

THE NATURE OF SPECIES IN EVOLUTION

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in S.M. Scheiner and D.P. Mindell (eds)

The Theory of Evolution
University of Chicago Press

Much has been written over the last few decades about the so-called “species problem,” which can be broadly characterized as the task of providing a functional species concept that picks out the “right” kind of entities. Yet, to date, no general consensus has been achieved on the individuation and definition of species, or whether a unique solution to the species problem exists. Some have gone as far as questioning whether contemporary biology requires species concepts at all. The goal of this chapter is to shed some light on the sources of the disagreement. We begin by drawing attention to two distinct ways species figure in biology, namely, as units of classification and units of evolution. Next, we introduce the so-called species problem and discuss a variety of ontological issues that pertain to the nature and role of species in evolutionary theory. In the second part of the chapter, we explore the interface between philosophical considerations and how species are conceived and used in biology.

1 Units of Classification or Units of Evolution?

A significant source of misunderstanding in species debates concerns whether species are conceived as *units of classification* or as *units of evolution* (Dupré 1994). Within contemporary evolutionary biology, including especially systematics and taxonomy, both views are widely prominent. It is not our intention to delve deeply into the complex history and philosophy of attempts to bring order to nature through classification (O’Hara 1992; Wilkins 2009; Wilkins and Ebach 2013). Yet, it is important to remember that, historically, species as units of classification long preceded species as units of evolution. Linnaeus saw his system as a means of categorizing nature and that the categories (ranks) of his system (e.g., *class*, *order*, *family*, *genus*, *species*, *subspecies*) were meant to be hierarchically-nested abstract concepts. These “invented” devices (in the

*We would like to express our gratitude to Patrick Forber, Roberta Millstein, Brent Mishler, and Matthew Slater for constructive comments on various versions of this essay. They greatly improved our thinking and the presentation. We are especially grateful to the editors, Samuel Scheiner and David Mindell, for inviting us to contribute to this volume and providing feedback and support.

words of Winsor 2006), are not concrete objects out there to be discovered but, rather, concepts that purport to facilitate a scientific understanding of nature's hierarchy. Taxa, in contrast, are scientific hypotheses about the boundaries of evolutionarily related groups—either a species or a group of related species—and thus are widely considered to be discoverable natural entities.

The above distinction between taxa and their rank is significant because understanding that taxa of a given rank are not thereby anointed with some equivalence has important empirical consequences. For example, many studies about biological diversity count taxa ranked at the levels of families or genera (*Hominidae*, *Asteraceae*, etc.). Although those groups may be discrete historical entities, they have no comparative equivalence merely because they are classified as families or genera. Each is simply a clade of species identified with a taxon name that happens to have a Linnaean rank. These taxa could just as easily have been ranked as a genus, tribe, or subfamily by another taxonomist. Categorical ranks only have meaning in relation to one another, hierarchically within a group. Although this distinction between taxa and ranks is widely recognized, it is also frequently ignored.

Once the idea of natural classification in which groupings represent things that exist in the world irrespective of the process that might have produced them became more common in the 19th century, classification took on a larger intellectual role in subsequent debates about species (Wilkins and Ebach 2013). Simply put, Darwin provided a rationale for seeing species and groups of species as the result of an evolutionary process, as historical entities (Kearney, Chapter 7). Yet, the idea of using classification to impose order on our exponentially increasing knowledge of living and fossil diversity also set the stage for confusion over species themselves. This increasingly contentious situation arose because many taxonomic philosophies were being applied to ranking through the 19th and into the middle of the 20th century, and this was amplified with the development of the Modern Synthesis (Huxley 1942; Simpson 1953; Mayr 1942, Smokovitis Chapter 2). Arguably, evolutionary taxonomy fostered the breakdown of the recognition of “natural” groups, including species. The science of using taxonomy and classification to represent natural order became, to a great extent, infused with the art of ranking that was designed to determine the Linnaean category in which the taxon should be placed. As Simpson (1961, pp. 222-23) described it, “The eventual rank of the taxon thus initiated is usually proportional to the degree of distinction of the [adaptive] zone entered, hence the amount of basic divergence involved...”

If one were just looking at the relevant literature, or most general textbooks on evolution, one might have the impression that in the world of systematics, there is chaos over what species are and how to classify them; (Mayden 1997) catalogs a hierarchy of dozens of species concepts. Yet, if one views the development of systematics within a historical context, this apparent chaos is arguably due more to linguistic parsing than to real differences in the biological structure of the world. First, the vast amount of the worlds discovered and described biodiversity was known prior to the species debates of the past forty years. Contemporary arguments about species have had a marginal effect on

our current knowledge about global diversity, 95+% of which includes arthropods and other highly speciose invertebrate groups. Second, a decided majority of that diversity was described using a basic empirical idea of what a species is: if the specimen(s) is morphologically different from other described species taxa, it generally represents a new species. This phenotypic approach, often criticized from a methodological perspective, becomes less surprising when one realizes that the majority of species are known from a relatively small number of specimens and restricted geographic distributions.

So why all the contemporary fuss about species? The debate concerning the nature of species—what species are—often reflects different thinking about the speciation process, which itself can influence how species are conceived or defined (Edwards et al. Chapter 15). A well-known example is the conflation of reproductive isolation and the speciation process versus how species are defined. The debate also has to do with how taxa are *classified* as species, that is, how they are ranked. These two complex, and sometimes conflicting, ideas have propelled the species problem and related debates. Finally, views of species have been influenced by studies of particular kinds of organisms (e.g., animals vs. plants vs. bacteria) and how investigators conceive of them as biologically different, or as having evolved differently.

Darwin saw species as distinct groupings of individuals, kept separate by infertility, which arose gradually over time beginning as geographic variants or races, proceeding to subspecies, then to species. This conceptual view of speciation as a gradual process of differentiation proceeding until there is a sufficient difference to *rank* a population (or set of populations) as a species is a foundational principle of the evolutionary synthesis (Mayr 1942; Simpson 1961).

Thinking about speciation as a gradual process and juxtaposing it with the practicalities of classifying variation in nature through ranking has done virtually nothing to advance either enterprise. Both Simpson (1961) and Mayr (1942) suggest that species somehow have a status different from taxa in other categories. Yet, their ontologies do not map cleanly onto one another: Simpson saw species in terms of evolutionary lineages, whereas Mayr generally did not; in contrast, while Mayr saw reproductive isolation as a relatively sharp boundary, Simpson was not convinced.

