

# Darwin's solution to the species problem

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**Abstract** Biologists and philosophers that debate the existence of the species category fall into two camps. Some believe that the species category does not exist and the term 'species' should be eliminated from biology. Others believe that with new biological insights or the application of philosophical ideas, we can be confident that the species category exists. This paper offers a different approach to the species problem. We should be skeptical of the species category, but not skeptical of the existence of those taxa biologists call 'species.' And despite skepticism over the species category, there are pragmatic reasons for keeping the word 'species.' This approach to the species problem is not new. Darwin employed a similar strategy to the species problem 150 years ago.

**Keywords** Darwin · Species · Species problem · Species category · Family resemblance · General lineage concept · Homeostatic property cluster theory

## 1 Introduction

The debate over the nature of biological species has many aspects. One question is the biological nature of species: are they groups of interbreeding organisms, phylogenetic branches on the Tree of Life, or something else? Then there is the ontological question: are species natural kinds, sets, or individuals? Recently, the debate over species has been pitched at a higher hierarchical level. Instead of arguing over the nature of species taxa, much discussion focuses on whether the species category—the theoretically defined category of all species taxa—exists. Those biologists and philosophers that discuss the existence of the species category fall into two camps. Skeptics argue

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that the species category does not exist (Ereshefsky 1998, 2001; Mishler 1999, 2003; Hendry et al. 2000; Pleijel and Rouse 2000a,b; Fisher 2006). Many of those skeptics also suggest that the term ‘species’ should be eliminated from biology. Defenders of the species category respond that with more theoretical knowledge and perhaps a bit of philosophical reasoning we can be confident that the species category exists (de Queiroz 1999, 2005, 2007; Mayden 2002; Pigliucci 2003; Pigliucci and Kaplan 2006; Lee 2003; Wilson 2005; Wilson et al. 2009).

This paper suggests a different approach to the species problem. This approach is far from new, because Darwin employed a similar strategy to the species problem 150 years ago. Darwin’s solution, as I will call it, is threefold. First, we should recognize that the species category is not a real category in nature. Second, despite skepticism over the species category, we should not be skeptical of those taxa biologists call ‘species.’ Third, despite skepticism over the species category, there are pragmatic reasons for retaining the word ‘species’ in biology. The claim that Darwin was skeptical of the species category is not new (Ghiselin 1969; Beatty 1992; Hodge 1987), though it is contested (Stamos 1996, 2007). What is new is the relevance of Darwin’s solution to current debates over the species problem. On the theoretical side, Darwin’s solution is supported by contemporary biology and offers a stronger answer to the species problem than recent attempts to save the species category. On the practical side, Darwin’s solution frees us from the endless search for the correct theoretical definition of ‘species,’ while at the same time not requiring that we reform biological discourse by dropping the word ‘species.’

The next section of the paper outlines Darwin’s solution to the species problem. Section 3 suggests that Darwin’s solution is confirmed by contemporary biological theory. Section 4 critically evaluates prominent biological and philosophical defenses of the species category. And Sect. 5 explains why we ought to keep the term ‘species’ despite skepticism over the species category.

## 2 Darwin and the species problem

The distinction between species taxa and the species category is central to Darwin’s solution. *Species taxa* are groups of organisms. *Homo sapiens* and *Canis familiaris* are examples of species taxa. The *species category* contains all species taxa, but is not merely the class or aggregate of all species taxa. If the species category exists, it is distinct from the other Linnaean categories. Furthermore, the species category, as a scientific category, should be an explanatory category (Devitt 2008). Knowing that a taxon belongs to the species category should help us understand why that taxon has certain features. For example, if we know that a taxon is a species and we adopt the interbreeding approach to species, then we can cite that taxon’s being a population of interbreeding organisms to explain why that taxon evolves as a cohesive evolutionary unit (see Sect. 3).

Darwin’s solution relies on the distinction between species taxa and the species category. As we shall see, Darwin believed that those taxa called ‘species’ by competent naturalists exist, but he doubted the existence of the species category. Let us start with

Darwin's observations concerning the species category, and then turn to what he said about species taxa and the term 'species.'

A good place to start is with Darwin's letter to his friend Joseph Hooker.

It is really laughable to see what different ideas are prominent in various naturalists' minds, when they speak of 'species'; in some, resemblance is everything and descent of little weight—in some, resemblance seems to go for nothing, and Creation the reigning idea—in some, sterility an unfailling test, with others it is not worth a farthing. It all comes, I believe, from trying to define the indefinable. (December 24, 1856; in [Darwin 1877](#), vol. 2, p. 88)

In this letter, Darwin highlights the species problem by observing that biologists offer different definitions of 'species.' Darwin's diagnosis of the species problem is that biologists are trying to define the "indefinable." Notice that in discussing the species problem, Darwin is not discussing whether a particular species concept is right or wrong. His concern is broader: he questions the entire project of trying to define 'species.'

Why did Darwin think that 'species' is indefinable? Because he doubted the distinction between species and varieties. For example, in the *Origin of Species* he writes, "I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety" (1859[1964], p. 52). Similar remarks are found in his manuscript *Natural Selection* (1975, p. 98). It might sound odd to assert that Darwin doubted the distinction between species and varieties. After all, he wrote a famous book called *On the Origin of Species*, and much is made of the word 'species' in that title (see [Mayr 1963](#), p. 12; [Futuyma 1998](#), p. 449). However, that was not the original title Darwin had in mind for the *Origin*. He first suggested *An Abstract of an Essay on the Origin of Species and Varieties* ([Browne 2006](#), p. 82). His publisher thought that title was too long, so Darwin dropped the words 'an abstract of an essay' and 'and varieties.' We should not read too much into the occurrence of the word 'species' in the title of Darwin's famous book.

