

January 2017

Species Pluralism: Conceptual, Ontological, and Practical Dimensions

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A thesis submitted in partial fulfillment of the requirements for the degree in Doctor of Philosophy

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Abstract

Species are central to biology, but there is currently no agreement on what the adequate species concept should be, and many have adopted a pluralist stance: different species concepts will be required for different purposes. This thesis is a multidimensional analysis of species pluralism. First I explicate how pluralism differs from monism and relativism. I argue that we must re-frame the species problem, and that re-evaluating Aristotle's role in the histories of systematics can shed light on pluralism. Next I consider different forms of pluralism: evolutionary and extra-evolutionary species pluralism, which differ in their stance on evolutionary theory. I show that pluralism is more than a debate about the species category, but a debate about which concepts are legitimate and a claim about how they interact with one another. Following that, I consider what sort of ontology is required for different forms of species pluralism. I argue that pluralists who deny the unity of biology will require a further plurality of frameworks, while those that ground their pluralism in evolution need only one framework. Finally, I consider what pluralism means for biological practice. I argue that species concepts are tools, and reflect on how pluralism can illuminate the way systematists approach the discovery of new species of yeast. Pluralism can make sense of the way species concepts are used, and can be developed to aid researchers in thinking about how to use the right tools for the right jobs.

Keywords: Pluralism, species, evolutionary theory, scientific unity, systematic biology, yeast, Aristotle

Acknowledgements

I would like to thank my supervisors Eric Desjardins and Devin Henry for countless illuminating discussions on the nature of species, pluralism and the entire history and philosophy of biology, and for pushing me far further than I thought possible. Thank you to everyone who participated and suffered through my various presentations at BiPED, especially Gillian Barker, Marc-André Lachance, and Sheila M. Macfie. A special thanks goes to my mentor Shari Monner and to Veromi Arsiradam for helping me both professionally and with the many other obstacles that affect us poor souls as graduate students. Thank you to Nic Fillion for showing how to make my thesis more true by writing it in LaTeX. Thank you to audiences at the Western Philosophy Graduate Student Association Colloquium, the Canadian Society for the History and Philosophy of Science, the International Society for the History, Philosophy, and Social Studies of Biology, the European Philosophy of Science Association, the International Society for the History of Philosophy of Science, the Philosophy of Science Association, the Western Canadian Philosophical Association, the Phoenix Colloquium at Mount Allison University, and the Atlantic Regional Philosophical Association, for hearing both various versions of my chapters and materials long since excised from my thesis.

I would like to thank my Master's supervisor, Rhonda Martens, for allowing me to carry my thoughts from the problem of induction to Popper's degree of corroboration to the philosophy of biology. Without that freedom, I never would have stumbled upon the 5% of biologists that care about the philosophy of science. I would like to thank David Bourget and the Centre for Digital Philosophy for teaching me how to do research in the digital era. I would also like to thank Patrick Walsh for being the first philosopher to show humility, and for being more than willing to steer me from a dead Great Books education into the real, living world of philosophy. A special thanks goes to Jack Bailey, for without his ranting and raving about birds, the problem of free will, and teaching me logic, I could have been a real doctor.

I would like to thank Paolo Biondi for introducing me to Aristotle, the first philosopher I ever felt I truly understood. Although I no longer feel like I

understand Aristotle, I would like to thank the many souls who have helped me bring his Greek to life, including, but not limited to Michael Stack and Dave Howarth at the University of Manitoba, and to John Thorp, Sean Coughlin, Cecilia Li, Adam Woodcox, Matt Watton and the rest of the Greek Gang at Western. A special thanks goes to Devin again for proving to me that the biological works are not quite as boring as some have claimed.

I would like to thank Mom, Tato, my brother Calvin and the rest of my family for putting up with and unwittingly participating in all my navel-gazing over the years. I'm sure I could have turned out much worse if it wasn't for all of that. Most of all I would like to thank Jessica and our daughter Vivienne for showing me both my own and our future, and for suffering my feeble and sometimes dangerous attempts at becoming an amateur naturalist.

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Chapter 1

Introduction

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.

Darwin, *Origin*, 1st Ed., 484

This is a dissertation on species pluralism. As such, I will consider debates about what ‘species’ means, and how species are supposed to figure in biological theory. In this introductory chapter I will set the stage by disentangling these debates from pluralism, thus introducing some of the terminology relevant for the following chapters. I will first present the different understandings of the so-called species problem, or the fact that no one seems to agree on what ‘species’ means in biology, and some of the different solutions. The species problem is thorny not because it is insoluble, but because it has too

many alleged solutions. Following this, I will then highlight the importance of distinguishing pluralism from two other approaches to the species problem: monism and relativism. As this dissertation shows, pluralism puts an entirely new spin on various problems that concern species, and gives us new insight into biological theory and practice.

1.1 The Species Problem Problem

In this section I will survey several common attempts to elucidating what the so-called species problem. This in turn will help us understand what solutions might be required.

There are two common ways of disambiguating ‘species.’ The first disambiguation of ‘species’ is that it can sometimes refer to the species category, the class to which all species taxa belong, or to the properties which make a species a species and not a genus or some other taxonomic class of entities higher or lower on the so-called ‘Tree of Life.’ The second disambiguation is that ‘species’ can sometimes refer to particular species taxa, (e.g., *Canis lupus* is a species, rather than a genus) or even all of them at once, without really specifying criterion for what makes them a species, but just taking for granted that there are such things as *Castor canadensis*, *Lactobacillus fermentum*, and the like. This disambiguation is thought to repair a lot of confusion about how ‘species’ is used, but in fact the distinction between the species category and species taxon problem has led to a cottage industry of formulating different species problems, and solutions to them. This work merely skims the surface of the very sophisticated ways that some biologists use species concepts, and talk about particular species. This thesis aims to rectify this problem by putting species pluralism into practice.

One might think that the two species problems are separable. That the species category problem is something for biologists, and that the species taxon problem is a problem for philosophers. This separation is not that simple. Sokal (1974), one of the founders of numerical taxonomy, believes that the species problem is two-fold. First, it is a problem of definition. Here the is-

sue is how to define the species category. Second, it is a problem of genesis, i.e., how to understand speciation: the many different ways new species come into existence. Some think the species problem is just that there are different, partly incompatible definitions of the species category (de Queiroz, 1999, 2005b). There is however another species problem that pertains to species taxa, the things to which our binomial nomenclature is said to refer to (e.g., *Castor canadensis*, *Gadus morhua*, etc.). This problem concerns whether or not species taxa are real things, as opposed to mere taxonomic conveniences useful for human purposes. Even if we agree that they are real, it's not clear what sort of thing they might be, whether they are natural kinds, sets, processes, individuals or something else. This species problem is ontological, and concerns how species come into and go out of being.

Would taking a pluralistic stance, and allowing for multiple solutions to these problems help in any way? In order to answer this question, we need to first get clear about what pluralism means when it comes to species. In the next section I will go over the sort of pluralism that is contributing to one aspect of the species problem, i.e., the conceptual pluralism surrounding the species category.

1.2 Conceptual Pluralism

There are now an astounding number of species concepts, and in this section I will only go over some of the more prominent ones ¹. A species concept is an attempt to answer the following general question: “How do we adequately define what a species is?” Here we must take ‘adequate’ in the broadest possible sense of the term: theoretically, so that it fits with our best biological theories, operationally, so that we know what operations to perform to demarcate particular species, practically, so that it meets our overall classificatory aims, etc. Species concepts are generally taken as definitions of the species category. However, a careful consideration of the differences between competing

¹See Mayden (1997) and references therein for a list of 22 species concepts (cf. Wilkins, 2011)

species concepts shows that many species concepts are also saying something about speciation. Further, though there is no universal agreement about which species concept is the correct one, some general desiderata for species concepts have presented themselves (cf. Wiley, 1978, 18), e.g., that a species concept be theoretically sound, or have operational consequences, i.e., that it can provide some actual guidelines for how to demarcate species. Part of the problem is that not everyone agrees on which desiderata ought to be captured by a species concept. The one desideratum that pluralists generally give up on is that a species concept be universalizable: different species concepts will be required for different jobs.

In this introductory chapter I will consider six ways of usefully defining species: (1) the typological species concept (TSC), (2) the phenetic species concept (PhSC), (3) the biological species concept (BSC), (4) the ecological species concept (EcSC), (5) the phylogenetic species concept (PSC), and (6) the evolutionary species concept (EvSC). There are many more species concepts out there. Concepts (3-5) are perhaps the most commonly cited as concepts applied when a new species is delineated (e.g., Mayden and Wood, 1995). Concepts (1-2) are not often referenced as decisive for marking out species, though they may still be useful for some aspects of systematic research. Concept (6) is admittedly not an operational concept, given that it does not tell us how to pick out species in the world, and is an early progenitor of modern species pluralism. I will explain how each concept characterizes or constrains what sorts of things count as species, and why there are real differences among each concept. As I will show in the following section, the fact that there is conceptual pluralism about species is distinct from species pluralism properly construed, which is the view that more than one species concept is correct. As I will show in Chapter 3, species pluralism is a view that must be tied to biological theory. I will also show in Chapter 5 that species pluralism needs to be tied to biological practice.

1.2.1 The Typological Species Concept

The typological species concept (TSC) appears in the introductory literature to the species problem or to systematics without a clear reference to anyone who explicitly advocates or advocated it, and in some ways used as a foil for the other species concepts (e.g., Mayr, 1957; Slobodchikoff, 1976; Cracraft, 2000). The **TSC** is more like a spectre that haunts biologists from time to time, and leads them down unscientific, non-evolutionary paths. The **TSC** is commonly characterized as recognizing species by their degree of phenotypic difference. **TSCs** are often conflated with the view that species have essential properties, but biologists have a peculiar understanding of essentialism. One way of formulating the **TSC** is as follows:

(TSC) ‘A typological species is an entity that differs from other species by constant diagnostic differences, but it is subjective what one may consider a diagnostic difference. The so-called typological species concept is simply a biologically arbitrary means for delimiting species taxa’ (Mayr, 1982, 176).

Mayr often ties the **TSC** to a reliance on morphological features, though that reliance isn’t necessary. The main point is that the **TSC** leads to an arbitrary way of classifying species. However, given the tie to morphological features, Mayr (1957, 12-14) argues that **TSC** fails for at least the following three empirical reasons. First, the fact that we often find polymorphism within populations (e.g., the light and dark-morphs of the jaguar (*Panthera onca*)). Second, because we often find geographic variation within species. Third, because of the existence of what are called ‘sibling’ or ‘cryptic’ species. Species that have the same phenotype, but differ in their reproductive capacities or differ genetically (e.g., recent DNA analysis the Two-barred Flasher butterfly (*Astrartes fulgurator*)). Applying the **TSC** to such populations would unnecessarily split such groups into separate species. What this means though, is that the **TSC** conflicts with sorts of classifications of organisms into species offered by some of the following species concepts. I will discuss the relationship between the **TSC**, Aristotle, and other species concepts further in Chapter 2.

1.2.2 The Phenetic Species Concept

The phenetic species concept (PhSC) is a concept that is currently quite out of fashion, though mostly for the ‘theoretical’ reasons driving it. This was the concept of the numerical taxonomists, an approach to taxonomy that is also quite out of fashion due to its attempt to provide a ‘theory-free’ approach to taxonomy, an approach that supposedly makes no assumptions about what forces hold species together nor about those which generate new species. In the early days of twentieth century systematics numerical taxonomy was one of three competing schools. The other two schools, cladistics or phylogenetic systematics, and evolutionary taxonomy both rejected the focus on the **PhSC**, but differed in the role they attributed to descent. A common definition of the **PhSC** is as follows:

[T]he species level is that at which distinct phenetic clusters can be observed (Sneath, 1976: 437).

Here “observable, distinct phenetic clusters” means that species are groups of organisms that are delineated by how similar they are overall. Sometimes this is taken to refer to traits that refer to a species phenotype, but other times it can also refer to the genetic makeup of a species. Many have argued against this species concept on the grounds that it is in essence a version of the **TSC**. I will speak in more detail about the role that the **TSC** plays in debates about species in the following chapter.

1.2.3 The Biological Species Concept

What is perhaps the most popular species concept, at least among zoologists, is misleadingly referred to as the biological species concept (BSC) (Dobzhansky, 1935; Mayr, 1940, 1942, 1963, 1970; Mayr and Ashlock, 1991).² An often cited early definition of the BSC is as follows:

²The reason this concept was called ‘biological’ is because Mayr believed that the **TSC** (or essentialist species concept) could apply to inorganic kinds, like species of molecules or minerals (1982, 251-252;272). However, calling something ‘biological’ within biology is uninformative at best. This would be like calling a proof method in a mathematics textbook the ‘mathematical proof method.’ Secondly, as many have pointed out, calling this concept

(BSC) **The Biological Species Concept**: “species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups” (Mayr, 1942, 120)³

According to the **BSC** gene flow, the transfer of genes from one population to another, keeps species together, and reproductive isolating mechanisms⁴ restrict gene flow and keep species apart.⁵ The **BSC** puts a great deal of emphasis on sexual reproduction. Due to this emphasis, the **BSC** will be useful for a zoologist⁶, especially with respect to the notion of “cryptic species”: species that are very similar morphologically speaking, but fail to successfully interbreed. However, the **BSC** will not be useful for a microbiologist or virologist who wants to sort entities that reproduce by clonal means.