In sum, contemporary views of the nature of species and the process of speciation cannot be divorced from the historical imprint of classification. Different species concepts have implied different conceptual and methodological approaches to speciation and to classification. Confusions over species-as-units-of-classification versus units-of-evolution are still with us, leading to the so-called “species problem.”

2 The Species Problem

Mayr (1996) argues that the species problem actually comprises two distinct issues. The first is the question of how to circumscribe species-taxa, i.e., how populations are grouped relative to other taxa. Many definitions of species, Mayr

claims, including the phylogenetic and cohesion species concepts, are “nothing but a recipe for the demarcation of species taxa” (p. 267). The second is how to rank taxa so that they fit the species category of the Linnaean hierarchy: “The species category is the class that contains all taxa of species rank. It articulates the concept of the biological species and is defined by the species definition. The principal use of the species definition is to facilitate a decision on the ranking of species level populations. . .” (Mayr 1996, p. 267). Mayr’s thinking does not clarify the problem because it focuses not on what species are, but on how to rank (classify) species given the acceptance of his own view as the definition of species.

In order to assess species concepts, their consequences for the demarcation of taxa, and their use in biological science, one must determine what kind of entities fall under the concept(s). In short, the species problem has not two, but three components:

- (i) *Nature*: what is the ontological nature of species; what kind(s) of entities are they?
- (ii) *Definition*: what is the conceptual scientific framework for a definition of species; which concept(s) is (are) consistent with that framework?
- (iii) *Demarcation*: how do we individuate species-taxa that fit the definition(s)?

In principle, the nature of species is independent of both their definition and their applications in practice. Many debates about species, in both the biological and philosophical literature, have intermingled these problems. Conflation of ontological and epistemological questions is common in the vast literature on species, often causing scholars to talk past one another. In an effort to bring conceptual clarity, we provide a philosophical analysis of various approaches to species. We attempt to parse out some of this confusion in the conviction that one of the major roles for philosophy in the species debate—and within science more generally—is to scrutinize the commitments that various species definitions leave more or less implicit. To avoid potential misunderstandings, we shall treat the notions of “species concept” and “species definition” as synonyms, a simplification that we take to be consistent with most of the relevant literature.

3 Species in Evolutionary Theory: Philosophical Issues

Species are not the only entities of evolutionary theory whose ontological status is of importance. Below the species level, the nature of populations is also of concern because under conventional speciation models, populations are the entities postulated to become isolated and, then, differentiate into taxa. Similarly, in population genetics, whether or not populations are considered to be concrete individuals has broad implications for the analysis of processes such as

selection and drift (Millstein 2009, Frank and Fox Chapter 9). Yet, our focus here will be on species. In this section, we address some general issues that intersect ontological thinking about species, their origins, and their presumed participation in various evolutionary processes.

3.1 Individuals vs. Natural Kinds

Philosophers of biology and biologists interested in the foundations of the species problem are divided into opposite camps by two *prima facie* contrasting views, according to which species are *individuals* or they are *natural kinds*, that is, the basic ontological categories that “carve nature at its joints.” What is at stake here is an answer to the “nature” component of the species problem: what kind of entities are species? Are they individuals or are they kinds? The question then becomes: what exactly makes a species an individual or a kind?

Many authors in the individuality camp (e.g., Ghiselin 1966, 1974; Hull 1976, 1989, 1999; Wiley 1978; Coleman and Wiley 2001; Crane 2004; Brogaard 2004) see the debate here as absolute: if species are individuals, they cannot be natural kinds, and vice versa. Others, usually adhering to the species-as-kind perspective (e.g., Wilson 1996, 1999; Mahner and Bunge 1997; Ruse 1998; Boyd 1999; Griffiths 1999; Hey 2001; Grene 2002; Reydon 2003; LaPorte 2004; Rieppel 2007, 2013; Brigandt 2009), maintain that this assumption is unwarranted, as these two ways of looking at species are not mutually exclusive.

Unfortunately, different authors seldom adopt the same definition, making their claims difficult to assess. To illustrate, consider five necessary and jointly sufficient criteria for individuality advanced by one of its original proponents and most adamant defenders, Michael Ghiselin (1997, pp. 37-49): (i) It is possible for a class, but not for an individual, to have instances; (ii) Classes are spatio-temporally unrestricted, whereas individuals are spatio-temporally restricted; (iii) Individuals are concrete, as opposed to abstract; (iv) Individuals have no defining properties; (v) An individual is logically prior to being the member of any class, i.e., an individual is not an individual by virtue of its membership in some class. Now, contrast Ghiselins five defining features with the characterization of the individuality of species offered by Rieppel (2007, p. 376): “To consider species as individuals is to reject the idea that parts of species, i.e., the individual organisms that ‘belong to’ the species, share universal properties.” It should be evident that the individuality thesis bears very different ontological burdens for these authors. Under Ghiselins view, individuality is a demanding ontological thesis, which entails an outright rejection of species having instances or defining properties, an explicit commitment to their physical concreteness and spatio-temporal restrictedness. In contrast, Rieppel’s commitment to individuality basically amounts to a rejection of essentialism, the discredited thesis that all and only members of the species share a set of universal properties. While Rieppel’s characterization is not incompatible with Ghiselin’s, it is much weaker. Indeed, it is hard to see how the claim that species are both individuals and kinds could be reconciled with a more demanding notion of individuality.

These considerations illustrate a troublesome aspect of the species problem

that is often overlooked. Authors who argue for or against broad metaphysical positions, such as the individuality thesis, often have very different concepts, definitions, and commitments in mind. Some have argued that it is a mistake to interpret the dispute in ontological terms (Kitcher 1989). This does not merely implicate a nitpicky difference in terminology for without some provisional agreement on these foundational matters, broad consensus or even meaningful debate becomes hard to obtain.

3.2 Concrete vs. Abstract

Given the theoretical nature of metaphysical disputes such as the individuality thesis, we suggest that the crucial ontological question underlying the species problem might stem from a different, more fundamental, and more general issue, namely, whether species are *concrete* or *abstract* entities. We realize that this distinction might be orthogonal to the individuals vs. kinds one; for example, Ghiselin’s multifaceted definition of individuality includes concreteness as a defining condition. Yet, concreteness appears to be a less theoretically loaded and potentially confusing property than individuality.

