

Why does the species problem still persist?

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Summary

Despite many years of discussion, the species problem has still not been adequately resolved. Why is this the case? Here I discuss two recent suggested answers to this question that place the blame on the species problem's empirical aspects or on its philosophical aspects. In contrast, I argue that neither of these two faces of the species problem constitute the principal cause of the species problem's persistence. Rather, they are merely symptoms of the real cause: the species problem has not yet gone away because of a failure to recognize that not one but a number of distinct concepts are at the heart of the problem. To illustrate this point, a recently proposed solution to the problem is examined: the suggestion to understand the concept of species as a family resemblance concept. *BioEssays* 26:300–305, 2004.

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Introduction

Almost half a century ago, in his preface to a special symposium volume on the species problem,⁽¹⁾ the biologist Ernst Mayr summarized the situation with respect to the issue thus:

“Few biological problems have remained as constantly challenging through the past two centuries as the species problem. Time after time attempts were made to (...) 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.”

Unfortunately, Mayr's words still apply today; several dozens of competing definitions of the notion of species are readily available in the literature (for a sample, see Ref. 2), but no solution has yet been found that can put the species problem to rest once and for all.

Since the species problem has certainly not suffered from a lack of attention, one may wonder why it is that the problem still

continues to persist and whether a definitive solution is at all possible. In the present paper, I address this question by considering two issues. The first pertains to the nature of the species problem. In recent discussions of this topic,^(3–5) the problem's empirical side and, alternatively, its philosophical aspects have been advanced as the primary factors responsible for the problem's persistence. In contrast, I suggest that the empirical and philosophical issues that arise in the context of the species problem are, in most cases, merely the symptoms of the real reason why the species problem continues to resist a definitive solution. This underlying reason is the failure to recognize that the problem is not one regarding a single scientific concept, the concept of species, but rather one that involves a number of distinct scientific concepts, conflated under the same name. In other words: 'species' is a homonymic term. I have extensively discussed this position (which has been pointed out earlier by Kornet⁽⁶⁾) elsewhere⁽⁷⁾ and I shall outline it only briefly here. The second issue considered here, as an illustration of the above point, is the recent proposal that the species problem can be resolved by understanding the notion of species as a family resemblance concept. I argue that because of the failure to distinguish between the different meanings of 'species', this proposal cannot yield a final solution to the problem.

Why is the species problem still here and whose problem is it anyway?

Recently, it has been questioned why the species problem continues to persist, rather than having been resolved decades ago. Hey,^(3,4) for example, suggested that a wrong approach to the species problem had been taken all along: in addressing the problem, too much emphasis has been placed on philosophical matters. Instead, the problem should be conceived as primarily a scientific problem, to be tackled by means of empirical investigation. At the root of Hey's position lies the observation that “[t]he 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” (Ref. 3, p. 329; cf. Ref. 4, pp. 105–110). According to Hey, the first motivation cannot be realized in any nonarbitrary way. That is, attempts to devise categories that can be used to order organismal diversity will not generally result in natural categories, i.e., categories that exist independently of the context of human investigation. Primacy, in Hey's view, should therefore be placed on the latter

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motivation, i.e., the study of the units that feature in evolution. And this is in the first place a task for empirical science.

Contradicting Hey's suggestion, Pigliucci⁽⁵⁾ has recently argued that the species problem cannot be solved by empirical investigation alone:

“the species problem has not gone away for the all-important reason that it is not the sort of empirical problem that can be solved by biologists alone. (...) it is a prime example of a philosophical question that requires input from empirical science (...)” (p. 599).

This view of the problem has also been taken by other participants in the discussions on the topic. In a classic paper from 1974, for example, the biologist Ghiselin⁽⁸⁾ stated that “[t]he species problem has to do with biology, but is fundamentally a philosophical problem (...) [W]e should note that we often fail to solve our problems because we cannot even identify them. Under such circumstances, conceptual investigations do more than just help. They are the only way out” (pp. 541 & 543).

