistent with evolutionary theory. At the most basic level, the theory of evolution tells us that there is change over time. Darwin thought that this involved the origin of new species through divergent change, whereby mere varieties become species. [15] This principle of divergence then explained the branching evolutionary tree diagram that in turn served to illustrate his approach to classification.

I request the reader turn to the diagram illustrating the action, as formerly explained, of these several principles; and he will see that the inevitable result is that the modified descendants proceeding from one progenitor become broken up into groups subordinate to groups... So that we here have many species descended from a single progenitor group-ed into genera; and the genera are included in, or subordinate to, sub-families, families and orders, all united into one class. [15]

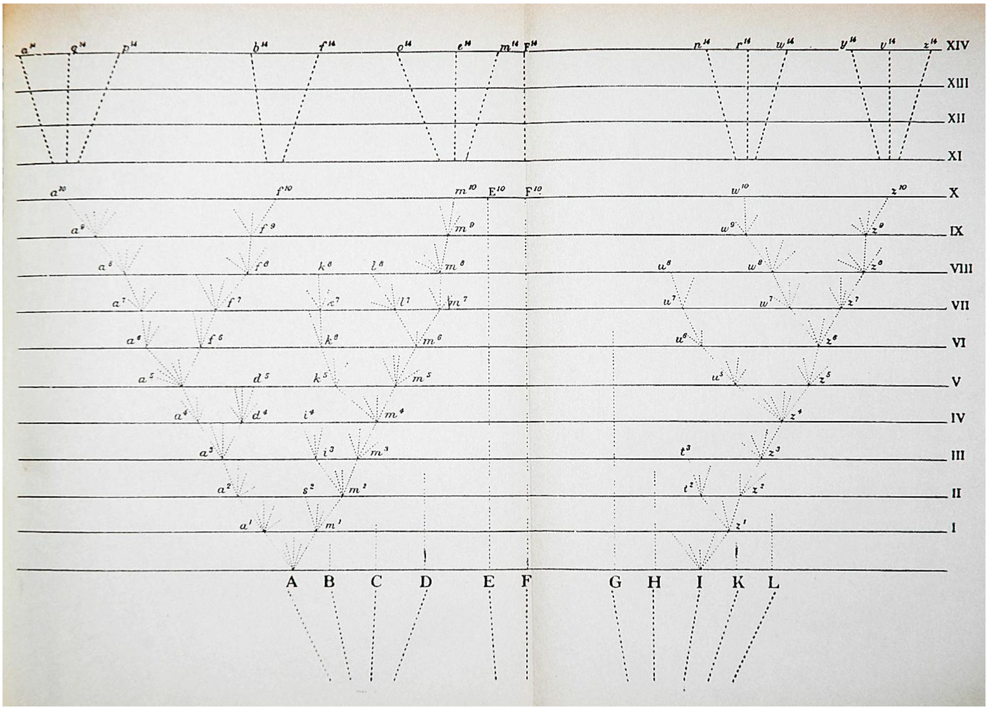

Figure 1.

What is important here is that this tree (figure 1) [16] emphasized the temporal, historical dimension of evolution, and the branching associated with speciation. It tells us that species have beginnings in speciation events. They have duration. They change. And they have endings. Since Darwin, this historical component has become further entrenched in evolutionary thinking about species.

This is not to say, of course, that species taxa are *just* historical entities. Evolutionary theory tells us that they exist as well, as groups of organisms at particular times, groups that share similarities, sometimes interbreed, occupy ecological niches, vary geographically, form gene pools, and have a variety of social structures. This way of thinking about species has been developed and refined most notably by the thinkers of the Modern Synthesis, such as Mayr, Dobzhansky, and Simpson. This *population* dimension, along with the historical, suggests that there are two ways to think about species taxa. We can think about them over time, as historical, *diachronic* entities that originate, change and go extinct. Or we can think about them at a single time, as *synchronic* groups of organisms that are connected or given some sort of structure by some biological process. If so, then evolutionary theory tells us that whatever else species taxa are, they have two dimensions – diachronic and synchronic, and an adequate theoretical species concept must reflect that fact.