Most biologists, if asked whether species are “concrete” entities, would answer affirmatively. Yet, this does not necessarily imply any deep ontological commitment. Many evolutionists do not articulate a strong metaphysical preference for a particular species concept. Similarly, most systematists are hardly concerned with the nature of species; rather, they devote their energies to the older endeavor of discovering and naming what they believe to be the taxonomic structure of the world. At the same time, some contemporary biologists have taken ontological questions quite seriously (Mayr 1996; Ghiselin 1997; Wheeler and Meier 2000). In such cases, the commitment to the concreteness of species and its metaphysical implications is not a byproduct of technical jargon, but the result of conscious philosophical reflection: “The term ‘species’ refers to a concrete phenomenon of nature and this fact severely constrains the number and kinds of possible definitions” (Mayr 1996, p. 263).

The strong inclination to treat species as concrete entities derives from the impression that what systematists count, organize, and, ultimately, classify are physical features of nature. Sure, one cannot directly observe a species in the same way we interact with an organism or a rock; still, the existence of species seems to many as uncontroversial as the existence of hydrogen atoms. This intuition seems directly opposed to the view that species can be conceptualized as abstract types. But what does it mean for entities to be “abstract” or “concrete”? Oversimplifying a bit, let us call “abstract” any object that lacks a spatiotemporal dimension, such as sets, numbers, properties, and various other mathematical constructions.

Whether species are concrete individuals or abstract types is a fundamental metaphysical question that underlies much debate over the nature of species, evident, for instance, in the above discussion of individuals and natural kinds. There is, however, a widespread tendency, in both the philosophical and biological literature, to label the thesis that species are concrete natural entities

as “realism” (Gourbière and Mallet 2009; Claridge 2010; Mishler 2010). This, we maintain, is a mistake. The theses that species are real and that they are concrete are conceptually independent and should not be conflated. For this reason, we suggest the introduction of a term of art, “concretism,” to capture the very idea of species being physical objects, as opposed to being abstract, while avoiding the quagmire of philosophical disputes between “realism” and “antirealism.”

Real, *physical*, and *natural* are all distinct predicates. First, there are myriad examples of entities that, like tables and cars, are perfectly “real,” but they are not natural the way quartz crystals are. Likewise, fictional characters (Sherlock Holmes) and musical pieces (Beethoven’s Ninth Symphony) surely do not qualify as natural objects, *sensu* Mayr, or as physical ones. In short, unless one is willing to stretch the meaning of “natural” and “physical” to include virtually anything, there are entities that are real without being natural or concrete, substantiating the claim that naturalness, physicality, and reality are distinct predicates.

In sum, the claim that species are abstract entities should be contrasted not with the reality thesis (“realism”), but with their status as natural objects (“concretism”). Hardly anything hinges on the reality of species, for virtually anything can be dubbed as real, in one sense or another. What is relevant, for the sake of determining the nature of species, is whether or not they are concrete natural entities. Thus, we suggest, it is concretism and not realism that is significant for the species problem. Indeed, many biologists seem to agree, more or less explicitly, with this claim (Hey 2001). Yet, as we will argue below, many entities designated to be species under some influential conceptions may sometimes be interpreted as being neither natural nor concrete.

3.3 Species Monism

Species monism, simply put, is the thesis that there is a single correct species concept, and the job of systematists is to discover and apply it. This is a widespread position. Advocates of some of the most influential species concepts including the biological, phylogenetic, and evolutionary ones, typically believe that their very own definition provides the one true path to grouping organisms into species:

“[T]he Evolutionary Species Concept [ESC] is the only concept currently capable of recognizing all naturally occurring biological taxonomic entities” (Wiley and Mayden 2000a, p. 73).

“The reconciliation of alternative and incompatible species concepts derives from the recognition of a more general concept of species [the Metapopulation Lineage Concept [MLC] that is shared by all contemporary species concepts and definitions. All modern species concepts and definitions conform to this general species concept and can therefore be considered variants of it. This general species concept, not Mayr’s more restricted species definition, is the true biological species concept” (de Queiroz 2005, p. 6601).

The monistic intuition is a strong one. However, a burning question remains,

namely, why there are so many concepts and why no monistic concept seems to cover them all (Wilkins 2003). The large number of competing species definitions, together with the failure of the biological community to achieve any general consensus on which is better or more fundamental, has seriously undermined the faith in the existence of a single correct species concept in favor of an apparently less dogmatic pluralism, which has led some to claim the in principle impossibility of any general agreement on what species are.

At first glance, monism goes hand in hand with concretism and, indeed, the two tenets are sometimes conflated. After all, if species are concrete entities, then could not one find a general way to characterize all of them unambiguously? Things, however, are not that simple. On the one hand, the concreteness of an entity does not entail the existence of defining or diagnostic properties. On the other hand, monism can also be reconciled, fairly straightforwardly, with the idea of species being abstract. For instance, if one could provide a set of necessary and sufficient conditions for organisms to belong to species, construed as sets (a version of the old-fashion and discredited essentialism), one would thereby have obtained a monistic definition of abstract species. To complicate things further, some pluralists have endorsed some version of concretism (Ereshefsky 1992, 1999). Without entering the details of the dispute, the issue of monism is independent of whether species are concrete or abstract and, consequently, these theses should not be conflated.

3.4 Pluralism vs. Heterogeneity

The puzzling nature of species in biology is reflected in their multifarious definitions, but can any particular definition capture all of them? Could it be that there are different and equally legitimate kinds of species and, therefore, there is no way of encompassing all of them under a single overarching concept? Or, perhaps, what counts as a species cannot be captured independently of the particular inquiry or scientific goal at hand. This thinking leads to the idea of *pluralism*, the thesis that one needs multiple species concepts and definitions to individuate all of the kinds of taxa. Directly opposed to the monistic orthodoxy, the pluralistic approach has thrived over the last few decades not only among philosophers (Kitcher 1984, 1989; Dupré 1993; Boyd 1999) but also among biologists (Mishler 1999; Mishler and Donoghue 1982; Hey et al. 2003; Rieppel 2007). Biologists and philosophers alike have discussed species pluralism, but often with different meanings and contexts. Hence, some caution is required in presenting the idea, which evolved along two related but distinct strands (Boyd 1999, Hey 2006). On the one hand, species pluralism is sometimes identified with the thesis that different kinds of species can be found in nature, and, consequently, different species concepts are required to account for this diversity. To illustrate, if birds evolve by different processes than bacteria, the argument goes, different concepts need to be adopted when studying these groups of organisms. We call this thesis *heterogeneity*, since it postulates that species-taxa are heterogeneous, in the sense that a variety of phenomena may underlie species entities (Ereshefsky 1999).

Heterogeneity: different speciation processes may produce different kinds of species, making species-taxa heterogeneous. The individuation of species thus requires different concepts to accommodate this diversity.