‘biological’ suggests that all other concepts that biologists use are somehow ‘non-biological.’ Simpson (1951) preferred the term ‘genetical species concept’ for Mayr’s version of the **BSC**. Others have called the **BSC** the reproductive isolation concept. Unfortunately, the name has stuck.

³Mayr offers this definition after quoting an earlier one: “A species consists of groups of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers” (1940, 256).

⁴Mayr (1942, 247-248) gives a taxonomy of four sorts of isolating mechanisms: ecological, ethological, mechanical, and genetic-physiological.

⁵See Beurton (1995) for some potential problems and a solution to the standard way of understanding gene flow associated with the **BSC**. For our purposes we can take a broader gloss on the **BSC** that encompasses both this and even further disagreements about how to define this concept.

⁶Interestingly most of those who were behind the early development of the **BSC** were zoologists. Mayr, for example was an ornithologist, and Dobzhansky worked on *Drosophila*. So in a way the **BSC** is zoocentric. The limitations of the **BSC** were not unintended by-products of a blind attempt to define species. In fact, problems with the concept were noted even earlier than Mayr’s (1942) particular formulation. Dobzhansky, for example, in discussing the limits of his own version of the **BSC** states that “Among organisms reproducing exclusively by parthenogenesis or asexually, species in our sense do not exist at all. The classification of these organisms must be based solely on the observable discontinuities in their morphological structures and physiologies.” (1935, 355). That is, where the **BSC** fails, we must use another ‘species’ concept.

1.2.4 The Ecological Species Concept

The main claim of the ecological species concept **EcSC** is that species are, for the most part, maintained ecologically, not reproductively (Van Valen, 1976, 235). According to the **EcSC** species are distinct because they occupy distinct niches (what Van Valen calls “adaptive zones”), which are roughly the ecological role played by a population with respect to some environment. On this account of species, species can occupy distinct niches even though, in some cases, the more inclusive group forms a ‘syngameon’: a cluster of species and subspecies between the members of which natural hybridization occurs. This phenomena, and limitation of the **BSC**, was already noticed by Simpson, who stated that “quite extensive interbreeding may occur between adjacent populations which nevertheless retain their own individualities, morphologically and genetically, so clearly that any consensus of modern systematists would call them different species” (1951, 289). Different selection regimes preserve the stability of each group. The **EcSC** has been formulated in terms of the concepts of lineage, adaptive zone, and geographical range as follows:

(EcSC) **The Ecological Species Concept:** A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range (Van Valen, 1976, 233).

In contrast with **BSC** the **EcSC** allows for cases where isolating mechanisms are not what keep biological groups distinct. Consider some Canadian oaks like *Quercus macrocarpa* and *Quercus bicolor* that regularly exchange genetic material. Since these two groups readily hybridize where they co-occur, they would be the same species according to the **BSC**. According to the **EcSC**, on the other hand, these groups of oaks are distinct species because of the different and distinct niches they occupy. *Q. macrocarpa* has a far broader range than *Q. bicolor*. Isolating mechanisms fail, but we have reason to believe that different selection regimes, and difference in geographic range, are at work keeping the species distinct, which also causes them to have different phenotypes.

The issue at stake between the **BSC** and **EcSC** is what is the fundamental cause of species cohesion: reproductive isolation or ecology. Both concepts make species cohesion explicit, thereby providing a partial account of speciation. When new isolating mechanisms arise in a population, this may lead to a new ‘biological-species.’ When new niches arise in a population, this may lead to a new ‘ecological-species.’ Both concepts are wide-ranging and unify a disparate array of phenomena, so it is very appealing for a species monist to declare a winner, or find something in common between them. A species pluralist may argue that searching for one unified account of species cohesion is the same as pursuing a red herring.

Independently of this fundamentality issue, the **EcSC** may not be useful for classifying organisms that are manufactured or manipulated by human beings to only exist in the laboratory. In these situations some have argued that there may be no well-defined or stable ecological niches for sorting these sorts of organisms, but we may still have grounds to differentiate between species (Stanford, 1995, 76). Unless of course we take the human influence as part of the ecological factors that keep these populations isolated and in the form they have. If this is the case, then perhaps we would say that the **ESC** is rather useful in such contexts.

1.2.5 The Phylogenetic Species Concept

The phylogenetic species concept **PSC**, in contradistinction to the **BSC** and **EcSC**, leaves open what sorts of processes make species cohere. According to one version of **PSC**, species are the smallest ancestor-descendant lineages of populations, which form monophyletic groups (groups characterized by an ancestral species and all of its descendants) (de Queiroz and Donoghue, 1988, 1990). On this account, since species are lineages between speciation events, they may be able to drastically change their ecological and reproductive properties depending on how we define speciation. Given enough change in these properties within a lineage, a single species recognized by the **PSC** may be counted as multiple species by the **BSC** or **EcSC**. A benefit of the **PSC**

over the **BSC** is that it will classify asexual organisms, as long as they form monophyletic groups.

1.2.6 Cross-Classification

What is important to note about all of this is that species concepts are not just semantically different from one another, but lead to concrete operational discrepancies. Different species concepts produce classifications that will cross-classify the world's organisms (e.g., Ereshefsky, 2001, 133). If we apply the **BSC** we will get a classification different than that provided by the **EcSC**, **PSC**, and so on. Species concepts make a difference when it comes to biodiversity counts, which has implications for conservationists. An extreme example is Cracraft's (1992) review of the Birds-of-Paradise (Aves, Paradisaeidae), which recognized over ninety species using his version of the **PSC**, whereas previous counts, using the **BSC**, had only recognized about half the number of species using the very same data.

The **BSC** and **EcSC** conflict with one another because they have different understandings of what it is the primary cause of species cohesion. For the **BSC** the reproductive properties are more salient, and for the **EcSC** it is the ecological properties that we must investigate. Both of these can conflict with the more rigid genealogical understanding imposed by the **PSC**. The **PSC** takes species to be a special form of monophyletic groups, a group composed of all the descendents of some common ancestor. The **BSC** and **EcSC** take species to be genealogical entities, but not necessarily monophyletic groups. They permit paraphyletic groups, which are groups composed of some of the descendents of some ancestor that they share. The **BSC**, as noted above will not apply to asexual organisms, but the **PSC** and **EcSC** can be used to recognize species among such organisms. Furthermore, none of these concepts can be generally applied by paleontologists. Extinct species are generally delineated by using something like the **PhSC**. In fact, the **BSC** explicitly stipulates that species are extant, and rules out the question of whether ancestral species can survive speciation.

Given this discordance, and given the widespread use of many different species concepts, what stance are we to take toward this sort of conceptual pluralism? Everyone admits there is a plurality of species concepts in biology, but not everyone agrees that we should accept this plurality.

1.3 Pluralism, Monism and Relativism

Scientific pluralism or “the pluralist stance” (Kellert et al., 2006), is the view that it is possible, for some domain, that there is no singular, unified account of its phenomena. Pluralism is the denial of monism, which is the view that for any domain all correct accounts of its phenomena can be unified. This is not to say that a pluralist holds that there are *no* locally unifiable domains in the world, just that we can’t assume that the world will be neat, tidy, and unifiable. Pluralism in biology has been understood as the idea that one “keep an open mind about which particular causal agent is to be invoked as an organizing principle in any particular case” (Mishler and Brandon, 1987, 402). However, at the level of global description, it is not always clear what scientific pluralists are being pluralists about, whether it’s about explanation, causation, theories, concepts, models, or some further thing. Thus, the way many understand pluralism at the global level has ridden on the backs of local, empirical, investigations of pluralism, e.g., ‘sex,’ ‘behaviour,’ etc. (Kellert et al., 2006). It’s not clear that Mishler and Brandon’s conception of pluralism in biology is helpful for understanding species pluralism. The species debate is not solely about causal explanation. This is because species concepts like the **PhSC** and **TSC** don’t specify any causes, but demarcate species based on principles of sameness and difference. I will return to this conception and explore the role of causes in species pluralism in the last chapter.

In general, scientific pluralism has important consequences for how we interpret scientific disagreement, because pluralism implies that more than one account may be correct. The main implication for biological theory that species pluralism generates is that there is more than one legitimate species concept. In the past, biologists and philosophers have both tended toward

species monism. An examination of their arguments shows that it is implicitly assumed that one and only one species concept could be correct. One might think that species pluralism would then just be the denial of species monism, the view that there is *no* singular way of grouping organisms into species. But this way of characterizing pluralism makes it tread awfully close to a full-blown species relativism, which at its most extreme suggests that anything goes as far as species concepts are concerned. There can be of course more sophisticated versions of relativism that are constrained, the worry here is about the lack of constraints on what counts as legitimate science that many believe pluralism to entail. I won't directly deal with these sorts of worries in this thesis, but will showcase the grounds for a promising species pluralism that can suit the needs of biological theory and practice.

As I understand it, scientific pluralism is a belief that there is something about certain parts of the world that cry out for a pluralist interpretation. Species pluralism, then should be understood as the view that the world is such that there is no singular, unified way of grouping organisms into species. This leaves it open to what it is about the world that is responsible for the pluralism, but makes it distinguishable from relativism. In order to distinguish species pluralism from relativism further, we need constraints on what species concepts are admissible. This must be an auxiliary claim about why the world is the way it is. For this claim to yield us a scientific species pluralism, it must be supported by our best biological theory. I address the way biological theory relates to species pluralism in my third chapter. In order to better appreciate the differences between species pluralism, monism and relativism, I want to briefly address how species monists come to terms with the *de facto* conceptual pluralism that runs rampant in systematic biology.

1.4 The Monist Agenda

In this section I will briefly go over four different strategies for maintaining monism in the light of conceptual pluralism.

Monists believe there is one true species concept, even if it turns out that

we may never get at it. This has important consequences for how we resolve conceptual pluralism. What does a monist do with all the species concepts? Given say the **BSC**, **EcSC**, and **PSC** the monist considers the arguments for each concept and selects the best. This is the first strategy, to accept one, and show why the others would lead to illegitimate classifications of organisms into species. If this strategy does not succeed, there are three more: reduce, combine, or create.

G. G. Simpson's (1951) development of the evolutionary species concept **EvSC** provides one of the first instances of the reductionist strategy in the biological literature. Simpson's idea was to supplement Mayr's version of the **BSC** with an evolutionary criterion, one which he thought was already implicit in Mayr's formulation. This criterion then would make a species "a phyletic lineage (ancestral-descendent sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies" (1951, 289). In the more recent and frequently cited definition he drops the explicit mention of interbreeding, making the evolutionary species concept even more general:

(EvSC) A species is "a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies" (Simpson, 1961, 153).

Simpson wanted to take interbreeding as only one factor to consider in recognizing something as a species. Thus, he is reducing the **BSC** to the **EvSC**. The move to reduce species concepts has metamorphosed in recent years. There have been attempts to develop a hierarchy of species concepts that all reduce to a form of Simpson's **EvSC**. On this view the **EvSC** is the species concept to which all other are concepts are mere operational variants. This view treads very close to species pluralism (especially evolutionary species pluralism) (Mayden, 1997, 1999; de Queiroz, 1999; Shun-Ichiro, 2011; Kendig, 2014). I deal with this in more detail in my second chapter. The point here is that the reductionist strategy still preserves some of the virtues of competing species concepts, but attempts to show that there is something more basic, further

from the 'operational' level, the level at which the **BSC** operates in connection with other operational concepts. The **EvSC**, on the other hand, is guiding all, or at least some of the available species concepts from the 'theoretical' level.

Michael Ruse's consilience approach to the species problem attempts to combine species concepts. Ruse's approach stems from considering how multiple species concepts can be used to delineate one equi-inclusive group. On his view, only when there's a correspondence between reproductive groups and morphological groups do we think that the species picked out by the **BSC** is real (Ruse, 1971, 369). Consider the most famous statement of his consilience view of species: "There are different ways of breaking organisms into groups, and they *coincide!* The genetic species is the morphological species is the reproductively isolated species is the group with common ancestor" (Ruse, 1987, 238).⁷ In a response that captures many general sentiments about Ruse's suggestion, Ereshefsky has said "It would be wonderful if these different types of groups did coincide, but they do not" (2014a, 74). As already stated, there is just too much cross-classification occurring between competing species concepts for Ruse's hope to be realistic. It's true that there may often be a correspondence between morphological and reproductive groups, but one may respond to Ruse by considering, for example, the notion of a cryptic species. Cryptic species are usually a temporary stage in speciation. A cryptic species contains separate types of organisms that cannot interbreed, for whatever reason, but all of the members of the cryptic species are individuals that are morphologically identical to each other. According to the **BSC** there are in fact two different species, because reproductive criteria are more fundamental to the nature of species than distinctive morphological traits. Due to the fact that there are so many outliers, so many cases where the different species concepts do not line-up, there does not seem to be a good reason to adopt Ruse's strategy. Despite these worries, Ruse's take on the monist reductionist strategy has some merit. Biologists often use more than one concept when analyzing a particular group. For a discussion of species pluralism to be complete, one must take the sophisticated ways that multiple species concepts are

⁷See also Ruse (1969, 111-112) and (1988, 54-55).

applied in different contexts into account. I will return to this topic of application in more detail in Chapter 5 when I consider the ways in which some yeast taxonomists apply species concepts.