If Pigliucci's and Ghiselin's assertions are correct (and I think they are), this brings about some interesting issues regarding the division of labor between philosophy of science and science itself. For one, it would be desirable to specify which aspects of the species problem are to be addressed by means of philosophical inquiry and which aspects are more suitable to be addressed empirically. Another issue would be whether the philosophical and the empirical work on the problem can be conducted largely independently, or should be done in close cooperation between the two domains of investigation. These issues cannot be properly addressed here, but the history of the species problem indicates that the problem is a concern of both fields of investigation and that cooperation is a fruitful way to approach the issue.⁽⁹⁾ The extensive crossovers that have happened between the two domains of investigation on the species problem have not only resulted in a large volume of literature on the topic, but also in a couple of new philosophical insights. One of these, generally considered a major breakthrough in philosophy of biology and endorsed today by many participants in the debate on the species problem, is, for instance, the thesis that species should be attributed the ontological status of individuals rather than classes.^(8,10–12) Yet, this ‘species-are-individuals’ thesis has not been able to set the species debate to rest and has itself become a topic of discussion (for recent opposition against the species-are-individuals thesis, see for example Ruse⁽¹³⁾). The same holds with respect to other important insights regarding the species problem, such as species pluralism (which is discussed later in this paper). Notwithstanding the close cooperation between philosophy and science, the species problem still stands.

This indeed suggests that the philosophical aspects of the species problem constitute an important factor in the

problem's persistence, making it a problem that cannot be solved by gathering more empirical data alone. There is, however, reason to suspect that the philosophical aspects of the problem (as well as its empirical aspects, for that matter), however difficult they may be to resolve, by themselves do not constitute the fundamental cause of the species problem's persistence but merely constitute the symptoms of an underlying causal factor (cf. Ref. 1, p. 10). This can be seen by considering the multitude of extant definitions of the notion of species, many of which are applied regularly in empirical studies. The application of the different available definitions to a given group of organisms in many cases yields several incompatible groupings of these organisms into tentative species. All of these tentative species constitute useful groupings for scientific study, suggesting that they are associated with different scientific concepts. Moreover, investigators working in different domains of biological science often pose incompatible demands on the notion of species,^(6,14) depending on the role of this notion in addressing the particular research questions at stake in their field of investigation. The diversity of available definitions of the notion of species reflects this diversity of demands. The suggestion that these different demands pertain to one single scientific concept—one all-purpose species concept—inevitably results in failure to achieve a final solution of the species question in the form of a unique definition of the concept of species (or at least a set of definitions containing a unique definition for each organism group). After all, any solution to the issue that meets some of the requirements placed on the notion of species will fail to meet other, incompatible ones. One way to resolve this predicament is by recognizing that, in different contexts of investigation, distinct concepts are at stake that however all are denoted with the term ‘species’. This, then, is the underlying reason for the species problem's persistence. As a consequence, the empirical and philosophical questions that have been addressed extensively in the discussions on the species problem then also rise with respect to each of the involved concepts separately.

How did this situation come about? On several occasions in the developmental history of biological science, the term ‘species’ has taken on a new meaning. When the Modern Synthesis was created and the widely used *Biological Species Concept* introduced, for example, the meaning of ‘species’ changed from its traditional denotation of classes of organisms to denoting groups of reproductively connected populations. The old meaning of ‘species’ was however not abandoned completely and the two meanings continued to coexist and to be used in biological investigations (cf. Ref. 15, pp. 108–111). As a consequence of several such changes in the meaning of ‘species’, biologists today use the same term to denote a number of distinct scientific concepts. I have argued for this perspective on the species problem extensively in a different paper⁽⁷⁾ and shall illustrate it only briefly here.