Why was Darwin skeptical of the distinction between species and varieties? The *Origin* contains a number of reasons. Most focus on the lack of a process distinction between species and varieties. For instance, in Chap.8 of the *Origin*, titled 'Hybridism,' Darwin spends considerable time arguing against the idea that hybrid sterility marks a boundary between varieties and species. Earlier naturalists, such as John Ray and Buffon, held that interbreeding among organisms in varieties of the same species produces fertile offspring, whereas interbreeding among organisms from different species produces sterile offspring ([Ghiselin 1969](#), p. 94; [Beatty 1992](#), p. 299). Darwin lists numerous examples where this distinction between species and varieties fails (1859[1964], 248ff., 269ff.). He writes that from these examples, "It can thus be shown that neither sterility nor fertility affords a clear distinction between species and varieties" (1859[1964], p. 248). And he goes even further. In the summary of the chapter on hybridism he writes, "Finally, then, the facts briefly given in this chapter do not seem to be opposed to, but even rather to support the view, that there is no fundamental distinction between species and varieties" (1859[1964], p. 278).

According to Darwin, another key process that fails to distinguish species from varieties is selection. This is important, for as Mallet (2008) and Kohn (2008) argue, Darwin thought that the origin of both varieties and species is due to divergent selection. In Chap. 4 of the *Origin*, titled ‘Natural Selection,’ Darwin offers *The Principle of Character Divergence* (1859[1964], 111ff.). The Principle of Character Divergence has a familiar Darwinian starting point. Suppose that a geographic region contains several closely related groups of organisms. Within one of those groups, some organisms are selected because they have a trait that gives them an adaptive advantage. Divergent selection occurs in future generations when organisms with even better adapted forms of that trait are selected, eventually causing pronounced morphological gaps between that group of organisms and its parent and sister groups (1859[1964], 112ff.). Darwin illustrates this process with a number of examples. Consider his example of a pigeon fancier (1859[1964], p. 112). A pigeon fancier is struck by the slightly longer beak of some birds. He then selects birds with slightly longer beaks in that generation, and continues to do so in subsequent generations until there is a pronounced morphological gap between the selected group and the original stock. Along with this example, Darwin offers examples of divergent selection occurring in his own experiments and in the wild (1859[1964], 113ff.).

The relevant point for us is that no special speciation mechanism marks the difference between species and varieties. As Kohn (2008, p. 88) notes, Darwin did not use the word ‘speciation’ in the *Origin*. This word is familiar to us, but it is not a word that Darwin used. For Darwin, the origin of varieties and species is due to divergent selection. As Darwin writes: “The origin of the existence of groups subordinate to groups, is the same with varieties as with species, namely, closeness of descent with various degrees of modification” (1859[1964], p. 423).

Darwin had an overriding reason for tearing down the distinction between species and variety. Earlier versions of that distinction proposed by John Ray, Buffon, and Lyell relied on the assumption that the origin of species was due to a special process that distinguishes species from varieties: God created species but no other type of taxa (Coleman 1962; Ghiselin 1969; Beatty 1992). Darwin, of course, had a different view of the origin of taxa. For him all types of taxa are the result of the same process, namely selection. Thus at the end of the *Origin*, he writes, “On the view that species are only strongly marked and permanent varieties... we can see why it is that no line of demarcation can be drawn between species, commonly supposed to have been produced by special acts of creation, and varieties which are acknowledged to have been produced by secondary laws” (1859[1964], p. 469). Species and varieties are made by the same process. Hence the creationist distinction between species and varieties is disconfirmed.

So far I have suggested that Darwin doubted the distinction between species and varieties and without such a distinction there is no distinct species category in nature. What about those taxa that biologists call ‘species’? Was Darwin skeptical of the existence of those taxa? It seems fairly clear that he was a realist when it comes to those taxa identified by competent naturalists. An often cited passage from *Origin’s* chapter on classification, Chap. 13, confirms this. Darwin writes that “[f]rom the first dawn of life, all organic beings are found to resemble each other in descending degrees, so that they can be classed in groups under groups. This classification is evidently not

arbitrary like the grouping of the stars in constellations” (1859[1964], p. 411). Darwin thought the groups identified by competent naturalists could be real. His skepticism of the species category did not extend to taxa, and in particular those taxa called ‘species.’

Given that Darwin was skeptical of the species category, what did he mean by the term ‘species’? After all, he used that term throughout the *Origin* and elsewhere. Darwin was clear what he meant by ‘species.’ In *Natural Selection* he writes: “I mean by species, those collections of individuals, which have commonly been so designated by naturalists” (1975, p. 98; also see 1859[1964], p. 47). According to Beatty (1992, p. 231) and Ghiselin (1969, p. 95), Darwin used the terms ‘species’ and ‘variety’ in a referential way. ‘Species’ merely refers to those taxa that competent naturalists call ‘species.’ The meaning of ‘species’ is simply “those taxa that competent biologists call ‘species.’” For Darwin, the term ‘species’ has no theoretical meaning. Darwin is explicit about this in his letter to Hooker where he writes that the term is “indefinable” (December 24, 1856). But there still remains the question, why did Darwin keep using the word ‘species’ given his skepticism of the species category? Beatty (1992) suggests that Darwin kept using it for pragmatic reasons. Beatty argues that Darwin’s primary objective in the *Origin* was to convince biologists of his theory of natural selection. Attempting to reform language would get in the way of that objective. So Darwin kept using ‘species’ but denied it had any theoretical meaning other than that the word referred to those lineages called ‘species’ by competent naturalists. That way Darwin could communicate his theory to others by arguing that those lineages called ‘species’ are the result of natural selection. At the same time he did not have to undertake the impractical task of telling biologists to stop using the word ‘species.’

Not surprisingly, some biologists reject Darwin’s skepticism concerning the species category. A prominent response is given by Mayr (1963, 1969, 1982, pp. 265–269) and Ghiselin (1969, Chap. 4). They believe that Darwin was right to be skeptical about the existence of the species category, given the state of biology in his time. Their diagnosis of Darwin’s error is that Darwin was biologically naïve when it came to species. For example, Mayr writes “Darwin failed to solve the problem indicated by the title of his work. ... I have examined the reasons for this failure (Mayr 1959) and found that among them was Darwin’s lack of understanding the nature of species” (1963, p. 12). In brief, Mayr and Ghiselin argue that given today’s biological theory, Darwin’s skepticism of the species category is unwarranted.