Evolutionary theory also tells us that species are the things that evolve. First, they have beginnings and endings in speciation and extinction events. Accordingly, each species taxon also has its own distinctive fate, in its trajectory of change or stasis and ultimate extinction. But species taxa also have some sort of cohesion, whether through reproduction, social interaction, gene transfer or the operation of natural selection. But to be universal, a theoretical concept must be indeterminate about which processes produce these general features. If there is a solution to the species problem, as I think there is, it will surely be based on something like what Mayden and de Queiroz propose – a primary theoretical species concept that treats species taxa as segments of populations lineages with cohesion and distinctive fates. And the more researchers find out about the processes that segment these population lineages and that produce cohesion, and that preserve or produce morphological, behavioral and molecular similarities, the more correspondence rules they will have at hand to identify and individuate species taxa. Since these correspondence rules are subservient to the primary theoretical species concept, *when understood correctly* they cannot ultimately divide biodiversity in inconsistent ways. It is only when they are taken to be independent of a primary theoretical concept that they can conflict.

This is not to say, however, that the nature and application of the correspondence rules is obvious and unproblematic. It is not always obvious which correspondence rules are appropriate in particular instances. That will often depend on empirical facts about the relevant organisms and processes in question - facts that may or may not be known. Nor is the nature of the primary theoretical concept unproblematic. The lineage and population concepts both require clarification. It is not always clear what kinds of cohesion are relevant and operate in the various groups of organisms. But more pertinent to purposes here, this division of conceptual labor is only half of the solution to the species problem. The other half is found at a lower level, the level of the individual theoretical species concept, and how it functions.

3. Conceptual structure

Mayden and de Queiroz suggest that even with the use of multiple operational concepts/species criteria there is general agreement that species are segments of population lineages. This is what evolutionary theory requires. There is good reason to agree with them. Ironically though, an historical conception of species as lineages predates evolution in the ideas of John Ray and Linnaeus. [1] And Darwin noted that an historical way of thinking about species was largely accepted by his contemporaries.

> With species in a state of nature, every naturalist has in fact brought descent into his classification; for he includes in his lowest grade, or that of a species, the two sexes; and how enormously these sometimes differ in the most important characters, is known to every naturalist: scarcely a single fact can be predicated in common of the males and hermaphrodites of certain cirripedes, when adult, and yet no one dreams of separating them. The naturalist includes as one species the several larval stages of the same individual, however much they may differ from each other and from the adult... He includes monsters; he includes varieties, not solely because they closely resemble the parent-form, but because they are descended from it... [15]

But as Darwin's evolutionary tree diagram in the Origin shows, this historical thinking about species is also central to evolutionary theory. The idea here is that even with the use of other criteria for grouping into species, and identifying and individuating species taxa, there has been guidance from the basic conception that species are lineages. In Darwin's tree diagram, species are the branches of the tree. If so, a systematist might use morphological or molecular similarity to identify and individuate species, but in ways that are constrained by a population lineage conception of species. This requires that the systematist ignore irrelevant morphological traits based on sexual dimorphism and developmental stages. If so, then there is an implicit hierarchy here, ust as Mayden and de Queiroz have argued.

There are puzzles about actual usage that remain. When naturalists, evolutionists and systematists actually *use* the term *species*, they don't always seem to mean "segments of population lineages with cohesion and distinctive fates." Rather they seem often to have other things in mind, as Darwin recognized in his own time:

> [H]ow various are the ideas, that enter into the minds of naturalists when speaking of species. With some, resemblance is the reigning idea & descent goes for little; with others descent is the infallible criterion; with others resemblance goes for almost nothing, & Creation is everything; with other sterility in crossed forms is an unfailing test, whilst with others it is regarded of no value. [2]

This is still the case. One person might apply the term *species* to a frog population on the basis of a distinctive morphology and behavior, without consciously thinking or claiming that the morphological or behavioral similarities are subservient to some other theoretical concept. Another might take the term to mean interbreeding and reproductive isolation as applied to a population of birds. A geneticist might take the term to mean something related to genotypic similarity. The point is that even if there is a primary theoretical concept *available* to guide thinking about species, not always does this theoretical concept get manifest in the actual usage and meaning of the term *species*. A molecular systematist might mean one thing, a naturalist might mean another, and a geneticist might mean yet something else when using the term *species*. How do we account for this variability in usage, given a single primary theoretical concept? The division of conceptual labor doesn't seem to adequately answer this question. It just tells us that there are different ways *available* to think about species, some theoretical some operational. To answer this question we need to look more closely at how concepts get structured and actually used.