Examination of what biologists mean when they use the term 'species' shows the term to refer to four distinct kinds of things: units that participate as wholes in evolutionary processes (units of evolution), segments of phylogenetic trees (phylogenetic taxa, i.e., historical pattern segments), kinds of organisms, and kinds of populations. From an ontological point of view, units of evolution and phylogenetic taxa both are individuals (although they are individuals of different kinds), whereas kinds of organisms and kinds of populations have the ontological status of classes. The differences between these four kinds of things become clearer when their material composition is considered. Units that participate as wholes in evolutionary processes must be composed of synchronously living organisms, whereas phylogenetic taxa encompass organisms from the present as well as from the near and the more distant past. In addition, kinds of organisms have individual organisms as their members, while kinds of populations have populations rather than organisms as their members. For further discussion, I refer to Ref. 7, where examples are given that show that all these four kinds of things are being referred to as 'species' in current biological discourse. (It is important to note here that, in my view, the different concepts at stake are not *species* concepts in the sense that they are interconnected concepts that can be subsumed under one overarching concept of species; they are independent scientific concepts that merely share the same name.)

If the perspective on the species problem sketched above is correct, this sheds new light on several issues that have been topics of debate in the context of the species problem. Important topics among these are species pluralism, the species-are-individuals thesis and the question of species as natural kinds. To illustrate this, I now turn to a recent attempt to resolve the species problem by understanding the notion of species as a family resemblance concept. Because this attempt fails to distinguish between the different concepts called 'species', I argue that it fails as a definitive solution to the species problem.

Species as a family resemblance concept

The notion of family resemblance concepts was introduced by the philosopher Wittgenstein in his *Philosophical Investigations*.⁽¹⁶⁾ The classic example of a family resemblance concept is the concept of game. Although there is general agreement among the members of the language community in which the term 'game' is being used on which things are included in the category of games, it is not possible to identify any characteristics that all and only games have in common:

"What is common to them all? (...) if you look at them you will not see something that is common to all, but similarities, relationships, and a whole series of them at that. (...) We see a complicated network of similarities overlapping and criss-crossing (...)" (Ref. 16, sec. 66; cf. sec. 67).

In other words, games do not possess essential properties in the sense that they do not possess any properties that are both necessary and sufficient for a given phenomenon to be included in the category of games. Given the problems confronting classic essentialism regarding species taxa, it would seem a natural move to understand species taxa as family resemblance classes (cf. Ref. 9; an early example is Ref. 17, pp. 22–25 & 64ff.). Yet, in practical applications this approach is confronted with serious problems; the placement of species boundaries, for instance, seems to become too much a matter of subjective judgement rather than of finding the natural state of affairs (cf. Ref. 13).

In the above perspective, individual species taxa are understood as families in the Wittgensteinian sense. An alternative move is to understand not individual species taxa but the species category (i.e., the category containing all past, present and future species) as a family of natural entities. This move was recently suggested by Pigliucci,⁽⁵⁾ thereby presenting a novel application of Wittgenstein's notion of family resemblance in the species debate (but Ref. 17, p. 64, and Ref. 18, p. 53, seem to constitute precursors to this approach):

"species is a family resemblance concept whose underpinning is to be found in a series of characteristics such as phylogenetic relationships, genetic similarity, reproductive compatibility and ecological characteristics. These traits take on more or less relevance depending on the specific group one is interested as a function of the particular biology of that group" (Ref. 5, p. 601).

This position acknowledges that various types of species exist in nature and that, when studying a particular group of organisms, we ought to focus on those features that are the most important with respect to the origin and maintenance of species in the case at hand. Next to rendering the use of the notion of species in research practice more adequate to the messiness of biological reality (Ref. 5, p. 601; Ref. 18, p. 55), this perspective on the concept of species can according to Pigliucci also explain why biological science has been able to proceed successfully all this time without being bothered by the persistent unclarity regarding the nature of species. In the case of the concept of game, for instance, the impossibility of defining precisely what a game is does not hamper our ability to speak meaningfully about games and to illustrate what we mean by giving examples of actual games (Ref. 16, sec. 69 & 71). The same holds for the concept of species: "(...) as biologists we *teach* our students what species are by example. (...) For our purposes as biologists, we can draw on one set of threads or another to work with particular species, depending on what taxonomic group we are considering" (Ref. 5, p. 600). Thus, although there exists a single concept of species valid for the whole of biological science, it is associated with a category of very diverse species taxa and must consequently

be defined differently in different domains of biodiversity and for different research purposes. But can this approach constitute a solution to the species problem?