I disagree with this response to Darwin’s skepticism for two reasons. First, Mayr and Ghiselin miss the primary target of Darwin’s discussion of the species problem. Darwin’s concern was not getting the right species concept, but whether the species category exists at all. Recall that in his letter to Hooker, Darwin writes that the word ‘species’ is “indefinable” (December 24, 1856); and in the *Origin*, he writes that the essence of the term ‘species’ is “undiscoverable” (1859[1964], pp. 484–485). Darwin’s primary concern with the species category was the relationship between the species/variety distinction and his notion of divergent selection. Creationism supports that distinction, his theory of selection undermines it. Darwin’s principal concern with the species category was whether its existence is inconsistent with his theory, not choosing the correct species concept.

The second reason Mayr and Ghiselin’s response to Darwin’s skepticism fails has to do with the current state of biological theory. Mayr and Ghiselin write that if

Darwin were alive today, he would have a satisfactory account of species—namely the Biological Species Concept. Their writings imply the hypothetical: if Darwin had known about the Biological Species Concept, he would not have been skeptical of the species category. My concern is not with that hypothetical. My concern is that despite the development of the Biological Species Concept, we still have reason to doubt the species category. That is, I believe that Mayr and Ghiselin are wrong to say that the species problem has been solved by contemporary biology. In what follows, I argue that contemporary biology has not overturned Darwin's skepticism. Quite the contrary. Current biological theory confirms Darwin's solution to the species problem.

### 3 The species problem in contemporary biology

As we saw in Darwin's letter to Hooker, biologists in Darwin's time offered different definitions of 'species.' Biologists still disagree over the definition of 'species,' and the number of proposed species concepts has increased. A recent article on species lists no less than 24 species concepts in biology (Hey 2001). Let us focus on the two most prominent approaches to species in current biology, the interbreeding and phylogenetic approaches. The best known example of the interbreeding approach is Mayr's Biological Species Concept. Mayr writes that: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (1970, p. 12). According to the interbreeding approach, the members of a species exchange genes through interbreeding, and a species is protected from foreign genes by 'reproductive isolating mechanisms' that prevent successful interbreeding with members of other species.

The phylogenetic approach is proposed by cladists. Cladism's founder, Hennig (1966), suggested that biological classifications should represent complete branches on the Tree of Life. More technically, Hennig suggested that all taxa must be *monophyletic*: monophyletic taxa consist of all and only the descendants of a common ancestor. Hennig did not apply the notion of monophyly to species, but other cladists have. There are many species concepts with the name 'the phylogenetic species concept' and they offer different definitions of 'species' (Baum and Donoghue 1995). Here I will just focus on phylogenetic species concepts that require that species taxa are monophyletic. A representative sample of this type of phylogenetic species concept is found in the work of Mishler and co-workers. For instance, Mishler and Theriot write that species are "the smallest monophyletic groups deemed worthy of recognition" (2000, p. 47).

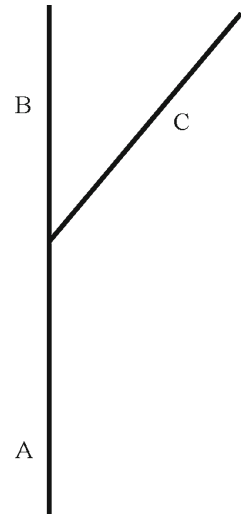
As many have observed, the phylogenetic and interbreeding approaches to species pick out different types of taxa in the world (Kitcher 1984; de Queiroz and Donoghue 1988; Dupré 1993; Ereshefsky 2001; LaPorte 2005). That discrepancy, I will suggest, implies that Darwin's skepticism of the species category is correct. Here is a quick sketch of that argument; the details will follow. First, the interbreeding and phylogenetic approaches to species carve the Tree of Life into different types of lineages: interbreeding and phylogenetic lineages. Second, each type of lineage is significant for understanding evolution on this planet, so neither the interbreeding nor the phylogenetic approach is more entitled to the term 'species.' At the same time, neither of

those approaches should be excluded, because each captures an important aspect of the organic world. Third, if the class of taxa called ‘species’ is truly heterogeneous, then we have reason to doubt the existence of the species category. The argument offered here has the same conclusion as Darwin’s solution, but it differs from Darwin’s argument. His argument is based on his skepticism of the species/variety distinction, while the argument offered here turns on the heterogeneous nature of the class of taxa called ‘species.’ Neither argument casts doubt on the existence of those taxa that biologists call ‘species.’ Let us turn to the details of the heterogeneity argument.

Evidence that the interbreeding and the phylogenetic approaches pick out different types of taxa is abundant. Here I focus on just two types of examples, one involving asexual organisms, the other concerning ancestral species. The interbreeding approach requires that the organisms of a species exchange genes through interbreeding. Asexual organisms do not exchange genes through interbreeding, but reproduce through other means, such as budding, binary fission, and vegetative reproduction. So lineages of asexual organisms do not form species on the interbreeding approach. When one turns to the phylogenetic approach, the perspective on asexual organisms is different. What is important for the phylogenetic approach is that a lineage of organisms is monophyletic, not how the organisms of that lineage reproduce. Phylogenetic species consisting of asexual organisms are maintained by processes other than interbreeding, such as genetic homeostasis, developmental canalization, and stabilizing selection. So the first discrepancy between the interbreeding and phylogenetic approaches is that many organisms form phylogenetic species but not interbreeding species. This is no small discrepancy, because asexual organisms outnumber sexual organisms in the world (Hull 1988, p. 429; Templeton 1992, p. 164). But given this observation we should not then conclude that the interbreeding approach is problematic and should be rejected. Far from it. The interbreeding approach and work associated with it have given us knowledge of an important type of lineage in the world: lineages of populations of interbreeding organisms (Coyne and Orr 2004). The claim here is that the phylogenetic and interbreeding approaches carve the world in different ways and each type of lineage is important.