Much modern thinking about concepts begins with a framework laid out by Gottlob Frege, in a classic German paper of 1892, and its English translation, "On Sense and Reference." [17] Here Frege addressed the question of how language can represent things in the world. He argued that linguistic entities such as concept terms function in propositions in two ways: first, through a "nominatum," what the term *refers* to (what it *designates* or *denotes)*; second, through the "sense," or *meaning* of the term. According to Frege, the sense of a term is grasped by anyone who knows the language, and is to be identified with the description that would be associated with the term in that language. The sense or meaning of the term *water* for instance would be identified with an associated description of *water*. The meaning of a term must be distinguished from what it refers to, or denotes, because, according to Frege, co-referential terms (terms that refer to the same thing) often have different meanings. Two terms that referred to the planet Venus, for instance, have different meanings based on the descriptions that designate different times of appearance in the sky: "The nominata of 'evening star' and 'morning star' are the same, but not their senses." [17] Meaning is therefore more fine-grained than reference, in that two terms can refer to the same thing, yet still have different meanings. (As we shall see, the meaning of 'species' is more fine-grained than its reference.)

If meaning is to be associated with some descriptive content – a description that gives conditions for the application of the concept, then to understand the meaning of a term we need to know the descriptive content. One standard, "classical" approach conceives the description in terms of a definition with a particular definitional structure, a set of singly necessary and jointly sufficient conditions for falling under the concept. The meaning of the concept term is then this set of necessary and sufficient conditions. [18] This does not rule out non-definitional descriptive content though. Alongside the definitional core is a set of conditions that are associated with the term, but in an "accidental" way.

The term *water*, for instance, has a theoretically provided definitional core based on its particular composition of two hydrogen atoms and one oxygen atom. But it also has a descriptive periphery: its density, freezing point, where it is found, its taste and appearance, recreational potential etc. On the classical approach, the term *species* similarly has a definitional core based on a set of singly necessary and jointly sufficient conditions, and a descriptive periphery. As argued here, the definitional core of *species* is constituted by the conditions that species are segments of a population lineage with cohesion and a distinct fate. These are singly necessary conditions – each one is required, and together they are sufficient for being a species taxon.

There are, however, other ways to think about definitional structure. One limitation of the classical approach is that it implies that falling under a concept is all or nothing. Either the necessary and sufficient conditions are satisfied or they are not. But it seems possible for this to be a matter of degree. The "cluster" approach asserts that something can fall under a concept to varying degrees depending on how many conditions are met, and how typical or characteristic the particular conditions satisfied are. [19] This way of thinking about concepts as probabilistic clusters of conditions has lead some to advocate a "prototype" or "exemplar" approach, where some instance of the concept that instantiates the core set of conditions comes to represent it as an exemplar or ideal instance. [19] Here there are then degrees of concept application. Something can more or less fall under a particular concept depending on how many and which conditions are satisfied, or how close the analogy is with the exemplar. Definitional structure on the cluster approach then, is a conceptual core that has greater definitional weight than other conditions, without thereby constituting a set of singly necessary and jointly sufficient condition. The definition of a term would then be some weighted cluster or other of the descriptive properties or conditions associated with the concept.

On this approach, *water* would still have a conceptual core, its molecular composition, but that may not be strictly necessary or sufficient. It might be that we would require some additional conditions. To count as *water*, there must some cluster of other conditions met. Perhaps we might require that it be made of up a certain range of proportion of "light" (with protium hydrogen atoms) versus "heavy water" (with deuterium hydrogen atoms). Or perhaps we might require some set of conditions related to functioning – safe for humans to drink etc.