Species pluralism and family resemblance concepts

Answering this question invokes the idea of species pluralism. Although Pigliucci (Ref. 5 and pers. comm.) rightly emphasizes that his approach is different from the various pluralist approaches that are already available in the literature, there seems to be an important similarity between these two types of approach that is fatal to both. To clarify this point, let us see how Pigliucci's position relates to the different forms of pluralism.

Notwithstanding their sometimes profound differences, the various pluralist positions regarding the notion of species that have been proposed can be classified into two overarching (but not sharply delimited) types.^(7,19,20) The more radical type of species pluralism holds that the species concept can be broken down into a number of—to some extent—independent subconcepts that can be applied to *the same* organisms depending on the question under consideration. Ereshefsky, for example, holds that “An organism may belong to two different types of species at the same time. For example, a single organism may belong to both an interbreeding species and a phylogenetic species even though those species are not fully co-extensive” (Ref. 21, p. 106). This type of pluralism has also been prominently advocated by philosophers such as Dupré⁽²²⁾ (although in later work Dupré took a less radical position; Ref. 23, p. 18) and Kitcher.⁽²⁴⁾ The other, less radical, type of species pluralism is purely definitional in nature; this form of pluralism is advocated by, among others, Mishler and Brandon: “a single, optimal general-purpose classification exists for each particular situation, but (...) the criteria applied in each situation may well be different” (Ref. 19, p. 403). Here it is not the case that there are several distinct species concepts that can be applied to the same organisms depending on the research question at stake, but rather there are several different definitions of the concept of species that each apply to particular organism groups for all research questions that can be considered with respect to these groups. This less radical type of pluralism is only pluralist insofar as it allows the existence of different kinds of species; in holding that these different kinds of species exist in different regions of the organismal world and that every organism belongs to precisely one species, it is a monist rather than a pluralist position. (Ereshefsky,⁽²¹⁾ for example, places emphasis on this difference between his type of species pluralism and Mishler and Brandon's less radical type.)

The difference between the two types of pluralism may be illustrated as follows. From a radical pluralist perspective, when studying for example the cichlid fish in Lake Victoria we may choose the concept adequate to our investigatory

purposes: a historical concept based on common descent when investigating the phylogenetic relations between the various groups present in the lake and a concept based on structural similarity when studying their functional morphology. (Note that although these concepts are to some extent independent, they are similar at a basic level in that they all are *species* concepts. One can be a pluralist, after all, only with respect to things that are at some level the same. Cf. Ref. 7.) From a less radical pluralist perspective, no such thing is allowed: one unique definition of the species concept applies to the Lake Victoria cichlids, but this may very well be a completely different definition from the one that applies to, say, the orchids in the forests of Java. Yet, all definitions are definitions of one concept, i.e., the species concept.

The position that the concept of species is a family resemblance concept is opposed to “[t]he pluralist suggestion (...) that there are equally legitimate, *conceptually independent*, species concepts that can be used depending on the interest of the investigator” (Ref. 5, p. 601, original italics). Instead,

“species represent one large cluster of natural entities, quite independently of the interests of human observers. This cluster, however, is a loose one, with its members connected by a dense series of threads, not all of which go through every single instantiation of the concept” (*ibid*).