Another discrepancy concerns a type of species called ‘ancestral species.’ A commonly recognized form of speciation often occurs when a population becomes isolated from the main body of a species. That isolated population undergoes a ‘genetic revolution’ and becomes a new species. The parental species, the ancestral species, remains intact. While the interbreeding approach allows the existence of ancestral species, the phylogenetic approach does not allow such species. This discrepancy can be seen with the help of Fig. 1. According to the Interbreeding Approach, when such speciation occurs, there are two species: C, which is the new species; and A + B, which is the ancestral species. However, the phylogenetic approach denies that there are two species in such cases. For the phylogenetic approach, a species must be monophyletic and contain all and only the descendants of a common ancestor. The ancestral species A + B is not monophyletic: some of A’s descendants are not in A + B. So, on the phylogenetic approach, there are not two species present, but either one species or three species. Either there is one species containing A, B, and C; or three species: Species A, which has gone extinct, and species B and species C which currently exist. Either way, the interbreeding and phylogenetic approaches give different answers to

**Fig. 1** According to the interbreeding approach: A + B is a species and C is a species. According to the phylogenetic approach: A, B, C are each subspecies; or A, B, C are each species



the number of species present in this situation. Again, the point of this type of example is not to argue that the phylogenetic approach is problematic, but merely to illustrate that the phylogenetic and interbreeding approaches carve the world in different ways.

So far we have just seen discrepancies between the interbreeding and phylogenetic approaches. There are other discrepancies between major approaches to species. For example, the ecological approach to species picks out lineages of organisms that share the same ecological niche (Van Valen 1976). According to the ecological approach, selection is the main cause of species cohesiveness. And with the ecological approach, we have a third way the organic world is carved. Ecological species can consist of asexual organisms, so the organic world consists of ecological species that are not interbreeding species (Templeton 1992). Furthermore, ecological species can be non monophyletic, so the world consists of ecological species that are not phylogenetic species (Ereshefsky 2001, p. 137).

Stepping back from these examples, we have seen that the interbreeding, phylogenetic, and ecological approaches to species pick out different types of lineages in the world. Those approaches highlight different unifying processes: interbreeding for the interbreeding approach, genealogical relatedness for the phylogenetic approach, and selection for the ecological approach. Those approaches to species also pick out lineages with different types of structures: phylogenetic species must be monophyletic; ecological and interbreeding species can be monophyletic or paraphyletic. And, as we have seen, in many cases those approaches pick out different groups of organisms as species. What are we to make of these differences among various approaches to species? First let me point out that these different types of lineages each play a significant role in the history of life on this planet. Lineages of asexual organisms are no less important than lineages of sexual organisms in the evolution of life (Mishler and Budd 1990). Paraphyletic species are no less real and important than monophyletic species (de Queiroz and Donoghue 1988). Many interbreeding species are not monophyletic but have population genetic parameters for being stable evolutionary

units (Frost and Hillis 1990). And lineages bound by ecological forces are no less significant than those bound by other forces (Templeton 1992). The point is that each of these different types of lineages is important in evolution, so no approach is more entitled to the word ‘species.’ Conversely, no particular type of lineage highlighted by these approaches should be excluded from being called ‘species.’

We have seen that the class of taxa called ‘species’ is heterogeneous. Let us now turn to why that heterogeneity casts doubt on the existence of the species category. If we are to believe that a putative category, as a scientific category, reflects nature, then that category should meet some minimum threshold. Let me suggest such a threshold. First, most of the entities of that category should share a common feature. Second, that feature should help us understand the nature of the entities in that category. Third, that feature should distinguish most entities in that category from entities in other categories. The first criterion requires that a putative category has predictive value. If no feature occurs in most of the members of that category, then that category has no predictive value. The second criterion requires that a category have explanatory value: it should cite some feature that helps us understand the nature of the entities in that category. For example, if the Biological Species Concept is correct, then citing interbreeding relations and reproductive isolation mechanisms helps us understand the nature of species, such as why adaptations are spread within and not among species. The third criterion requires that we can in most cases distinguish entities in a category from entities in other categories. Together these requirements place predictive and explanatory requirements on a scientific category. But these requirements, taken together, are weaker than essentialism: no property must occur in all or only the members of a category. This requirement is even weaker than Mill’s (1843[1963], vol. 8, p. 714) and Hempel’s (1965, p. 147) accounts of scientific categories. Mill requires that the members of a category share a number of common features that allow for new inferences about those members. Hempel requires that the members of a category share an extensive cluster of theoretically useful properties. The threshold offered here is weaker: no extensive cluster or large number of properties is required. All that is needed is a property that has predictive and explanatory power, and distinguishes most species from other types of entities.

When we turn to the species category, it seems doubtful that the heterogeneous class of taxa we call ‘species’ meets the suggested threshold for being a natural category. There is no explanatory property that is distinctive and common to most taxa called ‘species.’ Most of life is asexual, so interbreeding will not explain the cohesiveness of most taxa called ‘species.’ How about the property of being monophyletic? Much of life’s history consists of non monophyletic ancestral taxa. Furthermore, some argue that much of life does not form monophyletic basal taxa because most of life is bacterial and is infused with horizontal gene transfer (Doolittle and Bapteste 2007). Perhaps clades of bacteria can be constructed on the basis of gene phylogenies. But many prominent microbial systematists doubt that there are (or will be) objective grounds for determining which gene phylogeny among a set of conflicting phylogenies highlights a species’ phylogeny (Roselló-Mara and Amann 2001; Stackebrandt 2006; see Sect. 4.5 below). Still, there is an important explanatory property that all those taxa called ‘species’ share: they are lineages of populations. However, that

property does not distinguish those taxa called ‘species’ from other types of taxa, because all Linnaean taxa are such lineages.