The combinatorial strategy need not work in isolation from the reductionist strategy. Mayden (1997) for example, while attempting a ‘theoretical’ reduction to a slightly different formulation of Simpson’s **EvSC** shows how many of the available ‘operational’ concepts amount to the same thing. That is, even though there are over twenty different species concepts, Mayden argues that many of them are synonymous. This might not give us monism, but it will at least make species pluralism more constrained. Further, if the reductionist or combinatorial strategies fail, the monist may still avail herself of her imagination and create a new species concept. Every few years the total count of species concepts seems to increase in the biological community, with some species concepts even being developed by philosophers, e.g., the synapomorphic species concept of Wilkins (2003).

These are then the strategies for the monist. The pluralist may avail herself of bits and pieces of these strategies, but must be ready to graciously accept defeat at the hands of the world. The trick is to know when, where and why one must accept defeat. Pluralists want to have constraints on species concepts, but these need to be objective, well grounded, and there must be a legitimate purpose put to their use. Species pluralism, as I show in my second chapter, is just as multifarious as species monism, but in different ways. There is a plurality of ways of being a species pluralist.

1.5 Ontological Pluralism

Before we conclude this chapter I want to briefly touch upon a further form of pluralism that is relevant, related, but distinct from pluralism about species concepts: ontological pluralism. So far what we’ve discussed only directly pertains to resolving the the so-called species category problem, ontological pluralism pertains to the species taxon problem. Species taxa are again whatever individual species names refer to (e.g., *Escherichia coli*, *Poecile atricapillus*,

Beroe compacta, etc.),). When it comes to discussing species taxa from a philosophical point of view, this is where the question of realism most obviously comes into play. Are species real or are they just convenient ways of classifying organisms for purposes? If they are real, then what sort of ontological status do they have? This is the species taxon problem.

Many different answers have been proposed to this second question. The so-called traditional, or pre-Darwinian answer is that species are natural, rather than artificial, kinds with fixed unchanging essences. The so-called received, or post-Darwinian answer is that species are spatio-temporally restricted individuals with organisms for parts. In recent years many more different realist views of species have developed, some in the wake of species pluralism.

In this thesis I will not be directly engaging in the topic of species realism, which, as I understand it, pertains to the species taxon problem, though I deal with this problem in Chapter 4. As I show throughout this thesis, there are other realism related issues at play in that do not pertain to that problem. I will question whether or not a further plurality of ontological frameworks is required for species pluralism. My view is that if one accepts a certain theoretical unity to biology, but also accepts a certain kind of species pluralism, then one does not require a plurality of ontological frameworks. However, if one does not accept a certain theoretical unity to biology, but accepts a different sort of species pluralism, then one does require a plurality of ontological frameworks. The former sort I call evolutionary, the latter sort I call extra-evolutionary species pluralism. These two types of pluralism are further distinguished in Chapter 3.

1.6 Chapter Synopsis

In Chapter 2, ‘Aristotelian Species Pluralism,’ I deal with the following problem: Why has pluralism only recently been considered as a framework for systematic biology? I show how an Aristotelian species concept was used as a foil in part of a rhetorical strategy developed by Ernst Mayr (1940; 1942; 1957; 1963). With the prevalence of this strategy in subsequent disputes about

species, many were too distracted by the essentialist witch-hunt that ensued to notice whether or not anything was wrong with the assumption of monism. The essentialism story that Mayr's rhetorical strategy was built upon is incorrect, but has framed the way species concepts have been introduced in biology. I show that we can still use Aristotle's account of species as a foil, but as a foil for current accounts of species pluralism given a pluralist reading of Aristotle. Aristotelian science allows for a pluralistic approach to classification (Henry, 2011, 2014; Leunissen, 2014). From this perspective we can use Aristotle's approach to help better understand four issues at stake between modern species pluralists. First, pluralists need to consider the explanatory power of *all* taxonomic ranks. For Aristotle species are not necessarily the basal taxonomic units. Modern pluralists generally do hold that they are, even if there are different ways of conceiving of them (e.g., Mishler and Donoghue, 1982). Another way of saying this is that Aristotle has no fixed ranks, but since Linnaeus there is generally a fixed hierarchy of ranks in taxonomy. Second, pluralists must reconsider the significance of the species category in light of Aristotle's lack of explicit concern for providing a unitary definition of it. Third, pluralists ought to consider whether intrinsic, rather than relational or historical properties, are required to group and rank species. Modern pluralists remain divided on this (e.g., Kitcher, 1984b; Ereshefsky, 2014b), and Aristotle gives us a valuable means of comparison. Lastly, Aristotle can help us interpret the "cross-cutting" metaphor endemic to the pluralist literature (e.g., Dupré, 1999; Ereshefsky, 2001). For species pluralists to truly disabuse us of our unwarranted monistic assumptions, the essentialist story needs to be rewritten with these four issues in mind.

In Chapter 3 '(Extra-)Evolutionary Species Pluralism' I deal with the following problem: What sorts of arguments are there for being a species pluralist, and how do these arguments affect the form that species pluralism takes? I distinguish two main types of species pluralism, and discern three implications that follow from them. I first distinguish evolutionary from extra-evolutionary species pluralism. The debate amongst pluralists is about whether evolutionary theory alone ought to dictate which conceptions of species are legitimate,

and how we ought to interpret the relationship between biological theory and the different species concepts. Ereshefsky's (2001) account best showcases what I mean by evolutionary species pluralism by grounding pluralism in the various cross-cutting forces of evolution. Comparing his view with similar arguments (Mishler and Donoghue, 1982; Mishler and Brandon, 1987; de Queiroz and Donoghue, 1988) shows a range of interpretations of the role evolutionary theory ought to play in grounding species pluralism. Dupré's (1993) 'promiscuous realism' best shows what I mean by extra-evolutionary species pluralism, by grounding species pluralism in the disunity of biology. Comparing his view with Kitcher's (1984b; 1984a; 1989), I argue that Dupré (1981; 1999) fills in the needed theoretical support that Kitcher's lacks. Following this analysis, I examine both forms of species pluralism with respect to three main implications: (1) the nature of the species category; (2) (in-)admissible species concepts; (3) the nature of the "cross-cutting" kinds. Much has been written about pluralism and the species category, but I argue that determining the implications species pluralism has for the species category is only a first step toward developing a discerning species pluralism. The latter two implications make species pluralism a worthwhile contribution to systematic biology. I classify pluralists systematically and show how they have failed to resolve their views with respect to these two implications, and close by making some suggestions for how pluralists might make good on these ontological commitments.

In the fourth chapter 'Ontological Frameworks for Species Pluralism' I deal with the following problem: What sort of ontological framework(s) do different forms of species pluralism require? Debates about what species are have also been framed by monistic assumptions. Many different ontological frameworks have been developed to explicate the nature of *species taxa*: (1) species as individuals (Ghiselin, 1974; Hull, 1976), (2) species as natural kinds (Boyd, 1999a,b), (3) some mixture of both (Griffiths 1999; Millikan, 1999; Rieppel, 2013), (4) species as plural particulars (Slater, 2013; Simons, 2013), (5) species as sets (Kitcher, 1984a,b; Valen, 1988), or (6) species as processes (Rieppel, 2009; Dupré, 2012). Most have assumed that only one ontological framework will be correct. Contrary to this assumption, I argue that the debate is not

about what species are, but about which properties are more important for grouping species taxa (historical or intrinsic). On the account I develop, some species taxa may belong to different ontological categories. Different properties, historical or intrinsic, can be more important in certain cases than they are in others. Determining which species require which ontological category is partly empirical, and requires determining the role evolution plays on a group-by-group basis. Pluralism is compatible with almost any view of what species are, but “there may be more than one.” However, in order to be distinct from relativism, pluralism must be tied to biological theory. I show that evolutionary species pluralists favour ontological frameworks which are better suited to capturing historical properties (e.g., Ereshefsky, 2001; Wilkins, 2003), and that extra-evolutionary species pluralists will need frameworks that can capture intrinsic properties (e.g., Dupré, 2001).

In my final chapter ‘Species Concepts as Tools’ I deal with the following problem: What does species pluralism imply about how we use species concepts? I sharpen modern accounts of species pluralism by exploring the ‘species concepts as tools’ metaphor on the basis of a case study in yeast systematics. Yeast systematics provides many examples where multiple species concepts are used together. This is important because many species pluralists assume that each species concept should be used separately. That is, that there is still a one-to-one correspondence between successful applications of species concepts and species. The case study shows that there can be a many-to-one correspondence between species concepts and species, and that this doesn’t necessarily imply species monism. Generalizing from this case, I explain how the ‘species concepts as tools’ metaphor can be used to develop a rationale for determining when a concept is being used appropriately within a pluralistic framework by applying Waters’ (2011) account of ‘Toolbox Theorizing.’ Waters’ distinguishes between two sorts of realists: fundamentalists and toolbox theorists. For fundamentalists the world is made up of natural kinds of processes, and there is a one-to-one correspondence between a token process and its true model. For toolbox theorists there is a possibly messy world - for a given token process, some concepts and models might be useful

for constructing correct accounts of some aspects of this process, others for other aspects. Species pluralism if understood along these lines can not only make sense of the way species concepts are used, but can be developed to aid researchers in thinking about how to use the right tools for the right jobs.

Chapter 2

Aristotelian Species Pluralism

Linnaeus and Cuvier have been my two gods, though in very different ways, but they were mere schoolboys to old Aristotle.

Darwin (1882) to Ogle, on the publication of his translation of Aristotle's *Parts of Animals*.

2.1 Introduction

Species pluralism allows for multiple species concepts. Given the overwhelming number of such concepts (cf. Mayden, 1997; Wilkins, 2011), this seems like an obvious interpretation of how ‘species’ is used in contemporary biology. But why has it taken so long for this approach to be considered? I argue that part of the reason pluralism was overlooked due to the widespread use of a particular rhetorical strategy developed by Ernst Mayr. This strategy provided a framework for debates about the correct conception of species. That is, the strategy offered a means of comparing modern concepts with a monistic-essentialist understanding of species. I ask what would happen if we replaced this concept with Aristotle’s own pluralist-essentialist understanding

of species. As recent scholarship shows, Aristotle’s philosophy of biology allows for an approach to classification that is in practice highly pluralistic (Henry, 2011, 2014; Leunissen, 2014). From this new perspective we can understand what sort of assumptions are at stake when it comes to modern forms of species pluralism. My analysis shows that the essentialist story told by Mayr and others left us asking the wrong questions about how to conceive of species in an evolutionary world. Having a deeper understanding of Aristotle’s approach to the classification of animals allows us to shift focus from the so-called species problem in order to raise four issues that are relevant to current debates. These are questions about: (1) the explanatory power of taxonomic ranks, (2) the importance of the species category problem, (3) whether species are constituted by intrinsic or extrinsic properties, and (4) how to interpret the “cross-cutting” metaphor endemic to the pluralist literature. In order to get to these questions, I will first explain what sort of claim species pluralism is at the most general level, and motivate this chapter by showing how I’m enhancing the standard interpretation of the historical shift from species monism to species pluralism.

2.2 From Species Monism to Species Pluralism

The distinction between species monism and species pluralism suggests they are contrary views. Thus, a first pass would designate species pluralism as:

(SP*) There is no singular, unified way of grouping organisms into species

Pluralism allows for multiple, non-unified systems of classification. Monism allows for only one true system and only one true species concept.¹ Pluralism allows for many species concepts. Holding either view dictates the way we argue about species concepts. Monists seek general and unified criteria for ruling out false concepts. Pluralists maintain that these criteria are too strict, because they weed out concepts we ought to retain.

¹See Sterelny (1999); Brogaard (2004); Henry (2011).

Some worry that pluralism is dangerously close to relativism (e.g., Hull, 1999). A relativist would deny that there are principled and objective constraints on species concepts. If humans were to categorize species by how they taste, or by how cute they are, then this would be a legitimate concept. Denying relativism suggests a second pass at capturing species pluralism:

(SP) The world is such that there is no singular, unified way of grouping organisms into species

Pluralism requires constraints on which species concepts are admissible. This must be a claim about why the world is the way it is, which must be supported by our best biological theory.

Two *prima facie* and interrelated reasons for the shift from species monism toward species pluralism in and around the beginning of the 1980s suggest themselves. First, species pluralism is a consequence of the rise of pluralism in philosophy of science. Pluralism in philosophy of science is relatively recent, and is partly due to concerns about the feasibility of reductionism and unification (Suppes, 1978; Dupré, 1993). The true reasons why pluralism has become fashionable are not important here, for this is a very complicated story. What is important though is that it is not always clear at a global level what pluralists are being pluralist about, whether it's about explanation, causation, theories, concepts, models, or some further thing. This Chapter will make important steps towards clarifying these difficult issues. However the way many have understood pluralism at the global level has ridden on the backs of local, empirical, investigations of pluralism (Kellert et al., 2006). Arguments for pluralist approaches to explanations of sex (Fehr, 2001, 2006), pluralist interpretations of behaviour (Longino, 2005, 2006, 2013), pluralist interpretations of how “concept” is used in psychology (Machery, 2009), etc., have also lent credibility to arguments for species pluralism.

Second, theorizing about species has reached *conceptual overload*. Monism makes more sense when there's only a small handful of competing species concepts, but when the number of concepts keeps increasing (cf. Mayden, 1997; Wilkins, 2011) there is eventually a point where pluralism becomes a more

reasonable view. This of course isn't itself a great argument for pluralism. A monist has many reasons to retain their position even in the light of conceptual pluralism. However, conceptual overload may still be part of the explanation for why species pluralism has become a more fashionable approach to dealing with conceptual pluralism. But, as I will now show, despite there being more species concepts today than there were during the time of the New Synthesis in the earlier part of the twentieth century, there was still a significant amount of conceptual tension and conflict then.