The species problem is thus seen as involving a single scientific concept. Since the members of the species category, i.e., all actual species taxa, are interconnected by a complex network of biological factors that hold between some but not all species taxa, the species issue is best approached on a case-by-case basis, focusing on those factors that are relevant in a particular case. While rejecting central parts of both types of species pluralism (i.e., the radical pluralist view that there exist several independent species concepts and the less radical pluralist view that the species concept is to be defined differently for different organism groups, with one definition per organism group), this position does retain other important pluralist aspects. Firstly, even though there is no property that all members of the species category have in common, they all are *species* in that they are considered instances of the same scientific concept. As species taxa, i.e., instances of the same concept, they occupy similar positions in biological theory. This corresponds to the basic assertion found (sometimes implicitly) in both the more radical and the less radical forms of species pluralism that, even though the species category consists of different kinds of things, it is still meaningful to retain the species category as a distinct scientific category.^(7,19,22–24) Secondly, emphasis is being placed on the need for various operational definitions of the species concept, rather than a single one, due to the diversity of natural factors that play a role in the origin and maintenance of

different actual species. This is illustrated by Pigliucci's⁽⁵⁾ suggestion that Templeton's^(2,25) *Cohesion Species Concept* comes close to the idea that the concept of species is a family resemblance concept. Templeton defines species as "populations of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (Ref. 25, p. 12), while various such cohesion mechanisms can be identified in nature (see Ref. 25, Table 2). This yields a situation in which different operational definitions of the concept of species exist, focusing on different cohesion mechanisms. Depending on the research question at stake and the particular biology of the species taxon under study, different operational definitions are to be used in different cases, although no single all-purpose definition exists in any case (Pigliucci, pers comm). While rejecting the idea of one all-purpose definition of species per organism group, the idea is retained that different operational definitions of the notion of species can be used that in the end all define *species*.

So, why does this approach fail as a definitive solution to the species problem? The main problem with species pluralism in any form is a clash with the practice of biological research. Several dozens of competing definitions of the concept of species are readily available in the literature. As said above, in many cases, the application of different definitions to the same group of organisms leads to incompatible groupings of these organisms into species (see Refs. 5,7,14,26, pp. 129,130; but see Ref. 13 for a dissenting viewpoint). When adopting a form of radical pluralism, these diverse groupings of the same organisms into species are all considered legitimate and scientifically useful (be it perhaps in various degrees). But, then, why do all these various ways of clustering organisms yield *species*? Less radical forms of pluralism avoid this issue by identifying one particular way of clustering into species as the correct one for a given group of organisms. The problem now is not so much why all the various legitimate ways of clustering organisms yield species, but which of the various ways of clustering is the one correct way of obtaining species as they exist in nature in any given case. This problem cannot be resolved, because the various possible groupings of the same organisms stand at the focus of different contexts of biological research where they are seen as natural groups that legitimately stand at the focus of scientific study (see Ref. 7 for further discussion). Although the position advocated by Pigliucci cannot be seen either as a form of radical pluralism or as a form of less radical pluralism in the sense discussed above (because of its rejection of the view that there is precisely one adequate definition of the notion of species per organism group—perhaps it should be considered a third form of species pluralism for this reason), it does face this latter problem. Central in his position is the assumption quoted above that "species represent one large cluster of natural entities, quite independently of the interests of human observers" (Ref. 5, p. 601). Given that the various species

definitions available in the literature yield different clusterings of organisms when applied to the same group of organisms, the question is thus how to identify which definition gives us *the* natural clustering into species. (Note that on the view that the term 'species' denotes multiple concepts the above problems do not arise, for each grouping of organisms into tentative species can be understood as being associated with a different concept.)

Conclusion

It is certainly true that the species problem is "a paradigmatic example of a philosophical question that requires empirical information (provided by science) to be settled, not of a scientific problem with unwelcome philosophical characteristics" (Ref. 5, p. 596). But despite the large amount of work that has been done on both the empirical and the philosophical aspects of the problem, still no adequate solution to the problem has been found. In the above discussion, I have attempted to show that the reason for this failure to resolve the species problem has more to do with the historical development of biological science than with the philosophical nature of the problem: the term 'species' has come to denote a number of distinct scientific concepts that occupy different positions in the conceptual framework of biological science. From this perspective on the species problem it can be seen why the various forms of species pluralism, as well as the view of the notion of species as a family resemblance concept, cannot constitute good solutions to the problem. In addition, it provides a new starting point for further empirical and philosophical work on the species problem.

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