Biologists often straightforwardly conflate this criterion of heterogeneity with pluralism. This, however, is problematic, because it obliterates the distinction between heterogeneity—the mere denial of species universalism (Hull 1997, 1999)—and a much stronger thesis that is independent of whether prokaryotes and eukaryotes can be clustered in the same kinds of species. This more radical and more controversial thesis involves a commitment to the claim that the assignment of species-level taxa is always relative to a particular scientific theory, aim, or classificatory purpose (Kitcher 1984; Dupré 1981, 1993; Ereshefsky 1992; Boyd 1999). We dub this position “pluralism” to distinguish it from heterogeneity, as defined above.

Pluralism: there is no single correct species concept. Assignments of species-level taxa are always relative to the organisms and processes being studied and the explanatory target at hand.

The general idea underlying pluralism, thus defined, is the following. Suppose that species-concept *A* individuates organisms (populations) *x* and *y* as conspecific, whereas concept *B* treats *x* and *y* as belonging to different species. Although a monist is committed to the claim that (at least) one of these incompatible hypotheses must be erroneous, a pluralist can argue that both are equally correct since they are relativized to different concepts. Because species are inquiry-dependent, there is no such thing as species existing independently of a theory that specifies their nature in that context and no species concept is more fundamental than any other. From this point of view, it makes no sense to ask whether the BSC or the ESC is “better” *tout court*; the two concepts can only be assessed with respect to, say, a given theory of origins. The pluralist claims, you specify your explanatory target, and I’ll tell you which species concept(s) works better.

In order to unveil the philosophical commitments underlying pluralism it is crucial to dispel some common misunderstandings.

First, from a general methodological perspective, pluralism is more radical than heterogeneity. Whereas heterogeneity can be consistent with the existence of a single correct way of clustering a particular group of organisms into species, pluralism overtly rejects this idea because, in principle, there is no single correct standard for uniting organisms or populations as members of a species. According to the pluralist, two incompatible groupings of organisms or populations into species can be equally correct, when relativized to different goals or theories.

Second, some authors criticize pluralism on the grounds that it fails to “settle” the species problem. Hey (2006, p. 448) laments that “Even if one commits to pluralism, there are still many ways of being philosophically pluralistic about species . . . In short, species-concepts pluralism can be seductive, but it might

not actually help to settle anything.” Hey is surely correct that there is a pluralism of pluralisms in the literature. However, as a general critique, this line of thought also reflects a misunderstanding. Pluralism does not offer an easy answer to which species-concept is better because it was never intended to do so. Pluralism purports to offer a sketch of an explanation of why there cannot be, in principle, a single best definition of species. In short, monism and pluralism are not *solutions* to the species problem; they are *frameworks* within which to work to (hopefully) find a solution to the debate. As such, we should not expect either philosophical stance to “settle anything.”

Third, pluralism does not necessarily imply that “anything goes,” although some pluralists come close to endorsing the position that any grouping of species is equally acceptable or that clustering of populations into species is partially, or even completely, arbitrary (Dupré 1993). Relativizing species concepts and definitions to biological goals need not completely forgo objectivity. There might be independent reasons to prefer some theoretical goals over others, leading one to adopt the concepts posited in such frameworks (Kitcher 1989).

Finally, a widespread idea is that pluralism can be reduced to a form of antirealism. Hull (1999), for instance, explicitly connects the biological dispute between species monism and pluralism with the philosophical debate between realism and antirealism. Specifically, he argues that whereas the realism-monism and the pluralism-antirealism combinations are rather natural, the association of monism with antirealism or of pluralism with realism would be rather weird. As peculiar as it may sound, a pluralistic conception that does not deny the reality of species has been articulated by various authors (e.g., Kitcher 1984; Dupré 1993, 1999; Boyd 1999; Wilkins 2003; Slater 2013). If pluralism is intended as heterogeneity, then it is not in tension with realism or concretism. The claim that no single species concept applies to all groups of organisms is compatible with both the reality and the spatio-temporality of species; at most, it amounts to a rejection of radical monism.

Yet, in asserting the awkwardness of the realism-pluralism combination, we surmise that Hull is referring to a stronger reading of pluralism, closely connected to our reformulation above. Indeed, the simultaneous correctness of conflicting or incompatible species concepts is more problematic to reconcile with concretism (Cracraft 1983; Hull 1999; Wilson 1999, but see Boyd 1999). According to the pluralist, species are inquiry-dependent; there is no such thing as a species independent of a theory that clarifies the intended meaning. Hence, Hull sets up the wrong opposition: it is concretism, not realism, which is in tension with pluralism. Realism is an extremely weak position that bears very little ontological commitment—virtually anything can be dubbed as real, including abstract, fictional, and theory-dependent entities. As a result, the claim that species are “real” is perfectly compatible with pluralism. Concretism, in contrast, is a much stronger position that is harder to reconcile with pluralism: putting together the claim that species are theory-dependent and that they are concrete natural entities requires additional philosophical work. In short, that pluralism is consistent with a modest reading of realism is hardly a vindication of pluralism and does not have significant biological implications. It is concretism

that has to be accommodated or, alternatively, explained away, if pluralism is to have its bite.

It should now be clear why we insisted in keeping realism and concretism distinct: it helps avoid misunderstandings and reveals the likely source of disagreement. Full-blooded pluralism (that is, what we here contrasted with heterogeneity) is a form of nominalism or conventionalism that goes well with the idea that species are sets or other abstract entities, but not with the idea that there are competing species concepts, all of which involve equally concrete entities. Some conceptions of pluralism have understood and made explicit this anti-foundational dimension according to which there are no bedrock entities that are theory-independent and thus constitute the foundation of a clustering of organisms into species taxa (Kitcher 1984; Dupré 1999). In contrast, other authors have attempted to promote a more ecumenical pluralism that retains the concreteness of species (Rieppel 2007). Such views, we maintain, have not (yet) solved the tension underlying the species problem. It is questionable whether a pluralistic view of species is compatible with their status as concrete natural objects.

In conclusion, both monism and pluralism are viable approaches to the species problem, but each comes at a cost. While monism can be straightforwardly reconciled with concretism, it faces the empirical difficulty of explaining the plethora of competing species-concepts and the source of the disagreement among theorists. If there is a single adequate species concept, what's wrong about all the others? Pluralism, on the other hand, accommodates this diversity of approaches. However, it likely necessitates abandoning concretism, an assumption that many scholars—biologists in particular—do not find negotiable

4 Species in Evolutionary Theory: Biological Issues

In this section we explore the interface between the philosophical considerations about species presented above and the biological world, including the theory, methodology and data impinging on how species are conceived and used by biologists. This is not an idle exercise. As Ghiselin (1989, p. 65) pointed out, perhaps with a bit of overstatement, “The philosophy of biology . . . should be an effort to come to grips with, and solve, problems in both branches of knowledge.” Our discussion largely mirrors that viewpoint, which is why we suggest that many of the differences among species concepts derive less from data or theory and more from different ways of seeing the nature of species entities and conceptually organizing those observations.