Returning to Darwin, we have evidence from contemporary biology supporting Darwin’s skepticism of the species category. Given the heterogeneity of the class of taxa we call ‘species’ we should doubt that the species category is a natural category. Of course the argument given here differs from Darwin’s: his argument turned on tearing down the distinction between species and varieties. Still, the conclusion is the same. Notice, also, that the heterogeneity argument offered here turns on the existence of different types of taxa we call ‘species.’ So we have reached the same end point as Darwin: though we should doubt the existence of the species category, we should not doubt the existence of those taxa called ‘species’ by biologists.

#### 4 In defense of the species category

In the last 20 years, biologists and philosophers have offered a variety of arguments to save the species category. Some of those arguments highlight a particular biological feature that is thought to unify the species category. Other arguments adopt philosophical ideas concerning natural kinds and concepts to save the species category. This section surveys a sample of biological and philosophical defenses of the species category. As we shall see, none of those attempts to save the species category rescues it from the heterogeneity argument.

##### 4.1 The preference for sexual organisms

One defense of the species category maintains that only groups of interbreeding organisms form species taxa. [Ghiselin \(1989, 1997\)](#), [Eldredge \(1985\)](#), [Lee \(2003\)](#), and [Coyne and Orr \(2004\)](#) argue that though different types of base lineages exist, lineages of sexual organisms are more important in the course of evolution than lineages of asexual organisms. So only lineages of sexual organisms form species. For example, [Ghiselin \(1989, p. 74\)](#) writes that “clones soon lose out in competition with [sexual] species. They are very short-lived, and rarely if ever give rise to significant adaptive radiations” (see also [Eldredge 1985](#), pp. 200–201). Ghiselin and Eldredge conclude that because lineages of sexual organisms have more significant adaptations and out-compete lineages of asexual organisms, we should reserve the term ‘species’ for sexual organisms.

This defense of the species category faces a couple of problems. First, the suggestion that asexual lineages “lose out” is challenged by the observation that the majority of life on this planet is asexual. As [Hull \(1988, p. 429\)](#) observes, sexuality “turns out to be rare on every measure suggested by evolutionary biologists—number of organisms, biomass, amount of energy transduced, and so on” (also see [Templeton 1992](#), p. 164). Add to this the observation that most of life consists of prokaryotes and most prokaryotes are asexual ([Doolittle and Bapteste 2007](#), p. 2046; [Tudge 1999](#), p. 107), then the claimed superiority of lineages of sexual organisms is further undermined. But stepping back from this numbers game, there is a more general point to make. Yes, there are differences between lineages of sexual and asexual organisms, but each

mode of reproduction has its advantages. Lineages with sexual organisms more easily adapt to changing environments with the aid of recombination, and lineages of asexual organisms do better in stable environments or in environments where conspecific mates are rare (Futuyma 1986, p. 282). Despite these differences, if we want to understand how life has evolved on this planet, we need to study both lineages of sexual organisms and lineages of asexual organisms. If we limit taxonomy to only classifications of sexual organisms, then most of life will not be classified. Such an approach to taxonomy offers an impoverished framework for studying the organic world.

#### 4.2 The general lineage concept

A recent defense of the species category is offered by de Queiroz (1999, 2005, 2007) and Mayden (2002). They recognize that there are discrepancies among prominent species concepts. But they contend that there is an important commonality among those concepts. All such concepts assume that species are “separately evolving metapopulation lineages” (de Queiroz 2005, p. 1263). de Queiroz (1999) calls this approach to species “The General Lineage Concept.” According to Mayden, this approach “serves as the logical and fundamental over-arching conceptualization of what scientists hope to discover in nature behaving as species. As such, this concept can be argued to serve as the primary concept of diversity” (2002, p. 191). Similarly, de Queiroz (2005, p. 1263) writes that all modern species concepts are “based on a single more general concept of species,” namely the General Lineage Concept. How is the General Lineage Concept related to all other species concepts? According to de Queiroz, the properties that advocates of other species concepts disagree over (successful interbreeding, monophyly, and so on) are merely properties that serve as “evidence for inferring the boundaries and numbers of species” (2005, p. 1264). Proponents of prominent species concepts are confusing “methodological” disagreements with “conceptual” ones (de Queiroz 2005, p. 1267). Consequently, their disagreements are not really over the definition of ‘species’ but over evidential and operational issues. In a similar vein, Mayden (2002, p. 191) writes that other species concepts are “secondary” and “subservient” to the lineage approach to species; they serve as mere “functional guides” for identifying species taxa.

As Lee (2003) and Pigliucci (2003) argue, the General Lineage Concept does not save the species category. A proper conception of species needs to capture what is common to most species taxa, *and* it needs to capture what generally distinguishes species from other types of taxa. The General Lineage Concept captures what is common to all species—they are lineages. But being a lineage does not generally distinguish species taxa from other types of taxa. All Linnaean taxa, genera, families, orders, and up, are lineages. De Queiroz and Mayden could respond that, yes, species taxa and higher taxa are both lineages, but only species are “separately evolving metapopulation lineages” (de Queiroz 2005, p. 1263). However, this response does not adequately distinguish species from higher taxa either. The claim that species but not higher taxa are evolving entities is suspiciously close to the thesis that species but not higher taxa are the ‘units of evolution’ (Eldridge and Cracraft 1980, p. 327; Wiley 1981, p. 75; Mayr 1982, p. 296). According to that thesis, the evolution of a higher taxon is merely

the aggregate effect of the evolution that occurs in the component species of that taxon. The problem with this distinction is that the evolution of many species is the aggregate effect of their populations' evolution. The evolution of an asexual species consisting of separate lineages is a by-product of evolution within those lineages. Similarly, the evolution of a sexual species consisting of geographically isolated populations is a by-product of evolution within those populations (Donoghue 1985; Templeton 1992). The point is that many (perhaps most) species evolve as the result of their component populations or lineages evolving. Thus such species are no more the units of evolution than higher taxa are (Mishler and Donoghue 1982; Ereshefsky 1991). In the end, the General Lineage Concept does not save the species category because it does not sufficiently distinguish species from higher taxa.