Species monism was not questioned during the New Synthesis (e.g., Dobzhansky, 1935; Mayr, 1940; Simpson, 1951), which marks the first period where biologists were offering and debating explicit definitions of "species" as a theoretical entity in evolutionary biology. However, at this time it was recognized that a monistic *classification* had problems: "No system of nomenclature and no hierarchy of systematic categories is able to represent adequately the complicated set of interrelationships and divergences found in nature" (Mayr, 1942, 103). This conflicted with the desideratum that a species concept should be universalizable and general. Holding onto monism in light of these conflicts involved what some have interpreted as *ad hoc* manoeuvres *sensu* Popper (e.g., Stanford, 1995, 76-77). One may wish to reserve one concept for 'species,' and have other concepts for other important biological groups. For instance, if we favoured a concept that requires sexual reproduction and interbreeding, then asexual organisms that reproduce by budding, binary fission, vegetative reproduction and the like will fail to form species. Many argued just this (e.g., Dobzhansky, 1935, 355), and continued to argue this (e.g., Mayr, 1987). Some have even claimed that species produced through polyploidy "have all the earmarks of blind alleys of evolution" (1942, 191), and some have even claimed that asexual groups are rare in comparison with sexual groups (Mayr, 1942). The majority of life on Earth, both in terms of the number of organisms and the percentage of biomass, is asexual (Hull, 1988, 429).²

While some were depriving asexual organisms rights to full species-hood, others were developing terms like 'agamospecies' (Cain, 1954) and 'uniparental

²See also Templeton (1989).

species' (DeBach, 1969) to aid in grouping asexual organisms. These were only pseudo-species concepts. Today many people think differently about asexual organisms, because we now have a better understanding of the continuum between asexual and sexual organisms, and we have reflected on the fact that sex itself is an evolved trait. Considerations like this have lead us to restore asexual organisms's full rights to species-hood. But it is important to note that this restoration has been achieved partly through the influence of species pluralism (e.g., Wilkins, 2003).

But why not consider pluralism, rather than seeking a unified definition of the species category? The *conceptual overload* story suggests a reason why pluralism took so long to develop. Up until around thirty years ago, there weren't enough species concepts on hand for pluralism to be considered. The development of pluralism in philosophy of science is certainly far more complicated than I have presented it here, and though pluralism of one sort or another can be traced back at least as far as the Vienna Circle and its critics, much of that approach to philosophy of science has taken a long while to trickle down to debates in biology itself. However, since there are longstanding ways of arguing that certain concepts are not *real* species concepts, perhaps neither the conceptual overload story, nor the top down story from general scientific pluralism are the whole story behind the rise of species pluralism. There may also have been deeper reasons for holding on to species monism. Biologists may have assumed that "species" designates a natural kind, and as such there must be one true species concept. Though we will touch on part of this ontological problem now, a fuller treatment will be put aside until the fourth chapter where we consider species pluralism and the ontological status of species.

2.3 The Rhetorical Strategy

A monist needs reasons that favour one concept. This often involves a critique of the competition: and through critique and comparison between different species concepts what is better on some grounds often slips into what is best

overall³. Mayr's strategy was built upon a complicated and deeply misleading story about how Aristotelian biology and evolutionary biology conflict at an ontological level. Winsor (2003; 2006) has dubbed this story "the essentialism story," which she argues was developed by Mayr (e.g., 1969a), Cain (1958) and Hull (1965a; 1965b).⁴ I will only focus on Mayr, because his version of the story has set the standards for how leading biologists debate about species concepts.

According to the story, after Darwin's development of evolutionary theory, species essentialism became untenable. Essentialism is roughly understood as the view that species have fixed, distinct and unchanging essences that all and only the members of a particular species partake in. In most versions of the story essentialism is not clearly understood, but the point is that essences make evolution impossible. Darwin's work was not just to revolutionize biological theory, but to revolutionize the very way that we conceive of species at an ontological level. Many believe that essentialism forestalled the development of evolutionary theory nascent in pre-Socratic biology (Simpson, 1961; Mayr, 1963; Ghiselin, 1969; Dobzhansky, 1970). Others have blamed the Aristotelian method of definition (Popper, 1966; Hull, 1965a), or method of logical division (Cain, 1958; Winsor, 2001). The evolutionary shift requires giving up species essentialism, and calls out for a conception of species that allows us to keep species real, but one that fits with the intrinsic variation demanded by evolutionary theory. I'll now show how this story provided a framework or set of assumptions for arguing about species.

Consider the different species concepts as falling upon a line. At one end of the line we have an essentialist species concept. Different species concepts are placed in degrees of closeness to the essentialist species concept. An essentialist concept requires a set of necessary and sufficient conditions for species membership. On the line, species concepts would be closer to an essentialist concept the less they modify the way a species is defined from the essentialist

³See Cracraft (2000) for an important discussion of this problem about rhetorical uses of language in species concept debates

⁴But see Stamos (2005) for some problems with Winsor's account.

starting point. For example, an ostensibly defined species (a species defined in reference to a type, or exemplar organism) might be considered further from essentialism than a species defined by a disjunctive definition (a species defined as satisfying either this or that set of properties). If an essentialist species concept requires that we specify a set of typical phenotypic properties, then the more a species concept makes use of these sorts of properties the closer it is to essentialism. There may be differing and competing orderings of species concepts as based on different understandings of essentialism, but that there is some single correct ordering is taken for granted. The reason I'm calling this a rhetorical strategy, rather than Mayr's argument, is that many other people have picked up a similar way of arguing to Mayr, but have substituted their preferred concept for his **BSC**.

Mayr's distinction between population (non-essentialist, post-Darwinian) and typology (essentialist, pre-Darwinian) thinking formed a basis for his reproductively based species concept, and is one of the most common ways that essentialism is still understood to this day in biology. On Mayr's account, *population thinking* concerns relating organisms to populations, whereas *typology thinking* is about relating organisms to types. According to population thinking, an organism belongs to a certain species in virtue of it participating in a certain population structure (gene flow) with other organisms. According to typology thinking, an organism belongs to a certain species in virtue of it sharing the relevant sort of intrinsic properties with its exemplary type. There is much to be said about the value of this distinction (e.g., Sober, 1980; Chung, 2003), but for our purposes it is more important to focus on how typological thinking translates into a definition of what a species is. Typological species concepts were based on species having essential properties. Though it is rare to find an explicit formulation, one can state that the "typological species concept," Mayr later formulates it as follows:

(TSC) 'A typological species is an entity that differs from other species by constant diagnostic differences, but it is subjective what one may consider a diagnostic difference. The so-called typological species concept is simply a biologically arbitrary means for

delimiting species taxa” (Mayr, 1982, 176).⁵

Whether or not anyone actually held a **TSC**, Mayr (e.g., 1996, 269-270) argues that it fails for at least the following three reasons. First, because of polymorphism within populations (e.g., light and dark-morphs of the jaguar [*Panthera onca*]). Second, because of geographic variation within species. Third, because of ‘sibling’ or ‘cryptic’ species: species with the same phenotype, but different reproductive capacities or genetic difference (e.g., recent DNA analysis the Two-barred Flasher butterfly [*Astraptes fulgerator*]). This story of how the **TSC** fails in the light of such and similar reasons is quite common in much of the introductory systematic literature even today (Winsor, 2006). Following this, Mayr then sets up the biological species concept (BSC) as the non-essentialist, post-Darwinian species concept that can account for the failures of **TSC**, which he formulates as follows:

(BSC) “species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups” (Mayr, 1942).

The **BSC** is better, because it can be used in explaining why there is a real boundary between species when the **TSC** cannot. To a certain extent polymorphic species, species with geographic differences, and cryptic species can be further understood by considering the reproductive, and thereby genetic connections that exist between them. Many people who do not adhere to the **BSC** will still set the problem of finding a post-Darwinian species concept in this very same way.

A further aspect of this strategy is to argue that any species concept that resembled a **TSC** can, and should be ruled out. A phenetic species concept, that uses an analysis of overall similarity, rather than the more constrained set of diagnostic features required by the **TSC**, fails for the same three reasons the **TSC** fails, and so we can label it “typological.” This is definitely an oversimplification, but it shows the general structure of the species concept dialectic.

⁵See Mayr (2000) and Lennox (2001).

In sum, on Mayr’s understanding, essentialism and monism were linked, and with the widespread adoption of his strategy, many were too distracted by the essentialist witch-hunt to notice whether or not anything was wrong with monism. I will now explicate Aristotle’s account of species, in order to show how we should interpret species in a pluralistic context.

2.4 Aristotelian Species Pluralism

Traditionally Aristotle is viewed as an essentialist species monist. On this view, Aristotle would allow for only discrete, non-overlapping natural kinds. However, a close examination of the ways he carves up animals into kinds makes pluralism a more likely interpretation. Aristotle offers multiple, overlapping classifications of animals. Each classification he offers appears useful for understanding some causal aspect of the animal world. Single organisms are often described along multiple lines. Henry’s (2011; 2014) recent work on Aristotle, following Pellegrin (1982), shows that essentialism and monism about species are not necessarily connected, despite what Mayr’s essentialism story indicates (see also Balme, 1962; Lennox, 2001). In this section I will show why that is the case through a brief explication of Aristotle’s approach to classification.

First, Aristotle has two relative terms for natural kinds: εἶδος and γένος. They have standardly been translated as ‘species’ (εἶδος) and ‘genus’ (γένος) via the Latin, into English. When applied to a group of animals, an εἶδος is almost always some further specification of a γένος, and a γένος isn’t what it is without having different εἶδη (*Metaph.* ζ. 12: 1036a6-9).⁶ Both terms are used at all levels of biological organization, and a particular γένος may be itself an εἶδος of some higher order γένος. Since these terms do not indicate fixed ranks in a hierarchy in the way that genus and species do for post-Linnaean, recent Aristotelian scholars have offered ‘form’ (εἶδος) and ‘kind’ (γένος) as more appropriate equivalents (Lennox, 2001). I will follow this translation of

⁶Aristotle is willing to count humans as a γένος that doesn’t differentiate into further εἶδη.

both terms.

Second, Aristotle seeks definitions of kinds and forms at various levels of generality, but explanations must be at the right level. For example, the reason an isosceles triangle's interior angles are equal to two right angles, is because isosceles triangle belongs to the kind triangle, not because having interior angles equal to two right angles belongs to the kind isosceles triangle. The isosceles triangle is a form of triangle, and many of the properties isosceles triangles have, they have because of belonging to the kind we call 'triangle.' In the biological case Aristotle presents an *aporia*. He asks about the proper level at which an investigation should be organized. Should we either start with each substantial being on its own, and by this he seems to mean something like the *infimae species* or ἄτομα εἰδῆ (indivisible species), or should we start with the more general kinds first (*PA* I. 1 639a15-19)?⁷ Though the answer Aristotle seems to give is that it depends on what we hope to achieve.

Further, even if we lack a name for a kind we still need to seek the right level for the explanation. Aristotle gives an example that involves considering how proportion (or ratio) alternates in the same way for numbers, lines, solids, and times (*APo.* A. 5 74a19-25). Though we didn't see the commonality between these four kinds of things at first, as we investigated ratio we came to recognize this new real kind: 'proportionate things.' In the biological case, Aristotle was willing to invent new kind terms (e.g., 'cephalopods,' 'selachians,' 'entoma'), if they revealed the common nature that pertained to such organisms.

According to Aristotle, we get at the nature of a kind by acquiring a definition of it. Definitions are reached through division. Aristotle takes great pains to show why Plato's method for seeking definition through bifurcating division (e.g., in the *Sophist*), which separates kinds by means of a single difference, fails to uncover true kinds. Aristotle urges that we ought to group important forms together with their respective kinds, and that bifurcating division "tears kinds apart," because there cannot be many differences under a single dichotomous division (*PA*. 1 3 644a1-11). For example, there are many distinct forms of bird and fish, and we ought to follow the common people, and recognize

⁷cf. *APo.* B 13 98a1-19.

birds and fish as genuine kinds of animals (*PA* I. 3 6439-16). Though some birds are water-dwellers, and being a water-dweller can explain some things about those birds, we would lose something if we failed to recognize birds as its own kind. Nor should we combine water-dwellers and flying animals into one kind, because some water-dwellers are not birds. For Aristotle, the true mark of a natural kind is that it differs by degree and what he calls “the-more-and-the-less” (Lennox, 1980, 2001; Henry, 2014). Bird forms differ by degree because they either have short or long feathers (*PA* IV. 12. 692b3-9), whereas birds and fish differ from each other by analogy because one has feathers and one has scales to fulfill analogous functions (*PA* I. 4. 644a12-23) (cf. Lennox, 2001). On Henry’s reading of Aristotle “a genuine kind is a group of individuals sharing a “common nature” . . . a nexus of correlations underwritten by a set of causally basic features (the kind’s real essence)” (2011, 201). There is something causally basic about being a bird that causes birds to have things like feathers and beaks that differ in different environments, which are there used for different purposes.