4.1 Individuality, Lineages, and the Boundaries of Species Taxa

The language of evolutionary and systematic biology is replete with confusion and controversy over evolving entities, e.g., genes, populations, species, lineages,

ancestors. A deep understanding of species will be difficult without placing that unit into a larger context that also addresses these other entities.

How are we to interpret the alleged concreteness of species in relation to its role in evolutionary theory? For instance, how, exactly, should we conceive of spatio-temporal restriction as a species boundary, which has clear implications for understanding and evaluating species concepts? Phylogenetic trees, as abstract representations of history, have branches (edges) that imply relative relationships among terminal concrete taxa, whether extant or fossil (Kearney Chapter 7). In a multidimensional tree-representation framework, Hennig (1966) depicted species branches as populational envelopes that have a temporal lower-bound in their origin via speciation (a branching event) and then later in time, when they themselves are subdivided into taxa or became extinct. This depiction is arguably the most intuitive way to think about the temporal component, but it is not the only one. Many paleontologists, for example, have interpreted stratigraphic sequences of specimens as a species transforming in situ over time into another species without branching (speciation by anagenesis).

This way of thinking about and representing the speciation process over time raises further philosophical and scientific issues. For instance, it calls for an ontological position regarding lineages (Haber 2012), a term that has been applied to virtually anything having a history, from cells to people to stars and is part of the fundamental principles of the theory of evolution (Table 1.3, Scheiner and Mindell Chapter 1). In the Hennigian view, lineages might be taken to be the populational envelopes (within branches), the species themselves (an individual branch), as well as monophyletic groups of species. In some sense, these branches can be interpreted as abstract concepts. If we say that branches are representational of an individual, continuously evolving species, this might imply that all but terminal branches are a series of ancestral species. Yet, specifying their ancestral status is nontrivial, both conceptually and methodologically. Given that these putative species end at a branching event whose subdivision is reconstructed, not directly observed, the “ancestral species” does not give rise to anything other than allopatric subpopulations. Those populations may or may not subsequently differentiate, and unless they do there is no speciation, only population fragmentation. Today, many, perhaps most, species are composed of populations that are fragmented across the landscape. Typically, there is interconnectivity among them over time, but a portion may be strongly isolated by a barrier that allows those populations to have an independent evolutionary trajectory. In a temporal context, therefore, the nature of a species would seem to be dependent on substantial theoretical preconceptions, and the notion of “ancestral species” is also ambiguous, from an ontological perspective (Cracraft 1983).

The spatial component of spatiotemporality is, likewise, problematic. In the neontological world of extant species, distributions are fuzzy and indeterminate. Consequently, at best we might draw a boundary around all the recorded observations, perhaps incorporating environmental information and modeling, and call that the distribution. As concrete entities, species exist in a place, but we just cannot specify it in a precise manner. Distributions in the paleontological

world, if anything, entail even more uncertainties. Alternative species-concepts rely on different criteria to individuate species boundaries. All concepts, it should be emphasized, must and do have a notion of populational (intrapopulational or interpopulational) cohesion, because none of them would place males and females, or life-stages, in separate species. This has been stated multiple times over the years, but some have argued against various species concepts using the spurious argument that those concepts are not populational. Thus, interbreeding is universally seen as a cohesive process which, in some sense, would seem to entail a boundary. Systematists have traditionally proposed shared phenotypes (e.g., diagnostic characters, behaviors) as indicative of boundaries, and in the fossil record the phenotype is all one has. Those shared phenotypes are often taken as evidence for the cohesive unity of populations into taxa, and differences among populations are interpreted as lack of cohesion across space.

One flip-side of cohesion, of course, is reproductive isolation (Edwards et al. Chapter 15), which is perhaps the most frequently invoked idea for a species boundary as it is the cornerstone of the widely-used biological species concept where it has been invoked as the basis for individuating concrete biological species (Mayr 1992). It would be a misreading of history to believe that the introduction of the biological species concept and reproductive isolation turned our worldview from seeing species as classes to seeing them as concrete entities. Moreover, reproductive isolation as a benchmark of species boundaries is fraught with difficulties and carries a steep burden as an arbiter of individuality, or concreteness.

Mayr (1992) argued that the biological species concept works because we can plainly see that isolation is everywhere in local communities. Reproductive isolation, however, is not an intrinsic characteristic of organisms or species, although the genetic and phenotypic changes resulting in reproductive isolation would be characters. Rather, it is a relational inference that can run from the trivial (“an oak tree and the squirrel in it are reproductively isolated”) to the more intellectually interesting (“these two oak taxa hybridize only occasionally”) (Kitcher 1989). By creating a “nondimensional” (Mayr’s term) setting of a local community that eliminates geographically isolated populations among which reproductive isolation cannot be measured, Mayr thought it made a stronger argument for the biological species concept in that it eliminated ambiguity when assigning populations to the same or different species. Instead, it further weakens the case because nondimensionality is not germane to most critical issues about species or their origins.

4.2 Species, Subspecies, and the Nature of Speciation

We now return to the influence of classificatory units on thinking about the evolutionary origin of species. In particular, we explore the ontological status of subspecies (or any infraspecific taxon) because they have long played a role in classification, evolutionary theory, and the species debate. Interestingly, subspecies taxa are used to characterize the taxonomy of only a small portion of Earth’s biodiversity. Subspecies are most commonly applied to birds, mammals,

some butterflies, and a few other groups in which attempts have been made to describe fine-grained geographic variation. Yet, subspecies are used sparingly (when used at all) in most of the diverse groups of invertebrates. Formal infraspecific taxa, such as varieties, are relatively common in plant groups. But it is in birds and mammals that subspecies have played a large role in species concepts and evolutionary theory.