Another problem with de Queiroz and Mayden's defence of the species category is their characterization of the debate over species concepts. Recall that according to de Queiroz and Mayden, disagreements among supporters of other species concepts merely concern evidence for inferring the boundaries and numbers of species. De Queiroz and Mayden claim that supporters of prominent species concepts mistake operational disagreements for ontological ones. Proponents of other species concepts should reject this characterization of the debate. When supporters of the interbreeding approach say that asexual organisms do not form species, they are making an ontological claim not an operational one. Similarly, when proponents of the phylogenetic approach say that species taxa must be monophyletic they are not making an operational claim, they are asserting that paraphyletic taxa are not real. Mayden and de Queiroz are wrong to claim that disagreements among advocates of other species concepts are merely operational rather than ontological. Mayden and de Queiroz too quickly relegate all other species concepts to a secondary status.

#### 4.3 Family resemblance

Given the disunity of the species category, perhaps that category can be saved by adopting a philosophical approach that better accommodates disunity. Pigliucci (2003) and Pigliucci and Kaplan (2006) suggest such an approach. They argue that the species category is a family resemblance concept, and they suggest that by recognizing that 'species' is a family resemblance term the species problem can be resolved (Pigliucci and Kaplan 2006, p. 207). Hull (1965) made a similar suggestion many years ago. The notion of family resemblance is from Wittgenstein (1958). Wittgenstein observes that there is no similarity found among all and only games, thus the word 'game' cannot be defined by a necessary and sufficient property nor by a necessary and sufficient set of properties. Instead, the meaning of 'game' is best captured by the cluster of properties that competent speakers attribute to games. Many of those properties occur in more than one type of game, so all games are related by a series of overlapping features. Turning to species, Pigliucci and Kaplan suggest that the species category is defined by such properties as genetic similarity, reproductive isolation, phylogenetic relationships, ecological role, and morphological similarity (Pigliucci 2003, p. 601; Pigliucci and Kaplan 2006, p. 221). Some species taxa have one of these properties, some have more; but no one of these properties is the defining characteristic of 'species.' Still,

many of those properties occur in more than one type of species, so the members of the species category (all species taxa) are “connected by a dense series of threads” (Pigliucci 2003, p. 601).

Does the application of Wittgenstein’s notion of family resemblance save the species category? It depends on what one means by ‘save’ here. Wittgenstein’s notion captures how we use the term ‘species.’ But I do not think its application to the species problem makes any headway in determining whether we should think that the term ‘species’ corresponds to a real category. When discussing the meaning of ‘game,’ Wittgenstein’s concern was how we communicate with one another and convey the meaning of ‘game’ though there is no necessary and sufficient definition of ‘game.’ Wittgenstein was not addressing the question of whether we have good reasons to think that ‘game’ corresponds to a real category. Such epistemological questions were not on the table for him in his analysis of the meaning of ‘game.’ The species problem, or at least a significant aspect of it, is very different. We want to know if we have good reason for thinking that a posited scientific category exists in nature. To address that concern we need to ask questions along the lines of the threshold suggested earlier for determining if a putative category tracks nature. When we say that a taxon is a ‘species’ can we make better than chance predictions about some features of that category? Does saying that a taxon is a species help us explain typical features of that taxon? Have we highlighted some features that are more likely found in taxa called ‘species’ than other types of taxa? A family resemblance analysis of how we use the term ‘species’ does not answer these questions. So the application of family resemblance to ‘species’ does not address the central issue of the species problem, namely whether the species category exists.

#### 4.4 Homeostatic property cluster theory

Boyd (1999) Homeostatic Property Cluster Theory (HPC Theory) is another philosophical account that has been applied to the species category. Boyd (1999, pp. 171–173) believes that species taxa are HPC kinds, but he does not think that the species category is a natural kind, citing significant discrepancies between major approaches to species. Nevertheless, other proponents of HPC Theory, in particular Wilson (2005) and Wilson et al. (2009), argue that HPC Theory can rescue the species category. Very briefly, HPC theory asserts that HPC kinds have two components. First, the members of an HPC kind must share a cluster of similar properties that are stable enough to allow for successful induction. Nevertheless, none of those properties is necessary for membership; they can co-vary and change over time. Second, the co-occurrence of properties among the members of an HPC kind is due to that kind’s homeostatic mechanisms. Turning to the species category, Wilson (2005, pp. 111–113) and Wilson et al. (2009) argue that the species category is an HPC kind because species taxa tend to share a set of features that cause them to be species taxa.

The following is a cluster of causally basic features that most *species* share:  
... gene-flow among species members; species members have the ability to interbreed with their conspecifics, but not with members of other species;  
species members occupy the same ecological niche; species members face

similar selection pressures; species members share similar developmental constraints; species behave as a unit in evolution and independently of other species. (Wilson et al. 2009)

Wilson et al. (2009) conclude that “Pointing out that the species *category* is an HPC cluster kind shows that the different so-called species concepts are commensurable.”

There are two problems with this attempt to save the species category. First, Wilson et al. (2009) write that their list highlights the “causally basic features that most *species* share.” However, that is far from obvious. They claim that most species have gene flow and conspecifics that interbreed. But as we have seen, most of life is asexual. They claim that species members occupy the same ecological niche and face similar selection features. Both claims are contested (Grant 1981; Ghiselin 1987; Templeton 1992). Wilson et al. assert that species are units of evolution. Do they mean that species are genealogical entities (Hull 1978) or cohesive interbreeding entities (Ghiselin 1987)? The first interpretation fails to distinguish species taxa from other taxa (Sect. 4.2); the second interpretation implies that most of life does not belong to a species (Sect. 4.1). Wilson et al. too quickly assert that “most” taxa we call ‘species’ conform to their list of biological properties.