According to Henry, Aristotle offers a realist and pluralistic, cross-cutting approach to classification (2011, 200).⁸ At the core of each ‘cross-cutting’ kind, there is an essence, which corresponds to a cause (*aitia*) (2011, 201). He presents two reasons for viewing Aristotle as a pluralist about biological kinds. The first involves considering the relationship between Aristotle’s four different major divisions of animals: by mode of reproduction, locomotion, mode of cooling, and the Greatest Kinds. The second involves the ‘dualizers’ (ἐπαμφοτερεῖς), organisms that straddle different forms. Both show that Aristotle is open to cross-cutting classifications of organisms, and that he is thus a pluralist. The first example shows this with respect to kinds, and the second with respect to forms themselves.

⁸There is some debate on how to understand Aristotle’s biological classification (Balme, 1962; Balme, 1987; Pellegrin, 1982; Lennox, 2001). Henry understands ‘classification’ as ‘the systematic arrangement of organisms into a hierarchy of kinds on the basis of shared similarities and differences.’ If that’s all we mean, surely Aristotle classifies animals. Other interpreters think that a classification of animals must be in some sense universal, and monistic in nature, but this assumption is certainly imposed upon our reading of Aristotle.

The first division is by *mode of reproduction*: live-bearers, egg-layers, larva-producers, and animals that are spontaneously generated (*GA* II. 1, 732a26-733a1). This classifies lizards, turtles, fish, birds and snakes as egg-layers; cetaceans, humans, elephants, and bats together as live-bearers; some of the insects as larva-producers; some of the insects and some of the testacea as spontaneously generated animals. The second division is by *mode of locomotion* (*IA*; *HA* I 1, 5). First, by their *type of locomotion* (*IA* III): jumpers, walkers, swimmers and fliers (*HA* I 1, 487b14-32; *GA* I 1, 715a28; III 1, 749a15). Lizards, turtles, humans, elephants, and crabs are classified as walkers; cetaceans, fish, water snakes, and crustaceans as swimmers; birds, bats, and (some) insects as fliers. Second, by the *parts* used for locomotion: bipeds, quadrupeds, polypods, and footless animals. This classifies birds and humans as bipeds; elephants, lions, lizards and crocodiles as quadrupeds; insects as polypods; cetaceans, fish and snakes as footless animals. The third division is by means of their mode of cooling (*On Resp*): lung-possessors, gill-possessors, and membrane-possessors. This gives us cetaceans, lizards, humans, and birds as lung-possessors; fish, cephalopods, and other marine animals as gill-possessors; insects as membrane possessors.

These different divisions cross-classify one another. None of differentiae of one division explain those of the other (*GA* II 1, 732b15-27). Having a certain number of feet doesn't help explain how an animal reproduces. What explains reproduction is the material nature of the organism. Live-bearers are hot and moist, and egg-bearers are cold and dry. Mode of reproduction also cuts across the division Aristotle makes according to an animal's type of locomotion and the division by an animal's mode of cooling. The egg-layers and live-bearers cross-cut the lung-bearers and gill possessors. Some egg-layers are lung-possessors (e.g., birds, lizards, turtles, all snakes except the viper), but some are gill-possessors (e.g., bony fish). Some live-bearers are lung-possessors (e.g., humans, cetaceans, horses, vipers), but some are gill-possessors (e.g., some sharks and rays). Mode of cooling cuts across the parts an animal uses for locomotion (*On Resp.* 476a5). The lung-possessors cut across the different divisions according to parts used for locomotion. Some lung-possessors are

bipeds (humans and birds), some are quadrupeds (e.g. horses, oxen), but some are footless (e.g. whales and dolphins). Some gill-possessors are footless (e.g., fish), but some are quadrupeds (e.g. the water newt). The four divisions also cut across the Great Kinds: the blooded animals: birds, fish, cetaceans, and the bloodless animals: the hard-shelled animals, soft-shelled animals, mollusks, and insects. Thus, Aristotle has no single unified classificatory scheme of animals.

The second reason for viewing Aristotle as a pluralist concerns his treatment of the ἐπαμφοτερεῖς ('dualizers'). For these animals more than one form is needed to explain why a particular organism is the way it is. The ἐπαμφοτερεῖς show how even the bottommost forms (the *infimae species*) can, in some cases, cross-cut one another at the organismal level. I will discuss the following examples of animal forms that fall into this category: the Libyan ostrich, ape, seal, and bat.

First, the Libyan ostrich. This animal is both a bird (its lower parts are covered in feathers and it's two-footed) and a live-bearing quadruped (its upper parts are covered in hair and it's hoofed) (*PA* IV 14, 697b13–28). It doesn't fly, and its feathers are not useful for flight. Aristotle calls these feathers "hair-like" (τριχώδη). The general size of the animal corresponds to that of a quadruped, and this is partly why it doesn't fly. Second, apes, monkeys, and baboons can be classified both as bipeds (human-like) and as quadrupeds, since they share in the essential properties of both kinds (*HA* II 8-9. 502a16–24). The ape is both a biped and a quadruped: "The ape, because it is intermediate between the two (ἐπαμφοτερίζειν) with respect to its form, and because it is neither and both, has neither a tail nor haunches: as a biped it lacks a tail, and as a quadruped it lacks haunches" (*PA* IV 10, 689b32–4). This explains why apes have hairy bellies and backs. Third, consider seals and bats (*PA* IV 13, 697b1-12). Seals are both land-dwellers and water-dwellers (the same for the cetaceans), because they have feet and fins (and their teeth are razor sharp). Bats are both flyers and land-dwellers, because they have feet, but lack tail and rump, and they lack tails because they are flyers, and have no rump because they are land-dwellers. Bats are membranous-winged,

and nothing has a rump unless it is split-feathered. Being split-feathered is what causes certain organisms to have rumps. Clearly, by his treatment of the ἐπαμφοτερεῖς, Aristotle takes a pluralistic approach, and recognizes that in some cases multiple classification schemes are required to explain the features of one organism.

In sum, these two sorts of cases, the higher order kinds, and the ἐπαμφοτερεῖς (‘dualizers’) clearly show Aristotle’s pluralism at work. However, before I conclude this section, there are a couple of concerns to flag, because they call into the question the relationship between reading Aristotle as a pluralist and accepting his doctrine of essentialism. I will suggest that Aristotle’s approach can help us understand what is at stake between modern forms of species pluralism.

First, one might worry that this reading will lead us to the view that a particular organism may have more than one essence. Henry argues that a particular kind (or form) on this account will still have only one essence: “The single essence of the Libyan ostrich will thus be defined by a single complex of multiple attributes, some of which are characteristic of birds and others characteristic of quadrupeds” (2011, 206). On this reading of Aristotle, the essences just are in the individual organisms and nowhere else. If this is correct, it still remains to spell out in more detail how Aristotelian kinds cross-cut the world, and not just each other. This is important to work out, because many scholars that want to bring Aristotle back into modern biology argue that he is not building a taxonomy, though they have a certain monistic understanding of taxonomy and classification (Walsh, 2006; Witt, 2011) I will gesture towards one way of working this out in the final section of this Chapter.

A second worry concerns how Aristotle held two seemingly opposed views. First, the view that forms of a kind differ only in the relative magnitudes of their structures (*PA* IV.5.681a12-15; *HA* VIII.1.588b4-22). Second, that there are complete discontinuities between one form or kind and all others. Lennox’s solution to this problem hinges on how we understand ‘the more and the less.’ His position is that: “For two individuals to differ in degree, they must both be the same general sort of thing. With respect to that sort they do

not differ in degree. But the general sort is constituted of features with range – any sub-kind may have these features exemplified by different specifications of that range” (Lennox, 2001, 167). This solution seems to involve being careful about the level of differentiation Aristotle is talking about when he uses ‘the more and the less.’ Thus, we must ask if he’s talking about some individual black-capped Chickadee as some form of bird, or as belonging to the kind bird. Henry’s (2014) alternative solution to this problem focuses on Aristotle’s conception of analogy. On this reading, kinds are distinct because they have parts that fulfil analogous roles (e.g., birds and fish are distinct because one has feathers while the other has scales). Now, whichever solution to this problem we opt for, we get a clearer understanding of how Aristotle’s hierarchy of kinds works, which is further complicated by his use of only two relational terms ‘form’ and ‘kind,’ as discussed above. This issue has some bearing on the explanatory nature of higher taxa, which I will raise in its proper context in the following section.

2.5 Rethinking the Rhetorical Strategy

I have argued that Mayr’s strategy allowed for the use of a particular understanding of an essentialist species concept to shape disputes about post-Darwinian species concepts. This still shapes the way species concepts are introduced today. In order for species pluralism to truly supplant monism we need to update our foil from the naive traditional to a comparison with the rich and sophisticated ways Aristotle treats species. Pluralists can also use a version of the rhetorical strategy that Mayr developed in order to introduce different versions of species pluralism. We can keep the comparison with Aristotle’s classification schema, but we can lose essentialism as the main point of comparison. Though we should again note that Mayr and Aristotle mean entirely different things by essentialism. In closing, what I want to suggest is that having a deeper understanding of Aristotle’s pluralistic approach to biology allows us raise at least the following four points of comparison: (1) the explanatory power of taxonomic ranks, (2) the importance of the species

category problem, (3) the question of intrinsicism, and (4) how to interpret the “cross-cutting” metaphor endemic to the pluralist literature.

First, Aristotle doesn't have a fixed hierarchy of definable ranks: “His approach to classification does not involve an attempt to pigeonhole animals into the fixed ranks of some predetermined taxonomic hierarchy” (Henry, 2011, 217). Aristotle's greater kinds, e.g., bird, fish, land-dweller, lung-possessor, etc., are real. That is, they have a mind-independent existence and are explanatory. We want to know why certain things have certain features. All animals have certain features because they are animals, and other features because they are certain kinds of animals. The work of the biologist is to explain each feature at the right level of biological organization (*APo.* β 14 98a9-19). Modern pluralists generally do follow Aristotle in arguing that we retain species concepts that are real. However, modern pluralism raises questions about the nature and usefulness of taxonomic ranks. Some species pluralists have argued that we ought to abolish the Linnean system of taxonomy (Ereshefsky, 2001), and others have argued that species are not real in any distinct sense when compared with higher order taxa (Mishler and Brandon, 1987). Those behind the development of the PhyloCode, a new classification scheme that is meant to be more general than existing codes of nomenclature (e.g., the International Code of Botanical Nomenclature), have found no use for a hierarchical system (cf. Rieppel, 2006; Ereshefsky, 2007), though this may be due to an preoccupation that exists amongst some biologists with the search for clades or monophyletic taxa (taxa that include a common ancestor and all of its descendants). With this in mind, one question Aristotle's pluralism allows us to ask is whether or not there is something real about bigger paraphyletic groups (e.g., Reptiles, Gymnosperms), taxa that include a common ancestor but not all of its descendants. The fact that these groups cross-classify doesn't make them any less real, and this is an option that modern pluralists should still consider, rather than only recognizing monophyletic groups. I address the role the concept of monophyly plays for different forms species pluralism in the remaining chapters.

Second, Aristotle has no definition of the species category. Quite often a

‘species concept’ is thought to be a way of defining the species category. By providing a definition of what it is to be a species, whether it’s the **TSC**, the **BSC** or something else, we provide a way of putting things into the species category. But, as we have seen, Mayr understood essentialism as a failed way of doing this. Aristotle has no hard and fast rules for what counts as a species and what does not. His approach usually involves starting at the widest explanatory kinds and working down to the narrowest. Aristotle also works up by grouping together previously unrecognized kinds, e.g., cephalopods, and follows the many in recognizing kinds that are differentiated by multiple factors, e.g., birds and fish. But sometimes, as in the case of humans, we need not seek a wider kind to explain most of the features the thing has. For these reasons, Aristotle’s approach to kinds and forms clearly doesn’t fit the earlier model developed by Mayr. Aristotle mainly uses his classifications of animals to explain why organisms have the various parts they have. However, this does not mean there are no constraints on what it is to be a form for Aristotle. A minimal condition is that a form is one of at least two ways of differentiating a kind. But the other key thing is that there are many different ways of satisfying this condition. Species pluralism in the modern context may also imply that we do not have a well-defined “species category” as many have pointed out (e.g., Ereshefsky, 1992), but we still need constraints on what is to count as a legitimate species concept. Aristotle presents constraints in terms of how forms relate to their respective higher order kinds, whether cross-cutting or not. Whether or not there should be any analogous sort of hierarchical constraint on species concepts for modern forms of pluralism is a question that needs to be raised. I address the relationship between species pluralism and the species category further in Chapter 3.

The third issue Aristotle helps us address, though certainly not solve, is the question of intrinsicism. There are many modern debates about whether species are relational entities, or whether there is something intrinsic to each organism that makes it a member of a particular species. Many seem to argue that a kind’s essence is limited solely to intrinsic, micro-level properties. Unfortunately, the issue of intrinsicism is not entirely clear even in Aristotelian

scholarship. Are essences just sets of intrinsic properties, or is there something more resembling relational properties that might be present in the essence of a particular form? Aristotle does say that animals differ from one another in their modes of subsistence, in their actions, in their habits, and in their parts (*HA* I. 1 487a11). If this is the case, Aristotle can provide a way for an essentialist view of species to move beyond the intrinsic properties of organisms. More work needs to be done to understand Aristotle's view on this issue, because in the modern context the debate over intrinsicism is alive and well. We still want to know the degree to which the properties of the organisms themselves determine their species status. I discuss the issue of intrinsicism in more detail in Chapter 4.