Subspecies have been said to give rise to species (Mayr (1942, pp. 154-55), Simpson (1953, pp. 280-81)), and like species, they could be judged to be concrete entities. Both Simpson and Mayr, like a host of systematic biologists after them, were conflicted over the ontological status of subspecies. Mayr, perhaps more than Simpson, saw subspecies as a concept of classification rather than of evolution (Mayr 1969, p. 193). Yet, both saw subspecies as things that often have something to do with the generation of species. Their ambiguity over subspecies characterizes much of the history of speciation analysis, namely as a progression of differentiation from small differences (subspecies) to bigger differences (species) that are inferred to be sufficient to result in isolation. This view, and the conflicts it raises, is alive and well in various biological disciplines (Haig and Winkler 2010).

These considerations raise important ontological issues. If one thinks of subspecies as units that can encompass any arbitrary set of organisms, or even part of a continuum, then how do we determine their boundaries? If subspecies are generated by a biological process of “subspeciation” (Phillimore 2010), or if subspecies can be actors in evolutionary processes, giving rise to species (Simpson, Mayr), they cannot be mere conveniences or artifacts of classification but must be concrete individuals. But if subspecies are concrete entities with diagnostic morphological characters, what is the ontological difference between them and species, which are also concrete and diagnosable? Are they only different from species in their degree of distinctness?

Notions of speciation are inextricably linked to ontological views of species. de Queiroz (2011) argues that Darwin saw species as segments of the branching process (either internodal branches or terminal branches). This view, discussed above, assumes that the branches themselves are taxa. Alternatively, those branching diagrams could represent simple population histories (gene lineages, for example) within a single species-taxon. Here, one’s view of species is important in rendering cartoons of the process of speciation.

In deconstructing such processes of speciation, the main issue is perhaps not the species, in all its definitional guises, but the taxon. Indeed, ranking seems to be getting in the way of thinking about the origin of taxonomic diversity (de Queiroz 2011). Would our ontology of the evolutionary process change if instead of speaking of the “origin of species” we were speaking about the “origin of evolutionary taxa”? Darwin himself, de Queiroz notes, was influenced by species-as-ranks, but his idea of seeing branching as key, as did Hennig, points to a different way of recasting the process in two ways: (1) conceptualizing a cohesive lineage of populations through time that becomes spatially isolated, and (2) recognizing those isolates as having become differentiated to the point of being recognizable (diagnostic) as evolutionary taxa. Effectively, recognizing

two taxa that are each others closest relatives with reference to a third is evidence that branching has occurred. Perhaps, the concern of what rank they are becomes immaterial relative to envisioning them as markers of a branching history. Cartoons of the historical process, especially paleontological cartoons, tend to obscure and constrain our vision, which can only be based on evidence provided by individual organisms and the similarities and differences among them. If one does not have an ontological commitment to taxa as concrete entities, then all bets are off.

In conclusion, a dissection of the ontological status of subspecies versus species creates problems for evolutionists who tie themselves to classification systems that treat subspecies taxa as if they were evolutionarily relevant, rather than being an artifact that systematists created at one time to deal with gradations in geographic variation. It is difficult to reconcile the idea that subspecies are not concrete yet name them, or that they are discrete entities but are effectively equivalent to species with respect to the processes that produce them (isolation and differentiation). This conceptual conflict has arisen from the long-term entanglement of classification and species biology, and it has served neither well. Of course, if we “solved” the species problem, then the “correct” analysis of species would, in some sense, dictate or suggest the appropriate approach to address subspecies. Yet, until we do so, the nature of classificatory units below the species rank remains problematic.

5 A Hierarchy of Species Concepts

Extensive taxonomies of species concepts have been proposed (Mayden 1997; de Queiroz 1998). Yet, minute differences among various definitions and strategies for individuating species have inflated the rhetoric and obscured similarities while, at the same time, diverting discussion about their ontological implications.

Our goal is to parse out some of the ontological underpinnings of four widely-used groups of species concepts. Although this list is not intended to be exhaustive, most current definitions fall into one of these families. Advocates of these four concepts tend to see species as concrete units, as individuals out there in nature. The central differences lie in how they circumscribe the boundaries of those entities. Thus, an ontological understanding of alternative concepts stipulates whether they individuate the world differently—cut nature at the same or different joints. On this latter point, it is essential to understand that we are talking about the boundaries of taxa. Presumptive joints exist on any branching evolutionary system (genealogies of genes, interbreeding organisms, populations), but the issue here is discerning boundaries between a population within a species and a resultant new species that is the product of population differentiation, as well as among taxonomic entities whose species status is being investigated. Finally, there is the intersection of the notion of concretism with the boundaries of taxonomic units. Systematists agree that a cluster of monophyletic species, termed a “clade,” is also a concrete unit in the sense

of being a unique historical entity. Those entities often have formal names (e.g., Mammalia). The important issue, therefore, is the distinction between the concreteness of species versus the concreteness of clusters of related species (Mishler 1999; Mishler and Theriot 2000). Species concepts must specify how, and in what respects, those two concrete “things” are different, that is, what is special about species entities in comparison to clusters of them.

Various species concepts have been advanced as primary because they are theoretically-based, as opposed to secondary ones, which are supposed to be more methodologically prescriptive, or diagnostic. We find this distinction to be suspect as all species concepts must entail inclusion or acceptance of multiple theoretical assumptions as well as other criteria noted above. Since the inception of contemporary biology, the fundamental function of species concepts has been to aid the discovery and recognition of diversity, not to convey a foundational, theoretical understanding of species, and this is still largely true today.

5.1 Evolutionary Species Concept (ESC)

“[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” (Wiley and Mayden 2000a, p. 73).

The evolutionary species concept (ESC) was originally proposed by Simpson (1951, 1961), and further developed by Wiley (1978, 1981) and Wiley and Mayden (2000a,b). It is avowedly a theoretical lineage concept, with “maintains its identity” signifying individuality and “independent evolutionary fate and historical tendencies” signifying divergence from other lineages as evidenced by character analysis (Wiley and Mayden 2000a, p. 75). Wiley and Mayden (2000a) argue for an ontological distinctness between species taxa and supraspecific taxa (two or more species-level taxa). Under their ontological distinction, parts of species (individuals, populations) have ancestor-descendent relationships, and, as lineages, species give rise to other species, but supraspecific taxa do none of these things. Despite its popularity and evolutionary context, the ESC raises some ontological quandaries. First, the boundaries of the entities specified by the ESC are ambiguous. The above definition does little to distinguish species from monophyletic clusters of taxa, which also have separate identities and histories as historical individuals. Moreover, independent evolutionary fates and tendencies, to the extent that they can be empirical descriptors, are not unique to species entities. For example, populations can “maintain their identity” over space and time, which is why they too can be considered individual entities (Millstein 2009). Populations can also split into subpopulations, suggesting populations can have independence, leaving the distinction between population and taxon up in the air. Although applying the ESC must depend on character evidence to establish the population-taxon boundary, the definition itself entails a fuzzy ontology. Wiley and Mayden (2000a) endorse Hennig’s (1966) idea of recognizing the “joints” of species at lineage branching events as a clear theoretical boundary for the beginning and end of a species taxon, but a boundary

must be explicit in separating the splitting of populations versus the splitting (origin) of taxa.