But neither of these theories of meaning is fully adequate. Neither can answer questions about what determines the inclusion of conditions in the definition, or about how these conditions are related. They only designate the structure of concepts. What then determines the descriptive content and makes it cohere? Recently, an approach known as the "theory theory," has provided an answer to these questions. The idea is that the definitional structure of concepts is filled out and made coherent by some *theory*, scientific or otherwise, that contains the relevant concept. Chemical theory, for instance, gives the definitional conditions of the concept of *water* (whether the structure is classical or cluster) based on its molecular composition of two hydrogen atoms and one oxygen atom. Other descriptive conditions provided include freezing point, density, appearance and so on. These conditions *cohere* because the concept of water is given its meaning – definitional and descriptive content – by a chemical theory that identifies which attributes or conditions are important and how they are related. 'Found in beer and wine,' for instance, is an attribute of water that is unimportant according to chemical theory and is therefore not included in the definitional content.

So given the *theory theory*, which of the competing conceptual models is correct? I suspect that they are both applicable, depending on the concept. In the use of everyday non-technical concepts, such as 'vegetable,' the cluster model may be better. What counts as a *vegetable*, for instance, depends on a variety of factors, nutritive functioning, tradition, menu organization, etc. In a typical "meat and three" restaurant of the southern United States, for instance,

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french fries and peach cobbler sometimes count as vegetables for purposes of ordering from the menu. But in science, the conceptual structure may typically be more tightly specified and the classical model may better. What counts as a *quark*, *electron*, *element*, *compound*, *gene*, *population*, *reproduction*, *neuron*, etc. is in normal situations tightly specified by a well-defined set of definitional conditions, and the descriptive periphery does not play a significant role in determining whether something falls under a concept or not. (This may not be true in cases where the concept is still contested.) Similarly, for *species*, there might be a tightly specified structure and what counts as a species is limited to a well-defined conceptual core. More specifically, what makes something a species is determined by whether it is a segment of a population lineage with cohesion and distinctive fate, and nothing else is ultimately determinative. This is clearly more consistent with the classical approach.

This is not to say that there is no vagueness in the application of classical concepts. The condition themselves may be vague. In the case of species, what counts as a population may be borderline vague in the way that *town* and *city* are vague. There is no well-defined boundary between the two even if there are clearly significant differences in terms of size. Instead there is a range of population values that are borderline and could go either way. Similarly with *species*, there may be borderline vagueness in terms of *population*. There are no well-defined boundaries that demarcate non-populations and populations. There may also be vagueness (or perhaps ambiguity if there are several well-defined alternatives) in the other conditions. There might be different kinds of lineages, different kinds of cohesion, and different ways to think about evolutionary fates or trajectories.

This vagueness goes hand-in-hand with a *referential indeterminacy*. If the definitional conditions are vague or ambiguous, in the ways just outlined, then we may not know precisely how to apply the concept to the world. There may be groups of organisms that might be populations but not clearly and unambiguously so. Or there may be within some populations some level of cohesion, but not clearly and unambiguously enough cohesion to count as a species. In these cases, there is referential indeterminacy. It is not precisely clear how to apply the term *species*. [1] That is not to say, however, that the application of *species* is not restricted in some way. There will be a *reference potential*, limits within which the concept might be applied. Some groups of organisms clearly do not count as populations in the right way, and are therefore outside the reference potential. [1] In short, even though the classical conceptual structure may be unambiguous, the application of the concepts may still be problematic.

It may also be that a concept is not yet settled on theoretical grounds, in that there is some dispute about which definitional conditions are correct. This may be because there is some disagreement about the theoretical significance of certain conditions. After Darwin's *Origin*, for instance, speciation processes came to be important theoretically in thinking about species in a way that they were not before. Later theorists, especially those associated with the Modern Synthesis, developed a framework for thinking about speciation. In the terms William Whewell used, a species concept may become "explicated" – developed, refined and clarified as it gets applied to the world. [20, 1]

There are some important implications to this analysis of species concepts. First, there is an abstract, objective meaning constituted by a descriptive content associated with the term *species*, that is independent of any particular use of the term. This content is structured into a definitional core, determined in large part by the overarching theory of evolution, and a descriptive periphery, established at least in part by the contingent, empirical facts about those things that satisfy the theoretical definition. Included here are facts about morphological, behavioral, molecular similarities, processes operating in speciation and cohesion in both sexual and asexual organisms.