Wilson et al. (2009) also tell us that the “metaphysical and explanatory integrity” of the species category “is captured by the HPC view.” They do not directly discuss that integrity, though Wilson (2005) does. Wilson (2005, p. 111) writes that “organisms in a given species share morphology in part because they share genetic structures, and they share these because of their common genealogy.” Wilson is correct that the properties and relations within a species taxon are interconnected. The similarities among the members of a species may be the result of interbreeding among those members and the selective forces they are exposed to; and their interbreeding mechanisms and the ways those organisms interact with the environment are causally related to their shared ancestry. However, the question under consideration is how such mechanisms are causally related such that there is unity within the species category, not just within a particular species taxon. Wilson has demonstrated that there is unity *within* particular species taxa, but he has not demonstrated that there is causal unity *among* different species taxa. The general problem with the HPC approach to the species category is that it does not provide a reason for thinking that the category is a natural one. No explanatory property, or set of properties, is cited that occurs in most taxa called ‘species’ that generally distinguishes those taxa from other types of taxa. Like the family resemblance approach to species, HPC theory offers no evidence that the term ‘species’ tracks a distinctive category in nature.

#### 4.5 Can genetics save the species category?

A different approach to saving the species category is a reductionist one. It might be thought that with advancements in genetic sequencing, genetics will save the species category. In the last several years, a group of biologists have worked on developing a quick and inexpensive method for classifying field and museum specimens. They have looked for short and stable segments of DNA—what they call ‘DNA Barcodes’ (Herbert et al. 2003). They have found that a segment of mtDNA called ‘COX 1’

accurately matches animal specimens to voucher specimens in known classifications (Waugh 2007, p. 190). Does DNA Barcoding provide a reductionist, perhaps essentialist, account of the species category? The answer is no, because DNA barcoding is not relevant to the species problem. Biologists developing DNA barcoding are clear that they are not offering a theory of species (Herbert and Gregory 2005, p. 853). DNA barcoding is not even used for constructing classifications (Herbert and Gregory 2005, p. 854). COX 1 is merely used as a marker to match a specimen to a voucher specimen that has already been classified. DNA Barcoding is like human fingerprinting: fingerprinting helps identify a particular person, but fingerprinting offers no theory of humans. To emphasize that DNA barcoding is not relevant to the species problem, note that though barcoding banks provide barcodes for species, the rank of ‘species’ is of no particular concern: the aim is merely to assign a specimen to a taxon in a classification, independent of the rank of that taxon.

Nonetheless, taxonomists frequently use genetic data for constructing classifications. Is there reason to think that a definition of ‘species’ based on some form of genetic similarity will unify the species category? Again, the answer is no. Consider the relation between overall genetic similarity and interbreeding. In some cases, genetic similarity does not correlate with reproductive isolation. There are cases of flies, fish, and frogs where there is more genetic variability within an interbreeding species than between two reproductively isolated species (Ferguson 2002). In other words, overall genetic similarity does not sort populations into taxa the same way that the interbreeding approach does. Bringing genetic data to the fore does not provide a method for unifying the species category; instead, it provides yet another way to classify organisms.

One might respond that instead of looking at the relation between interbreeding and overall genetic distance, we should focus on the use of genetic information to construct phylogenetic trees. Perhaps we could obtain a genetic–phylogenetic account of species that would be preferred over all other approaches to species. This suggestion is problematic as well. Different genes from the same group of organisms often have different phylogenies (Maddison 1997; Whitfield 2007). For instance, suppose we construct a phylogenetic tree of a group of organisms on the basis of gene A. We then sample another gene, B, from the group. The phylogeny of B may vary from the phylogeny of A, because B may arise after the inception of A and coincide with only part of A’s phylogeny. Think of cases where B is introduced to the lineage of organisms containing A by mutation or horizontal gene transfer (Maddison 1997; Doolittle and Baptiste 2007). This example highlights discordant gene trees for two genes. Add more genes to the data set and the number of trees increases.

There are two ways to address the problem that different genes from the same group of organisms have different phylogenies. One is to use genetic data in a statistical manner. However, overall genetic phylogenies of organisms may not match interbreeding groups or phylogenies based on non-molecular traits such as morphological adaptations (Wu and Ting 2004). Again, using overall genetic similarity adds another approach to species. Consider the second tactic, that of picking certain genes over others for constructing classifications. As others suggest, the choice of those genes is made on pragmatic grounds and not on the assumption that those genes better capture the nature of species (Stackebrandt 2006; Whitfield 2007; Franklin 2007).

Their point is not that we must temporarily choose which genes to use on pragmatic grounds because eventually we will find the right genes for classification. They argue that different classes of genes underlie different significant biological functions (niche use, reproduction, and metabolism), so there will always be multiple sets of genes that give rise to inconsistent phylogenetic classifications. In sum, then, genetic data, like all data, is useful for constructing classifications. But there is no genetic definition of ‘species’ that unifies the species category.

## 5 The term ‘species’

If the results of the previous sections are correct and we have reason to doubt the existence of the species category, then how we should understand the term ‘species’? Some biologists and philosophers suggest that we should eliminate the term from biology. Grant (1981) suggests using ‘biospecies’ for interbreeding species and ‘eco-species’ for ecological species. Ereshefsky (1992) adds the word ‘phylopecies’ for phylogenetic species. Pleijel and Rouse (2000a,b) advocate dropping the word ‘species’ and replacing it with the phrase “Least-Inclusive Taxonomic Units” or “LITUs,” where an LITU is a type of phylogenetic species. Mishler and Fisher (Mishler 1999, 2003; Fisher 2006) maintain that all taxa are clades, and argue that because there is nothing special about those clades called ‘species’ so we should junk the word ‘species.’ Similar approaches to ‘species’ are found in the conservation literature. Hendry et al. (2000, p. 74) suggest “abandoning the concept of species and replacing it with a new system... that describes groups of organisms based on the amount that they differ from other groups.” Hey (2001, p. 191) argues that conservation efforts should focus on preserving populations with certain quantitative measures rather than anything called ‘species.’ Hey et al. (2003, p. 600) propose that conservation efforts should focus on “Evolutionary Significant Units” or ESUs, rather than species. An ESU is a group of closely related populations that is genetically separate from other ESUs and contributes to the ecological or genetic diversity of a more inclusive taxon.