5.2 General Metapopulation Lineage Concept (GMLC)

de Queiroz (1998) introduced the general lineage species concept as a simplifying solution to the species problem. He argued that entities identified or implied as species under the available species concepts, despite definitional differences over criteria for delimiting species taxa, are consistent with his lineage concept, which was subsequently renamed the “general metapopulation lineage concept,” GMLC (de Queiroz 2005). While a formal concept or definition has not been stated, the general idea is rather clear:

“I do not mean to say that there are no conceptual differences among the diverse contemporary species definitions but rather that the differences in question do not reflect differences in the general concept of what kind of entity is designated by the term species. All modern species definitions either explicitly or implicitly equate species are segments of population-level evolutionary lineages. I will hereafter refer to this widely accepted view as the general lineage concept of species” (de Queiroz 1998, pp. 59-60).

Claiming all species concepts are consonant with a general lineage concept of species is little more than a tautology, given that species must necessarily be composed of population lineages, individual organisms, and so on. Moreover, the GMLC begs the question: if two or more of those species concepts actually individuate species taxa differently, then why do those conflicting hypotheses of species suddenly become consonant under a general lineage concept? In short, the GMLC leaves us wondering how many species there are, and most importantly, what they are.

Seeing species as little more than population lineages, or segments thereof, suggests that the boundaries of these species entities may be even more unclear than those under the other lineage concept, the ESC, although neither provides a basis for distinguishing a species-level taxon from groups of species. de Queiroz (1999, p. 63) seeks to avoid this by proposing that “there is only one necessary property of species—being a segment of a population level lineage.” Still, population histories can be expected to involve splitting and coalescing over time, and the mere fact that they do sometimes split does not constitute a necessary and sufficient framework for species boundaries, theoretically or empirically, unless it is *a priori* stipulated that the split results in two taxa, not two subpopulations. Under the GMLC, the boundary between an evolving population and an evolved taxon is not marked by anything other than a split: “metapopulation lineages do not have to be phenetically distinguishable, or diagnosable, or monophyletic, or reproductively isolated, or ecologically divergent, to be species. They only have to be evolving separately from other such lineages” (de Queiroz 2005, p.6005). It is well known that gene-tree branching does not necessarily map onto species entities, so why should we expect this with splits within populations? Again, the focus of species concepts does not involve population splitting *per se*, but

the individuation of taxa called “species.” Consequently, discernible boundaries of populations, on the one hand, and species, on the other, become an issue, inasmuch as the GMLC leaves this distinction hanging.

5.3 Phylogenetic Species Concept (PSC)

“[A species is] the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent” (Cracraft 1983, p. 170).

“[A species is] the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states” (Wheeler and Platnick 2000, p. 58).

“A species is the least inclusive taxon recognized in a formal phylogenetic classification... Taxa are ranked as species rather than at some higher level because they are the smallest monophyletic groups deemed worthy of formal recognition, because of the amount of support for their monophyly and/or because of their importance in biological processes operating on the lineage in question” (Mishler and Theriot 2000, pp. 46-47).

At first glance, these species concepts share similarities in acknowledging the theoretical distinction between populations (or population lineages) and taxa by stipulating the diagnosability of the latter. Thus, the concept of diagnosability (or detectable, character support) is critical for instantiating the notion of species units as concrete. These definitions also set a boundary between a single taxon and a cluster of taxa by stipulating that species are the smallest taxonomic unit, which increases the objectivity of species in the sense it eliminates infraspecific taxonomic units and any related ranking quandary. Thus, none of these concepts would admit subspecies to be concrete entities.

Over the years there has been substantial arguments between advocates of this species concept (e.g., Wheeler and Meier 2000). One recurrent theme has been whether phylogenetic species can and should be monophyletic. Many, perhaps most, phylogeneticists argue the term monophyly refers to shared relationship among species or groups of species (“species *A* is more closely related to *B* than either is to *C*”) and thus excludes species taxa in the sense discussed here. Others, such as Mishler (Mishler and Donoghue 1982; Mishler and Theriot 2000) stipulate that species must be monophyletic. Among these concepts, “diagnostic” takes on different meanings. Some want species to be characterized by unique derived characters (Rosen 1978, Mishler and his colleagues) whereas others contend that a species may be potentially primitive in all respects relative to its sister-species and thus be diagnosable (e.g., Eldredge and Cracraft 1980; Nelson and Platnick 1981). *Contra* Velasco (2009, p. 475), none of these notions of diagnosability is inherently at odds with phylogenetic theory, but as with any species concept, empirical mistakes can be made.

None of these disputes, in our opinion, creates a critical ontological divide in what species taxa are from a PSC viewpoint. There is, however, a potentially profound ontological issue associated with the above debates, namely that

species are not fundamentally different from higher taxa (Velasco 2009). To be sure they are similar in being taxa, allegedly concrete units out there to be discovered. Yet, we believe that there is a fundamental process—speciation—associated with producing species. Species as a concrete entity do not speciate, they are speciated (Cracraft 1989). Clades, on the other hand, cannot be said to be produced by any unitary process, rather they unfold as the summation of many speciation events taking place over time. The process often ascribed to the evolution of clades—diversification—is a distant analogue as it also includes extinction. This suggests that species might have a unique ontological status.

5.4 Biological species concept (BSC)

“Species is a dynamic rather than a static entity, and the essential feature of the process of species differentiation is the formation of discrete groups of individuals which are prevented from interbreeding with other similar groups by one or more isolating mechanisms” (Dobzhansky 1937, p. 419).

“Species are groups of interbreeding natural populations that are reproductively isolated from other such groups” (Mayr 1969, p. 26).