Lastly, Aristotle's pluralism allows for cross-cutting kinds. His higher divisions of animals cross-cut one another, and the ἐπαμφοτερεῖς fail to fall under one uncuttable form, though they still retain a complex essence. Aristotle allows for kinds and organisms cross-cut one another. Modern pluralists might require that populations and lineages be cross-cut, or even something further than that. There may be ways of cross-cutting for modern pluralists that accord with Aristotle's account. This is a metaphor that needs to be sorted out, and I will make further progress on this question in Chapter 3.

In sum, the importance of *these* questions to the modern species literature, especially when it comes to pluralist approaches to species, shows the importance of revisiting Aristotle's approach to biology, in particular, his approach to classification. I have here only begun to sketch the connections we can draw. The important part of this chapter is to note that there is much more to the essentialism story than what we find in textbooks, and much more that we ought to be putting in new textbooks. Mayr and others have assumed that essentialism must be a form of monism, but looking carefully at Aristotle, the archetypal essentialist, shows that this is not the case. I'm not suggesting that revisiting Aristotle will help clarify everything that is going on in modern systematic biology, for in many ways there is not a strong Aristotelian tradition for us to draw on (Lennox, 1994). What I am suggesting is that revisiting Aristotle's work on classification can help us raise more questions and hope-

fully disabuse us of some of the assumptions that plague contemporary debates about species concepts and the ontological status of species taxa. Mayr's interpretation of the history of biology before Darwin has set the standard for comparison among species concepts for far too long. A new, more pluralistic, essentialism story of pre-Darwinian taxonomy needs to be told, especially if Darwin is to be taken at his word when it comes to old Aristotle.

Chapter 3

(Extra-)Evolutionary Species Pluralism

Nothing in biology makes sense
except in the light of evolution.

Theodosius Dobzhansky, 1973

Introduction

In this chapter I show how taking on different assumptions about the theoretical role that species ought to play in biology will lead to different forms of species pluralism. There are two main kinds of species pluralism: evolutionary and extra-evolutionary species pluralism, with many different forms falling under each of these two kinds. Species pluralism raises three questions: (1) What sorts of things get to count as species? (2) How do the different sorts of species relate to one another? (3) What does species pluralism imply about the nature of the species category? This third question has been raised largely in relation to distinguishing pluralism from monism. The former two concern how to distinguish pluralism from relativism. To distinguish pluralism from relativism we need reasonable constraints on what sorts of species concepts are admissible. These constraints come from biological theory. I will argue that

just as species concepts constrain what sorts of biological entities can count as species, so species pluralism constrains what sorts of concepts count as species concepts.

The first section of this chapter will explicate the difference between evolutionary and extra-evolutionary species pluralism¹, and will develop a taxonomy of positions falling under these two views. Both forms of pluralism are constrained by biological theory, but they differ in whether they accept evolutionary theory as *the* fundamental theory that pertains to ‘species.’ Evolutionary species pluralists differ amongst themselves in the way they interpret the different evolutionary forces that produce, shape and maintain species, but agree that species are important evolutionary lineages (Mishler and Donoghue, 1982; Mishler and Brandon, 1987; de Queiroz and Donoghue, 1988; Ereshefsky, 2001). Extra-evolutionary species pluralists agree in denying that species must all be lineages, but differ in the sorts of non-evolutionary relationships that are recognized as important for how we think of species (Dupré, 1981, 1993, 1999; Kitcher, 1984b,a, 1989).

The second section will make explicit the ontological implications of each form of species pluralism with respect to: (1) the nature of the *species category*; (2) the species concepts that each reject; (3) ‘cross-cutting’. I overview four different accounts of the relationship between species pluralism and the species category, and show that this requires distinguishing pluralism from monism. The second implication concerns distinguishing pluralism from relativism, and the third from both relativism and monism.

3.1 Two Forms of Species Pluralism

One of the important debates amongst pluralists is about which theory or theories ought to dictate which conceptions of species are legitimate, and how we ought to interpret the relationship between theory or theories and the different species concepts. On my analysis, there are two main forms of species plu-

¹For a similar distinction between two different sources of species pluralism see Reydon (2003, 50-51).

ralism: evolutionary and extra-evolutionary species pluralism. Evolutionists think that species must be what evolutionary theory tell us they are, whereas extra-evolutionists disagree.

In order to streamline the argument of this chapter, I will re-introduce the distinction from cladistics between monophyly, paraphyly, and polyphyly. A *monophyletic group* is a group composed of a collection of organisms, which includes the most recent common ancestor of all those organisms and all the descendants of that most recent common ancestor. A *paraphyletic group* is like a monophyletic group, but does not include *all* the descendants of that most recent common ancestor, merely some of them. A *polyphyletic* taxon does not include the most recent common ancestor of all members of the taxon. Cladists focus on delineating monophyletic groups. Despite the fact that this terminology is tied to cladistics, one of the three major schools of taxonomy, and that not all pluralists follow the dictates of the cladistic school of taxonomy, it will prove economical for discussing the implications of a wide range of views referred to as species pluralism.

3.1.1 Evolutionary Species Pluralism

Evolutionary species pluralists make explicit appeals to evolutionary theory in the way they formulate pluralism. For example, “Species pluralism, according to current evolutionary theory, is a real feature of the world and not merely a feature of our lack of information about the world” (Ereshefsky, 2001, 139). Evolutionary species pluralism is the view that:

There are multiple, non-unified ways of grouping organisms into species, and evolution is the single cause of these different (‘cross-cutting’) species.

This view involves a commitment to fundamentalism about evolutionary theory with respect to species. Species on this view are considered to be important entities that evolve as a unit.² In this section I review three different arguments

²Evolutionary species pluralism bears many affinities with the species as individuals hypothesis offered by Hull and Ghiselin. I will return to this relationship in the following

for variants of this thesis.

Monophyletic Pluralism

Mishler and Donoghue (1982) offer perhaps the earliest argument for a form of evolutionary species pluralism, which is elaborated by Mishler and Brandon (1987).³ Though this sort of view is pluralistic, it is also a pluralism ruled by an interpretation of one particular species concept, the phylogenetic species concept, by way of its requirement that all species be monophyletic groups. Thus, it is in this way that the view is really quasi-pluralistic. Mishler and Donoghue's (1982) argument for species pluralism requires denying that species are the unique basal evolutionary unit. This makes the argument rest on a denial of monism. The assumption that species, whatever else they are, are evolutionary units, is what makes this an argument of evolutionary species pluralism. It can be formulated as follows:

1. Species are evolutionary units.
 2. There are many evolutionary (genealogical) units within any given lineage that can temporally and spatially overlap.
 3. If there are many evolutionary (genealogical) units within any given lineage that can temporally and spatially overlap, then there is no unique basal evolutionary unit
 4. If there is no unique basal evolutionary unit, there is no reason to pick out any particular group as the species.
 5. If there is no reason to pick out any particular group as the species, species pluralism.
- ∴ Species pluralism.⁴

The key premise here is the third. Species are typically thought of as the basal unit in taxonomy, and higher order taxa are simply groups of species. In

chapter

³See (Hennig, 1966, 5-7) for a similar suggestion. See Ghiselin (1989) for an early criticism of their view and defense of a monistic interpretation of the **BSC**. See Mishler and Brandon (1989) for a reply.

⁴See Dupré's (1999, 11-12) discussion for a similar formulation of their argument.

support of (3) they say that “in the search to find the evolutionary unit, one is on a very “slippery slope” indeed. Units all along this slope may be of interest to evolutionists, depending on the level of focus of the particular investigator. These units do require some sort of designation in order to be studied, but a formal, hierarchical Linnaean name is not necessary” (Mishler and Donoghue, 1982, 498). It is thus a slightly arbitrary decision as to which of these evolutionary groups should be considered species. There are many sorts of spatially and temporally overlapping units, though, according to this view, all of the units we recognize are more or less inclusive monophyletic groups. The other units they wish to exclude from consideration as species may be monophyletic, but too large or too small, so they should be recognized as either higher-order taxa (e.g., genera, orders, etc.), or sub-specific taxa (e.g., varieties). There are also evolutionary units that may be paraphyletic, but these, according to this view, should not be counted as species, nor as higher-order taxa or sub-specific taxa. In different situations, different biological properties will be required to rank a monophyletic group as a species apart from the higher and lower taxa. But these properties must always be consistent with monophyly, because for them, evolutionary units in general must be monophyletic. This claim is contentious, and as we will see, it is not one that many pluralists hold.

Monophyly and Interbreeding

A second argument for a form of evolutionary species pluralism comes from considering debates about the primacy of interbreeding versus monophyly for defining the species category.⁵ Some biologists want to focus on relationships of descent, and some consider interbreeding groups to play a special role in the evolutionary process. De Queiroz and Donoghue (1988) argue that descent and interbreeding are real processes that can hold species together jointly or separately. We should allow species concepts based on either to count, because neither one can meet the needs of all biologists. Either way, evolutionary theory has bearing on these two different sorts of species concepts. With this

⁵They are arguing that we should use both the **BSC** and the **PSC**. See the Introduction for more details.

in mind, we can formulate their argument as follows:

1. Species concepts make either interbreeding or monophyly the most important criteria for demarcating species.
 2. These two criteria sometimes cross-classify.
 3. If neither sort of species concept can meet all the needs of all comparative biologists and these two criteria sometimes cross-classify, then species pluralism.
 4. Neither sort of species concept can meet all the needs of all comparative biologists.
- ∴ Species pluralism.

The second premise marks a key difference between this and the last argument for pluralism, but I will leave spelling out what it means for two or more concepts to cross-classify in detail until we have all the positions on the table. One of the problems with many explications of pluralism is that it is not clear what it means to cross-classify, just as it is not clear what it means for a natural kind to ‘carve nature at its joints.’ What is also interesting about this argument is that it pays heed to the needs of different biologists. Thus, even though this form of pluralism is governed by evolutionary theory there still is a certain sense of disunity amongst the different sorts of research that different evolutionary biologists pursue. Both concepts are retained because they help us answer different sorts of questions about species.

Multiple Evolutionary Forces

Ereshefsky offers a more general argument for species pluralism, which he grounds in several forces of evolution, “[G]iven what current evolutionary theory tells us, the forces of evolution segment the tree of life into varying and opposing classifications. Species pluralism is the result of a fecundity of biological forces rather than a paucity of scientific information” (2001, 140). The forces of evolution create and maintain different, sometimes overlapping, lineages that we may all legitimately call ‘species.’ I have sketched what Ereshefsky (2001, 139-140) calls his metaphysical argument for species pluralism as

follows:

1. There are multiple species concepts that group and rank on the basis of evolutionary forces
 2. There are multiple evolutionary forces that make and maintain different sorts of species
 3. The different sorts of species cross-cut the Tree of Life
- ∴ Species pluralism.

According to this view, it is not the needs of different evolutionary biologists that are relevant, but it is the different forces of evolution (interbreeding, natural selection, genetic homeostasis, common descent, and developmental canalization, among other things (cf. Templeton, 1989)), which are the fundamental causes of species pluralism.

According to evolutionary species pluralism, it is something about evolution, or the needs of evolutionary biologists, that is ultimately responsible for all the different approaches to species. This may be because (1) there is a plurality of processes that make the monophyletic groups that are species, (2) there is a need for considering monophyletic groups and groups bound by interbreeding, or (3) there are many different groups shaped by the forces of evolution. In the final half of this chapter we will see in more detail what's at stake between these different forms. For now, we will turn to a radically different sort of species pluralism.

3.1.2 Extra-Evolutionary Species Pluralism

Some pluralists deny that species always need to be thought of as evolutionary units. According to this view, there are legitimate ways of conceiving of species that do not make reference to the role that species play in evolutionary theory. Thus, extra-evolutionary species pluralism is the view that:

There are multiple, non-unified ways of grouping organisms into species, and evolution is *not* the single cause of the different 'cross-cutting' species

I'm using 'cause' here in a very loose sense. The point is that those who hold this view reject fundamentalism about evolutionary theory. They point out that there is more to biology than just evolution (Dupré, 1999, 13). Biology is in an important sense disunified, which means that the entities different areas of biology require different ontologies. As we will see in Chapter 4, this may entail ontological framework pluralism. What is key to extra-evolutionary species pluralism, and what separates it from evolutionary species pluralism, is the claim that there is no fundamental science that governs the classification of species. The argument requires a similar intra-biological conflict to some of the forms of evolutionary species pluralism, but one that is wider in scope. I will now review and compare Kitcher and Dupré's different arguments for extra-evolutionary species pluralism.

Two Set Pluralism

Kitcher (1984b), most criticized for his view that species are sets (see Sober, 1984), offers a pluralism radically different from those so far considered. He argues that there are many different sorts of species, but there are two main types: "The species category is heterogeneous because there are two main approaches to the demarcation of species taxa ... One approach is to group organisms by structural similarities ... The other approach is to group organisms by their phylogenetic relationships" (Kitcher, 1984b, 309). By the latter, he means that species are a sort of lineage. We can roughly formulate Kitcher's (1984b) argument as follows:

1. Species are sets of organisms related to one another by complicated, biologically interesting relations
 2. There are many such relations, none of them are fundamental
 3. These relations lead to different cross-classifications of species.
- ∴ Species pluralism

There are ultimately two main types of species for Kitcher, though there are many sub-types that fall under them. The main criticism of his view that

comes from evolutionary species pluralists stems from the structural properties that he allows to define species. Classifying species according to the structural properties they bear would involve no reference to the evolutionary explanations of those structures, but would involve a measure of similarity and difference of structure. Further, it is not clear that defining species in this way explicates any aspect of contemporary biological practice. One might respond to this sort of criticism by appealing to approaches like phenetics or numerical taxonomy that have collapsed for reasons that I won't get into here. However, resting this sort of extra-evolutionary species pluralism on such a 'theory-free' approach to biological classification is dubious at best (see Sober, 1984). Evolutionists dominate discussions of species within biology, and it is no surprise that this is reflected in many forms of species pluralism. Kitcher's view is thus significantly out of touch with mainstream biology as compared with the last three forms of species pluralism. Despite these sorts of worries, there is an in principle argument for extra-evolutionary pluralism even in Kitcher's account that becomes much clearer in Dupré's work.