Despite these calls for replacing the word ‘species,’ I do not think we need to eliminate it. There are pragmatic reasons to keep the word, even if there is no species category in nature. ‘Species’ is well entrenched in biology and elsewhere. Students are taught the term from their earliest encounters in biology. Field guides and taxonomic monographs use the word ‘species.’ And the term is even found in our governments’ laws. From a practical standpoint, it would be hard to eliminate the word ‘species.’ Skeptics of the species category could reply that such practical issues should be ignored: if there is no species category in nature, then ‘species’ should only be used in the history of science and not in science itself. But this reply ignores the role that pragmatics plays in selecting which words are used in biological taxonomy. Biologists frequently cite such pragmatic virtues as stability (keep classifications stable), continuity (keep preexisting names), and generality (treat all taxon names the same) when choosing a school of nomenclature (Wiley 1981; Cantino et al. 1999; Forey 2002). The pragmatic virtues of stability and continuity speak in favor of keeping the term ‘species.’ The point here, however, is not to cite these virtues, but to highlight that practical concerns have weight when considering which words to use in biology.

Removing the term ‘species’ from biology would be an arduous task, and that speaks in favor of keeping it.

Perhaps more importantly, there is no pressing need to eliminate ‘species’ from biology, as long as we are careful in how we use the term. Still, some worry that if the species category is not unified and the word ‘species’ is ambiguous, then biology will be plagued with confusion (Hull 1987, p. 181; Mayr 1987, p. 165). There is a simple way to deal with this problem, and it is a way that biologists often use to avoid confusion over the meaning of ‘species.’ When the meaning of the word ‘species’ affects our understanding of a biological study, then biologists should be explicit about which approach to species they are using. Consider biodiversity studies that count the number of species in a geographic area. Marris (2007) cites an example where butterfly taxonomists count species using the phylogenetic approach, while ant taxonomists count species using the interbreeding approach. When it comes to comparing the diversity in these two groups, Marris (2007, p. 251) writes that “the number of ant species and the number of butterfly species are not comparable.” Two different kinds of biodiversity are being counted and that needs to be highlighted. Or consider a study of endemic avian taxa in Mexico. Peterson and Navarro-Sigüenza (1999) point out that if one uses the Biological Species Concept, then Mexico has 101 endemic bird species. But if one uses a phylogenetic approach, there are 249 species. How many bird species are there in Mexico? It all depends on what one means by ‘species.’ In such situations, it is important to say which type of taxa is being counted. Interbreeding species and phylogenetic species are different kinds of biodiversity (Sect. 3), and we may want to target a particular kind of biodiversity for preservation. Using the term ‘species’ without clarification in such cases masks relevant biological details.

Then there are cases where we do not need to highlight which approach to species is used in a study. If our use of ‘species’ does not affect our understanding of a study, then no clarification of the term is needed. For example, if a biologist highlights a particular taxon by calling it a ‘species’ and distinguishes it from its more inclusive taxon by calling that taxon a ‘genus,’ the idea that the species taxon is the less inclusive taxon is clearly conveyed. Similarly, if a biologist uses the word ‘species’ to convey a relation between two taxa, say a prey–predator relation, then referring to one taxon as the ‘predator species’ and the other as the ‘prey species’ is sufficient to illustrate that relation.

The approach to ‘species’ suggested here is similar to Darwin’s use of ‘species.’ Darwin was skeptical of the species category, yet he kept using the word ‘species.’ Why did Darwin keep using the word? As we saw earlier, Beatty (1992) argues that Darwin kept ‘species’ for pragmatic reasons: to communicate his theory with other naturalists, while at the same time not taking on the task of reforming biological language. We too can be skeptical of the species category and keep using the word ‘species’ for pragmatic reasons. Our continued use of ‘species’ is analogous to our continued use of the QWERTY keyboard. A different keyboard arrangement would make for more efficient typing. But the QWERTY keyboard is so pervasive that it would be hard to replace it; moreover its continued use has not caused any significant problems. Similarly, our use of the term ‘species’ is not the most efficient way to talk about some lineages. But the word ‘species’ would be hard to eliminate, and its continued use has not impeded scientific progress.

## 6 Back to Darwin

The thesis of this paper is that Darwin's solution to the species problem is the right solution for current biology. As Darwin suggested 150 years ago, there is no species category, so we should stop trying to provide the correct theoretical definition of 'species.' This conclusion is part of a general skepticism about the entire Linnaean Hierarchy. For many years, biologists have been skeptical about the higher Linnaean categories (Ereshefsky 2001). They have doubted whether such categories as genus, order, and family exist in nature. Nevertheless, those biologists that are skeptical of the Linnaean hierarchy tend to believe that the species category is an exception—they believe that the species category is a real category (Cantino et al. 1999). Given the arguments in this paper, such selective skepticism about the Linnaean ranks is wrong. Darwin's solution to the species problem shows that the species category is in the same boat as the rest of the Linnaean categories. The Linnaean hierarchy, including the rank of species, is a fictitious grid we place on nature.

As Darwin aptly wrote in the conclusion of the *Origin of Species*:

When the views entertained in this volume on the origin of species, or when analogous views are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history. Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. This, I feel sure, and I speak after experience, will be of no slight relief. (1859[1964], p. 494)

Let us follow Darwin's lead and stop being "incessantly haunted" by the need to define the word 'species.'

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