The biological species concept is the favorite of many evolutionary biologists, but it has received substantial critical analysis from systematic biologists and philosophers (Kitcher 1989; Velasco 2008). Its theoretical lynchpin is the idea of reproductive isolation of populations, which is used to establish boundaries between two taxonomic units (Edwards et al. Chapter 15). However, it is well known that reproductive isolation (for simplicity, the absence of production of viable F1 hybrids, themselves capable of interbreeding) can fail to develop among taxa that are phylogenetically and temporally deep. This presents the first problem for the BSC in establishing boundaries among units. The second problem is the ranking conundrum discussed earlier in which evolutionarily distinct taxa, sometimes not closely related, can be combined into a single biological species if it is known or suspected that their members might interbreed. Consequently, in many biological species, their boundaries belie the notion of the BSC as individuating a single concrete entity. And, even when all the taxa combined in a single biological species are discrete evolutionary units, that biological species is acting as a higher taxon. There are many cases in which biological species are monotypic and thus can be taken as unitary concrete entities, but at the same time virtually all other concepts would also recognize them as such. Yet, because the ontological status of biological species is ambiguous, its role in understanding speciation has been misunderstood. As noted, all species concepts include assumptions about reproductively cohesive populations.

6 Is There a Hierarchy of Species Concepts? Second-Order Pluralism

Some biologists, such as Mayden and de Queiroz, have attempted to reconcile the tension between concretism and pluralism by advancing a second-order plu-

realism with respect to species concepts. Roughly speaking, if the various competing species concepts are organized and visualized in a map-like structure, then they can all be equally correct, thus reducing all differences to an epistemological level, while maintaining both the monistic and the concretist intuition at the level of ontology. Assume that the dispute between species monism and pluralism is tied to the multiplicity of processes producing species-taxa. Thus, we might have agamospecies—a group of asexually reproducing organisms ? on the one hand, and everything else, on the other. One might argue in this case that there are two different kinds of species, hence the need for two definitions and a *prima facie* vindication of the heterogeneity thesis discussed above. But then, would instances of sympatric speciation or speciation through hybridization require different concepts? Even in a group dominated by allopatric speciation? But what if we expect that the evolutionary process, despite all the mechanisms that cause evolutionary change, always produces evolutionary taxa that have boundaries and can be distinguished from each other? Is that a (partial) solution to the species problem? Does it vindicate the existence of a single, general species concept?

One way or the other, we need to be a bit less prescriptive about how processes or products of evolution are imagined to be different across life. It is clear that we cannot build a comparative framework for biology if nature is incompletely or erroneously partitioned into different kinds of species, for then regularities or patterns could be difficult to discern. So thinking and arguing about what is out there—not the semantics of a definition—will remain an important issue. Regardless of the ecumenical effort to justify and give a role to several competing species concepts, both Mayden and de Queiroz turn out to be monists and, probably, concretists with respect to the nature of species. Differences between competing species definitions are said to be mostly pragmatic or epistemological. Mayden and de Queiroz appear to claim that several species concepts can coexist at the level of individuation, but that is an attempt to reconcile monistic metaphysics, which treats species as concrete entities in nature, with a pluralistic idea that there is no single correct way of individuating them. However, we have argued that this second-order pluralism does not do justice to pluralism because their frameworks do not agree with either of the two dimensions of pluralism discussed above.

This fuzzy ontology is a problem for a view of species-as-lineages. de Queiroz’s conceptual cartoon (2005, figure 2) mirrors ideas of advocates of the BSC: terminal lineages exhibit gradual evolution in divergence until, at the end, there is reproductive incompatibility. Within that evolving lineage, de Queiroz traces a *scala naturae* of species concepts that depend on the degree of divergence. This makes it difficult to reconcile species as being concrete, and harks back to the subjectivity of seeing ranking in terms of degree of divergence. Moreover, it reflects the idea that species might be concrete individuals ontologically but at the same time something akin to natural kinds from an epistemological perspective (Rieppel 2013). We earlier argued that epistemology—evidence, in our sense—may be relevant for discerning boundaries, but it is the ontological commitment to concretism that is primary.

7 Concluding Remarks

Throughout this essay, we have attempted to uncover some philosophical issues that underlie the debate over the nature of species and, more generally, questions about the ontology of biological entities. We argued that, despite the fact that both concretism and pluralism are compelling assumptions, they are extremely hard to reconcile. The species problem thus confronts us with a dilemma. Concretism pins down the pre-theoretical status of species, but faces the problem that no species definition may be comprehensive enough. Pluralism, in turn, acknowledges the difficulty of finding a single correct species concept, and explains it by appealing to the fact that the notion of species is theory-dependent or inquiry-dependent. Recent attempts to reconcile the two intuitions such those advanced by Mayden and de Queiroz do not solve the tension.

The main problem for pluralism is that it is not clear that one's view about species depends on which scientific aim she has in mind. The evidence for the existence of species seems to be independent of any particular theoretical framework in biology. It is certainly true that different views about the process of speciation have led to different species definitions or species concepts, but we suggest that the idea that organisms are organized into species is independent of any particular view of speciation. Indeed, the evidence that leads us to postulate the existence of species seems to be independent even of the whole framework of evolution. It could be argued that Aristotle had a notion of species that was not fundamentally distinct from contemporary concepts, and deeply essentialist taxonomic systems such as Linnaeus were not radically modified by the evolutionary world-view. What profoundly changed with the work of Darwin and Wallace was our understanding of the origin of these entities, not the evidence that we have for believing that organisms in nature are clustered into species. Hence, even without evolution, biologists still recognized species entities that needed to be explained.

On the other hand, the idea that species-level entities are concrete and natural would seem to suggest that they are actors in one or more processes in nature. After all, if species were inert bystanders, how would we justify their prominence within biology? But what exactly do species do? An answer to this question is likely to be independent of any particular species concept, although this would not be a common intuition in evolutionary biology for two reasons. First, a number of species concepts are framed around an understanding of various processes. Second, many evolutionary biologists think that species are active participants in multiple processes in nature. For example, species are said to speciate or go extinct, compete or predate, occupy niches or adaptive zones, interact with their environment and disperse. Without revisiting previous arguments (Holsinger 1984; Cracraft 1989; Williams 1989), species likely do none of these things as biologists have consistently misconstrued the locus of causality — directly, or through liberties of language. Rather, these are all things that individuals or populations do. So the most plausible conclusion is that species do little, or more likely, nothing. That is, they do not participate as actors in processes. Even assuming the lineage-through-time idea of “ancestral

species” discussed earlier, individually isolated populations are the entities that differentiate and can be said to turn into species (i.e., speciate, in the context of allopatric speciation models). It would seem, therefore, that even notions of “species as evolvers” (Williams 1989) needs to be revisited.

Our view of species-as-actors opens the door to thinking more mechanistically about many processes in nature and their importance by conceptualizing causation at a more appropriate hierarchical level, usually that of individual organisms. But, it also has implications for proposed selective processes of and among species within macroevolutionary theory (Jablonsky Chapter 17).

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