Second, this descriptive content is available in part or whole, to anyone who uses the term *species,* and has knowledge of evolutionary theory and the relevant empirical facts. Depending on context and interests though, focus may fall on either the definitional core or various parts of the descriptive periphery. Like the person for whom *water* means 'stuff to drink, bathe with, or swim in,' one could focus only on specific parts of the periphery. But he or she need not be thought of as denying that water is a compound of hydrogen and oxygen – whether or not he or she knows the molecular composition of water. Similarly, a person could concentrate on limited parts of the descriptive content of the term *species*, depending on theoretical or practical interests. This person could focus on reproductive isolation, genetic similarity or ecological functioning, without denying a theoretical definition of species that identifies species as segments of population lineages with cohesion and a distinctive fate – whether or not he or she is aware of that particular theoretical definition. So even if the subjective meaning of the terms *species* may vary in the actual usage of different researchers, there is an objective meaning of the term that is independent of the interests and backgrounds of those who use the term.

4. The demic structure of science

There is yet another factor relevant to a full understanding of the species problem. In the practice of science, scientists do not interact with *all* other scientists. Theoretical physicists, for instance, typically interact little with biologists. And even those within these disciplines scientists don't interact equally. Rather science gets practiced mostly within smaller groups. Vertebrate systematists, for instance, interact mostly just with other vertebrate systematists. And even within this group there are subgroups based on other factors such as the particular vertebrates studied, and whether molecules, morphology or behavior is the focus. Similarly geneticists who work on very specific problems are most likely to interact. There is then a hierarchy within the practice of science. Those within a particular discipline interact more than they do with those outside the discipline. And those within subdisciplines interact more. At the lowest level there are small groupings where the interaction is greatest. Following David Hull [21, 1], we can think of these small groups as *demes* - groups of interacting scientists that share distinctive subject matter, problems, methods and values.

Each of the demes may need to engage the species concept in various ways, depending on their distinctive interests, problems, methods and values. And most important for purposes here, each deme may focus on various parts of the descriptive content of the species concept, and ignore other parts. So a geneticist may not need to worry about the morphological similarity typical of species, or the historical dimensions of species in engaging the species concept. And an ecologist may not need to worry so much about genetic similarity. De Queiroz recognizes these differences in interests:

> The existence of diverse species concepts is not altogether unexpected, because concepts are based on properties that are of the greatest interest to subgroups of biologists. For example, biologists who study hybrid zones tend to emphasize reproductive barriers, whereas systematists tend to emphasize diagnosability and monophyly, and ecologists tend to emphasize niche differences. Paleontologists and museum taxonomists tend to emphasize morphological differences, and population geneticists and molecular systematists tend to emphasize genetic ones. [12]

We need not follow de Queiroz there though, in thinking of these as different concepts. Rather these are just different emphases on the descriptive content of the theoretical species concept. Moreover, researchers need not focus on just one part of the descriptive content. In behavioral genetics, both genes and behavior are obviously important. And for evolutionary theorists all aspects of species may be relevant.

What is important here is first that particular interests may guide how the members of each deme thinks about species. Second, this does not entail that across demes researchers are using different theoretical concepts. The primary theoretical concept is still available to all. And most importantly, the primary concept constrains the usage of the term *species*. A geneticist may, for instance, think about species in terms of genes, but not in ways that are inconsistent with the fact that species have two dimensions – populational and historical, as segments of population lineages. The bottom line is that researchers may focus on different parts of the descriptive content that constitute the objective meaning of the term *species*. Which part they focus on may be determined by contingent, pragmatic factors that are unique to their particular deme.

Not all of these uses of the species term across demes are equally authoritative though. There is a linguistic division of labor. Since evolutionary theory plays an important role in determining the definitional core of the term *species*, those who work most directly on evolutionary theory have some linguistic authority over the term *species.* Just as theoretical particle physicists have linguistic authority over terms like *quark* and tell us what quarks really are through a theoretical definition, evolutionary theorists have linguistic authority over the term *species*, and tell us what they really are through a theoretical definition. So what constitutes the definitional core of a term is determined by those with linguistic authority. What this means is that some uses of the term *species* are parasitic on other more constitutive uses. And just as anyone who uses the term *quark* should know and respect the authoritative meaning established by theoretical physicists, anyone who uses the term *species* should know and respect the authoritative meaning of that term as determined by those with linguistic authority.