Promiscuous Pluralism

Dupré (1981; 1993; 1999; 2001) has developed a related argument for species pluralism, which rests on the potential conflict between different classificatory practices in biology. Dupré (2001) focuses on defending the claim that species are units of classification, and that this doesn't mean that they are units of evolution. The general strategy that he has exploited is to display the ways in which all sorts of different scientific and folk practices govern our use of 'species,' and that if this is the case, then surely it cannot follow that evolutionary theory has exclusive rights to the term. For Dupré, all of these uses of 'species' pick out genuine real entities, and lead to conflicting classifications of the biological world. At his most radical, the way a cook classifies organisms is just as legitimate in Dupré's eyes as the way an evolutionary biologist does.

Dupré's (1993; 1996; 1999) argument for species pluralism has been given a great deal of criticism, partly because his attack on the claim that species are evolutionary units involves an advocacy for the legitimacy of folk taxonomy

or taxonomy based on the interests of non-biologists. Ereshefsky (2010) has argued against Dupré’s promiscuous pluralism, on the grounds of an analogy with the concept of ‘work’ as used in physics. In order to understand what ‘work’ in physics means, we don’t analyze ordinary sentences like “He’s a real piece of work.” Likewise, for Ereshefsky, the term ‘species’ is a theoretical term. To understand what ‘species’ means we don’t analyze the way it is used outside of that theoretical context, which for Ereshefsky means outside of evolutionary biology. The relationship between ordinary language classification and scientific classification is certainly a complicated issue with respect to ‘species,’ but this is where some of the debate has gone.

With this in mind, it is perhaps more promising if we sidestep this aspect of promiscuous pluralism. Let’s consider Dupré’s strategy as only pertaining to a more developed biological science, or at least one that could be potentially as developed as evolutionary theory. The claim then becomes about what sort of explanatory interests are at stake when we choose to develop a scientific classification scheme. For example, the interests of ecologists may differ substantially from those of evolutionists, and this may need to be reflected in a classificatory practice that involves a radically different conception of species. As Dupré claims, “Ecology may . . . in principle at least, require either coarser or finer classifications than evolution, and it may need to appeal to classifications that crosscut phyletic taxa” (Dupré, 1999, 14). This would then allow us to formulate his argument as follows, though many different versions that exploit different biological practices are possible.

1. Evolutionary theory classifies species one way
 2. Ecology classifies species another way
 3. Neither science is fundamental in its classification of species
 4. If two non-fundamental approaches cross-classify the organic world along the lines of species, species pluralism
- ∴ Species pluralism

Here it is nothing internal to any particular theory that is at fault. It is a problem with the broader unity of biology, and this is what makes this a form of extra-evolutionary species pluralism.

If we take this sort of view one way, it may mean monism for each sub-biological science. If we are being pluralists about the different classificatory practices in ecology and evolutionary biology, this may mean monism for the ‘evo-species’ and monism for ‘eco-species.’ To put the point another way, when we do ecology, we will use *one* system of organizing species, and for evolutionists, we will use another. I will deal with the problem of how these two more radically different understandings of species might relate to one another in what follows.

In sum, there clearly are a variety of ways of being a species pluralist. If we gloss over pluralism as a mere denial of monism, we lose this variety. All forms deny that there is one unitary, and fundamental way of conceiving of species. Evolutionary species pluralists argue that there are many, non-unifiable ways of considering species as evolutionary units. These sorts of pluralists, as we will see in more detail below, will sometimes allow for a plurality of classificatory schemes, and sometimes not. Extra-evolutionary species pluralists agree that there are many, non-unifiable ways of conceiving of species, but that these need not make any reference to evolutionary theory. These sorts of pluralists differ in what sorts of other theories ‘species’ may be interpreted in, for example, ecology or a theory of structural relationships.

3.2 Discerning Pluralism

We may have noticed that in the first half of this chapter we have several different arguments for species pluralism, but not one of them actually spells out what they are arguing for. They are all framed in a way to argue that species monism is false. But there is more to pluralism than just a denial of monism. In this half of the chapter I will analyze (1) what species pluralism in general implies about the nature of the *species category*: the category to which all species taxa belong; (2) what the distinctive rationale is for eliminating concepts provided by each form of species pluralism; (3) what it means for multiple species concepts to ‘cross-cut’ each other and the organic world. The first issue has generated the most discussion in the literature, and serves to

distinguish the different ways of understanding the difference between pluralism and monism in general. However, this is not enough to help us distinguish between different forms of species pluralism. The latter two issues do, and this is why they need to be answered for us to develop a species pluralism that is more discerning about species concepts. The second issue pertains to distinguishing pluralism from relativism, and the third, as we will see, is caught up in distinguishing pluralism from both monism and relativism.

3.2.1 The Species Category

We have grown accustomed to the disambiguation of ‘species’ into the species category and species taxa. Species taxa are whatever different species names refer to, e.g., *Castor canadensis*, but the species category is the class to which all the different species taxa belong. When we ask about the species category, we want to know what makes species different from genera, kingdoms, etc.,. When we ask about the species taxa, we want to know what sort of entity a beaver is, as opposed to that beaver over there. However, it’s not clear how profitable making this distinction explicit has been, or if anyone working on these matters has been confused by the ambiguity. Due in part to this disambiguation, there is now a huge body of literature devoted to species pluralism and the *species category*. Monists take one species concept, and allow it to define the species category, but pluralists must avail themselves of other resources. There are four general solutions to the species category problem that pluralists have posed: (1) Eliminativism (Ereshefsky, 1992, 2001); (2) Disjunctivism (Pigliucci, 2003, 2005); (3) Minimalism (de Queiroz, 1998, 1999, 2005a, 2007); (4) Pragmatism (de Queiroz and Donoghue, 1988; Dupré, 1999; Ereshefsky, 2014a).

Eliminativism

Eliminativists argue that if species pluralism is true, then it implies that the species category is empty. If the species category is empty, then we ought to eliminate it from scientific discourse. Ereshefsky (1992; 2001) provides

what he calls the heterogeneity argument, which shows that species pluralism implies that the species category should be eliminated (but see Brigandt, 2003): “Despite philosopher’s best efforts, the biological world is uncooperative when it comes to unifying the species category” (Ereshefsky, 2014a, 80). We may formulate his heterogeneity argument as follows:

1. Species pluralism.
 2. If the different concepts that compose a plurality share nothing in common with each other that distinguishes them from concepts outside the plurality, then we should eliminate the concept that governs the plurality.
 3. The different species concepts are heterogeneous.
- ∴ Eliminativism.

So if this argument is convincing, instead of retaining the species category, we should have several other categories, e.g., *phylospecies*, *biospecies*, and *ecospecies*.

An initial worry with this solution is that it is not *sensu strictu* representative of a pluralistic approach. If Ereshefsky is right, we are left with monistic approaches to the remaining categories. That is, we are monists about ‘biospecies,’ ‘phylospecies,’ and ‘ecospecies,’ for there is one clear definition of each of these categories, but nihilists about ‘species,’ because there is nothing to which species, as a theoretical term, refers to. So what then are we being pluralists about? One might respond that this is just a semantic issue with how to understand ‘pluralism.’ This, however, is not the biggest problem with eliminativism.

The main problem with eliminativism, is that it fails to capture something very important about biological practice, which is noted in de Queiroz and Donoghue’s (1988) version of evolutionary species pluralism. Two competing species concepts, e.g., in their case species demarcated by either interbreeding or monophyly, can sometimes classify the same organisms in the same way, and sometimes they can cross-classify. This is the main reason that we should reject eliminativism. Given situations where two species concepts yield equi-inclusive groups, it seems odd to say that we have two (or more) things, say a ‘biospecies’

and a ‘phylopecies’ that include the very same organisms, even though there are many situations where different criteria fail to yield equi-inclusive groups. Many species are named as such by way of congruence between many species concepts. Some have interpreted this use of species concepts as reason to conclude that different species concepts, by way of consilience, will ultimately classify organisms in a single way (Ruse, 1987). This claim is taken up in the final chapter, where I argue against both Ereshefsky and Ruse

Disjunctivism

Some argue that species pluralism only implies that the species category is undefinable in the traditional sense, by offering a set of necessary and sufficient conditions, and that we should treat the category either as a family-resemblance concept (Pigliucci, 2003, 2005), polythetic concept or cluster concept (Scriven, 1959; Hull, 1965a).⁶ Consider Hull’s (1965b, 13) disjunctive definition of the species category: something is a species just in case it is a population that either:

1. Consistently interbreeds producing a reasonably large proportion of reasonably fertile offspring, or
2. Consistently serially interbreeds with synchronic populations producing a reasonably large proportion of reasonably fertile offspring, or
3. Does not fulfil either (1) or (2), but have not diverged appreciably from a common ancestry which did fulfil either (1) or (2),

⁶The traditional sense is often taken as an essentialist or Aristotelian approach to definition, but we shouldn’t take this as a serious attempt to describe Aristotle’s own view on the matter. Hull, for example, claims that

[W]hat Aristotle was advocating in modern terms is definition by properties connected conjunctively which are severally necessary and jointly sufficient. For example, being a three-sided plane closed figure is necessary and sufficient for being a triangle. Such a mode of definition is eminently suited for defining eternal Forms. It is not very well suited for defining the names of evolving species or for ‘species’ itself.(1965a, 318)

First, Aristotle is not the eternal Forms guy, that is Plato. Second, as we saw in Chapter 2, Aristotle’s own view on the matter is far subtler. Despite Aristotle’s search for the essences of species taxa, he does not appear to have offered an essentialist definition of the species category.

4. Does not fulfil any of (1), (2), or (3), because they do not apply but are analogous to populations which do fulfil at least one of (1), (2), or (3).

Fulfilling any one of these conditions would be sufficient for something to be a species, and fulfilling at least one would be a necessary condition. The problem here, similar to the problem with eliminativism, is that these sorts of definitions often say nothing about what happens when something satisfies multiple conditions. That is, whether or not this lends more support to claims about whether or not this or that group is a species. I will address this problem in detail in the final chapter.

Pigliucci's (2003; 2005) suggestion that species pluralism implies that the species category is a family resemblance concept makes some first moves to getting around this problem. The term 'species,' on Pigliucci's view, "is a family resemblance concept whose underpinning is to be found in a series of characteristics such as phylogenetic relationships, genetic similarity, reproductive compatibility and ecological characteristics" (2003, 601).⁷ Pigliucci unfortunately does not develop the approach any further. What needs to be sorted out is how the different family members, i.e., species concepts, cross-cut each other and the world, and even before that, which ones are excluded or included. Sorting this out would actually make a difference to the way biologists apply species concepts. As it stands, such a disjunctive definition of the species category does nothing other than combine the available species concepts in a disjunctive fashion. And what may be worse is that "Rather than resolving the incompatibilities among alternative definitions of the species category, this interpretation encourages different authors to adopt incompatible definitions, thus perpetuating the current disagreements" (de Queiroz, 2005a, 1266).

⁷This view of species is meant to be close to Templeton's (1989) cohesion species concept. Templeton defines species as "the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms" (1989, 12). Cohesion mechanisms, for Templeton, include natural selection, developmental constraints, interbreeding, ecological similarity and common ancestry. Different mechanisms are thought to be important in different specific situations.

Minimalism

Minimalists give up on the quest for a operationalizeable definition of the species category, one where the definition gives us useful means of knowing how to determine whether we put this or that taxa into the species category, but require that it be universal and unified (de Queiroz, 1998, 1999, 2005a,c, 2007; Mayden, 1997, 1999; Shun-Ichiro, 2011; Kendig, 2014). Minimalism is thus *sensu strictu* a sophisticated monism. However, minimalism should be still considered in an examination of pluralism, because it constitutes a view that puts the pluralism somewhere else, as we will shortly see.⁸ de Queiroz (1998; 1999; 2005a; 2005c; 2007) argues that species pluralism implies not that we eliminate the species category, nor that we ought to treat it as a cluster concept, but that we ought to reconceive the species category more minimalistically (see also Kendig, 2014), but be pluralistic about certain aspects of the definition. I will refer to this view as minimalism about the species category.

De Queiroz (2005a) argues that we can still have a unified conception of the species category if we adopt his general lineage conception of species (GLC),⁹ which is a more sophisticated version of Simpson's (1951; 1961; 1978; 1981) evolutionary species concept.¹⁰ Species, according to the GLC, are defined by a single necessary and sufficient property: something is a species, if and only if, it is a separately evolving metapopulation lineage (de Queiroz, 2005a, 1264). He argues that according to all (modern) species concepts, a species just is a separately evolving metapopulation lineage. In fact, he even goes so far to say that "any definition that is inconsistent with this general evolutionary concept of species is probably sufficiently removed from the mainstream of contemporary biology that it need be considered no further" (de Queiroz, 1998, 62).