The species problem has been in part a consequence of the neglect of two facts: first, there is a social hierarchy in science that governs interaction, ultimately into demes; and second, there is a division of linguistic labor that arises out of this hierarchy. Those who work in these demes do not always recognize or respect this division of linguistic labor, and sometimes treat their own usage as authoritative. If so, then it would *seem* that there really are different concepts in use. The invertebrate systematist's concept is seemingly not the vertebrate systematist's, which is not the ecologist's, and which is in turn not the evolutionary theorist's. Here the use of apparently inconsistent concepts is an illusion, generated by a misunderstanding of the structure and content of the theoretical species concept, and a neglect of the division of linguistic labor. By understanding all this, we can, in effect, "dissolve" the species problem

5. Conclusion

Some conceptual problems are relatively easy to solve. We propose or invent a new concept that works better. Or we modify a current concept to better serve theoretical purposes. Both kinds of solutions are central to the practice and progress of science. While these solutions are not easy in the sense that the solutions are always or even ever obvious, they are easy in that they are straightforward and uncomplicated. The species problem is not easy in this way though. Its solution requires a sophisticated understanding of how scientific concepts work, are structured and get content. It also requires an understanding of how they work within the social structure of science. This complexity explains the long-endurance of the species problem. In part, the understanding of how concepts work was lacking. Only recently do we have the theoretical framework to understand such conceptual problems. So, just as we need evolutionary theory to understand what species are, we need a satisfactory conceptual theory to understand complex conceptual problems like the species problem.

There are, however, worries still lurking. What if there are theoretically important differences between the various segments of population lineages that we are identifying as species? Perhaps there are crucial differences between vertebrates, invertebrates, fungi and bacteria such that they should not all be regarded as forming the same kinds of species. What if, on our best theoretical understanding, there really do seem to be different kinds of species things? Is there really then, a single, fully adequate species concept? Or might there be multiple, irreducible concepts? If so, then the species problem returns, and not just as an illusion.

Marc Ereshefsky argues for just this kind of possibility. He accepts the basic idea that species are genealogical - historical lineages, but denies that they are all the same kinds of lineages. First he begins by noting there are three main ways of thinking about species - in terms of interbreeding, ecology and monophyly. Then he argues that these are different kinds of lineages produced by different evolutionary forces.

The positive argument for species pluralism is simply this: according to contemporary biology, each of the three approaches to species highlights a real set of divisions in the organic world… All of the organisms on this planet belong to a single genealogical tree. The forces of evolution segment that tree into a number of different types of lineages, often causing the same organisms to belong to more than one type of lineage. The evolutionary forces at work here include interbreeding, selection, genetic homeostasis, common descent, and developmental canalization… The resultant lineages include lineages that form interbreeding units, lineages that form ecological units, and lineages that form monophyletic taxa. [22]

These different kinds of lineage concepts apply in different ways to biodiversity. Some organisms, for instance, may not form ecological lineages. Consequently, that lineage concept would therefore not apply.

It is not initially obvious how to respond to Ereshefsky's pluralism. He considers and then rejects the suggestion that there is an additional parameter that can unite these three different kinds of lineages under one conception. [22] But at some level he seems to be already thinking of them under one conception. To even think of them *as three kinds of lineages* seems to assume that there is an overarching, more general way of thinking about species based on the idea of a lineage. It seems that if the theoretical concept is general enough, then surely it can be universal.

More worrisome perhaps, what if the species concept itself is ultimately unnecessary and misguided, the way the outdated ideas of *phlogiston* and *vital force* are? From my perspective as a philosopher, this anti-realist worry is abstract and not given much force by either evolutionary theory or what we know about the world. Nonetheless it cannot by dismissed on purely philosophical grounds. The answer, I believe, will be found ultimately in the practice of science. Is the theoretical species concept discussed here ultimately necessary for the practice of the biological sciences? It seems to me that it is, but the future might prove otherwise.

Author details

Richard A. Richards

University of Alabama, Tuscaloosa, Alabama, USA

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