⁸Whether or not a view should be called pluralism or monism is not really the issue. As Hull has pointed out for slightly different reasons, "One problem unfortunately characteristic of such contrasts as monism versus pluralism is that the apparent differences between them tend to disappear under analysis. Numerous senses of monism blend imperceptibly into just as many senses of pluralism" (1999).

⁹He also calls this a 'general metapopulation lineage concept of species' (de Queiroz, 2005b, 6602).

¹⁰See the Introduction for more on **EvSC**.

De Queiroz also draws on the fact that many modern species concepts explicitly mention that species are some kind of lineage in their very definition. Others, he notes, equate species with populations in the definitions or in the associated discussions. Populations are really just short segments of lineages. His strategy for subordinating all species concepts to his own, is to show that all of the different concepts either (1) describe the GLC itself (e.g., the evolutionary species concept), (2) describe criteria for delimiting species taxa (e.g., the reproductive isolation version of the biological species concept), or (3) some do both (e.g., the ecological species concept). Those that describe criteria for delimiting species taxa also give defining properties of subcategories of the general species category (de Queiroz, 2005a, 1264).

But if there is only one species concept, then where is the pluralism in all of this? De Queiroz suggests in response to Pigliucci (2003) that “in agreement with the cluster concept proposal, the idea of a metapopulation lineage may itself be best interpreted as a family resemblance or cluster concept” (2005a, 1267). In this way, he is suggesting that disjunctivism and minimalism are highly compatible with one another. The difference is that they put the pluralism, as interpreted disjunctively and not eliminatively, in different places.

Ereshefsky (2014a) and others (Pigliucci, 2003, 598) object that de Queiroz’ view is too permissive. According to the GLC ‘species’ applies to all separately evolving metapopulation lineages. One might agree with part of this, namely that yes, all biologists agree that species are metapopulation lineages, but disagree with the GLC, because not all metapopulation lineages are species. The disagreement over species concepts just is a disagreement about what kind of metapopulation lineage species are supposed to be. Thus, what were called sub-species, species, superspecies, and even demes would now also be considered species if they satisfy his definition. This is not very conservative! What sort of change in biological practice would this bring about? De Queiroz chooses to bite the bullet on this point, and offers an argument by analogy in support of his view, which I will now turn to.

De Queiroz (1998; 1999) argues for an analogy between the traditional notion of species and the GLC with organism and adult. The species cate-

gory should be treated as analogous to the organism category, rather than to the adult category. He grounds his analogical argument in a more abstract claim: “If the species category is to be truly analogous to the categories cell and organism and of similar general theoretical significance, then the species category must be the most general category at its particular level of biological organization. It cannot be a less general subset of this general category” (de Queiroz, 2005b, 6603). As usual, the analogy is based on an assumption of monism. We want a concept that covers all stages in the life cycle of a species. We may formulate his argument as follows:

1. If we choose any particular stage in either process (population lineage divergence or organismal development) as a necessary condition for species or organism, then the other stages where the condition is absent will be left in limbo.
 2. We do not want these stages left in limbo.
 3. So we should not choose any particular stage in either process.
 4. If for organisms we do not want stages in limbo, we should talk about the entire life-cycle of an organism.
 5. Likewise, if for species we do not want stages in limbo, we should talk about the species life-cycle.
- ∴ We should talk about species life-cycle.

With respect to (1), in the past “adults,” or “males” were privileged, over other stages. This focus was harmful to our overall understanding of organisms and the organism life-cycle. Thus focusing on species as anything more than this minimal view is also harmful to our overall understanding of species, and the species life-cycle. Even if we accept his arguments, it is hard to say how de Queiroz’s view would affect biological practice, though there have been some attempts to apply his general lineage conception of species. The point being that if we adopt his conception, we might be forced to classify many things as species that aren’t currently classified as species by most practicing biologists. This is just to show how seriously the effects of pluralism on our current taxonomic practice are taken by systematists themselves. Worry about these

effects has led many to a more pragmatic pluralism, which we will now turn to.

Pragmatism

Many have argued for putting the following pragmatic constraint on species pluralism: if species pluralism is true, ‘species’ should still be preserved in much the same way as it has been historically (de Queiroz and Donoghue, 1988; Dupré, 1999; Ereshefsky, 2014a). A common problem with all three solutions thus far considered concerns the extent to which they would, if implemented, effect biological practice. Reflecting on this has caused many pluralists to gravitate toward a sort of pragmatism from their initial, more revolutionary positions on the species category.

One way pluralism might affect biological practice is as follows. Some (Ghiselin, 1969, 1997; Hull, 1987, 1989a) have claimed that pluralism will ‘lead to Babel.’ This is also known as the communication objection to pluralism (Ereshefsky, 1992, 680-681). According to this objection, having multiple species concepts will make biologists unable to communicate with one another, just like having many languages caused the people of Shinar to abandon building their city. Following Ereshefsky (1992, 681), we can formulate this argument as follows:

1. Species pluralism entails that the term “species” is ambiguous.
 2. If the term “species” is ambiguous, then confusion will set in when biologists discuss the nature of species, for biologists will mean different things by “species.”
 3. But, we should avoid such confusion.
- ∴ Species pluralism should be avoided.

Typically speaking, pluralists have responded by denying the second premise (e.g., Kitcher, 1984b; Ereshefsky, 1992, 2014a). That is, monists are exaggerating the consequences of accepting pluralism. Pluralists have just suggested that biologists attempt to be clear about what sense they might be taking up in their particular uses of species. Kitcher, thinks an analogy can be drawn with

how biologists discuss the concept ‘gene.’ According to him, “Biologists have already learned to be responsible in discussions of genes. The same responsibility can be attained in the case of species. To allow pluralism about species and to deny the need for a “general reference system” in biology is not to unlock the doors of Babel” (Kitcher, 1984b, 327) However, though his analogy seems correct, it is far too simple a formulation of the problem. Even if the needs of academic biology take precedence, we must consider other uses of the term ‘species,’ though we needn’t quite go as far as Dupré into accepting a promiscuous pluralism. Ereshefsky, the staunchest advocate of eliminative species pluralism, has more recently argued, on pragmatic grounds, that we cannot eliminate ‘species’ because that would just be too hard: “The word ‘species’ is firmly entrenched in scientific discourse. It occurs in biology textbooks, field guides, and systematic studies. It is also entrenched in non-scientific discourse, for example, in governmental laws. Eliminating ‘species’ from biology and elsewhere would be an arduous task” (2014a, 81). The word plays too many roles in too many disciplines for it to be changed in any significant way, let alone eliminated from discourse.

Dupré (1999), has also has defended the reservation of the term ‘species’ for a general taxonomy on pragmatic grounds. According to Dupré we need a general, all-purpose taxonomy, and we can reserve the term species for the base units in such a taxonomy: “it would be best to reserve the term species . . . for the base-level categories of this general, pragmatic, taxonomy” (1999, 4). Though he admits that more specialized taxonomies will also be required for particular purposes.

What I am calling pragmatism is much weaker than either minimalism or disjunctivism. That is, even if we reject such cluster approaches to preserving the species category, we can always resort to this third option if we want to oppose eliminativism. However, as this position is weak, it really tells us nothing about what to do with the conceptual pluralism that has run rampant in biology, other than that we should just keep on trucking. In effect, it is rather worrisome, because it, of all the positions so far considered, is closest to relativism. Though perhaps it is not a relativism where anything goes, but

one closer to Kitcher's description of cynicism: "The most accurate definition of 'species' is the cynic's. Species are those groups of organisms which are recognized as species by competent taxonomists. Competent taxonomists, of course, are those who can recognize the true species" (1984b, 308).

Further, pragmatism about the species category is compatible with all the different forms of pluralism we have already considered. This again is the general problem with species pluralists solely focusing on the species category problem. In the next two sections I will explicate what is really important about distinguishing pluralism from relativism. We need to ask two questions. First, which species concepts are admitted as legitimate and which are eliminated from biology? Second, how do those that remain work in relation to one another? I will explore the ways in which the different forms of species pluralism answer these two questions, especially focusing on the distinction between evolutionary and extra-evolutionary species pluralism.

3.2.2 Which Species Concepts Are Legitimate?

I will now examine what sort of species concepts are rejected and which are permitted by evolutionary (ESP) and extra-evolutionary species pluralism (XSP) (Table 1). This is important, because it shows an important way in which pluralism makes a difference to taxonomic practice. For a monist there's one right species concept, for a relativist anything goes, but for a pluralist many things go. Further, the different assumptions that different pluralists make change the relationship between pluralism and biological practice. As will become clear, these consequences are largely independent of how we treat the species category. I will begin by describing the sorts of concepts eliminated by the three forms of evolutionary species pluralism discussed in the first section of this chapter. I will also compare these with the general lineage conception. Following this I will do the same for the two different forms extra-evolutionary species pluralism.

Table 1: Legitimate Species Concepts

ESP	XSP
Monophyletic	Historical & Structural
Monophyletic & Interbreeding	Evolutionary & Ecological
Evolutionary	

Evolutionists

Though it is a slight oversimplification of some of the subtle differences between the views, we can say that what evolutionary species pluralists have in common is that they rule out species concepts that do not treat species as evolutionary units. However, what is at stake between these evolutionists, is that there are different ways of interpreting what counts as a species sized evolutionary unit: (1) monophyletic groups, (2) either monophyletic groups or interbreeding groups (or groups that are both), (3) any lineage of a certain size, maintained by various crisscrossing forces of evolution, (4) the general lineage conception of species.

Mishler and Donoghue (1982) and Mishler and Brandon (1987) require that species taxa are monophyletic groups (assemblages of populations). This requirement rules out any species concept that does not require species taxa to form monophyletic groups. Since monophyly is one way of specifying the phylogenetic species concept, this in a sense is just a disjunctive version of that concept. They are thus monists about how species are grouped: they are grouped according to monophyly, but pluralists (disjunctivists) about how they are ranked. On their view, genera, and other higher-order taxa are also monophyletic, and so may be legitimate lower order groups, like sub-species and varieties. Thus, ranking criteria are needed to distinguish species from these other taxonomic ranks, both above and below.

de Queiroz and Donoghue (1988) accept that species may be held together by common descent (monophyly), but they argue that species can also be held together by interbreeding. They also argue that these monophyly and interbreeding can come apart. They are thus disjunctivists about the species category, though they admit that the two senses sometimes overlap. On this

account, any species concept other than these two is excluded.

According to Ereshefsky's account, evolutionary theory requires that species are some sort of lineage. Lineages, and thus species, can either be monophyletic or paraphyletic groups, but cannot be polyphyletic, because these sorts of groups lack spatiotemporal continuity (2001, 133-135). This form of evolutionary pluralism is thus more permissive, but still excludes any species concept that would allow us to consider a polyphyletic group (a group that fails to form a continuous lineage) a species. It is important to note that Ereshefsky's argument for pluralism can be made distinct from his argument for eliminativism, which is why I have separated them here (c.f. Brigandt, 2003).

According to de Queiroz's general lineage conception of species there is only one species concept allowed, but what of the competing approaches remains? These he claims we can either treat as synonymous with his concept, or we can interpret them as criteria for telling us what a separately evolving metapopulation lineage is (or they do both). The more criteria we have, given that they are compatible, the surer we are that we are talking about a species. However, a problem with this view is that it is nowhere explicit about exactly what his approach rules out. According to de Queiroz, "[A]lmost all modern biologists have the same general concept of species" (1998, 57). This is highly contentious, but if it is true, then this would at least rule out any pre-Darwinian conception of species. But would it rule out polyphyletic groups? These, for example, seem to be recognizable by the phenetic species concept, and de Queiroz is explicit in his ability to subsume such a concept. With respect to this he says "The fact that lineages can be paraphyletic or polyphyletic does not mean that the same is true for . . . species; some species definitions permit paraphyly and polyphyly while others require monophyly" (1998, 60). Elsewhere he is very clear that species recognized by his concept do not have to be monophyletic: "metapopulation lineages do not have to be phenetically distinguishable, or diagnosable, or monophyletic, or reproductively isolated, or ecologically divergent, to be species" (de Queiroz, 2005b, 6605).

From this discussion we see that, even among evolutionary species plu-

ralists, there are significant discrepancies about what are legitimate species concepts. Everyone tries to incorporate some portion of the wisdom found in the species concepts they rule out, but different concepts will play more prominent roles in different pluralities. We will also see how there are discrepancies between evolutionists about how these different concepts will be used to create (cross-)classifications of organisms. Before we get to that we will turn to the differences between different forms of extra-evolutionary species pluralism.

Extra-Evolutionists

Denying that evolutionary theory plays the ultimate role as arbiter among species concepts has been generally tied to the acceptance of more concepts than any of the pluralists just surveyed, though in principle it need not. Again, though neither Dupré nor Kitcher hold this view, an extra-evolutionary species pluralist could hold that there is one ‘evo-species’ concept and one ‘eco-species’ concept. But given that extra-evolutionary species pluralism is not meant to be a relativistic position, so what sorts of concepts are ruled out?

According to Kitcher’s two set pluralism, there are two sorts of species concepts: historical and structural. Evolutionists have argued against his recognition of structural concepts, so it is safe to say that he admits that the historical concepts fall under similar considerations as those the evolutionists favour, that is, they must pick out a certain sort of lineage. However, it is not clear whether he has a restriction to monophyletic groups or not. With regard to his structural species concepts, the main criticism has been that these do not correspond to any recognizable way that biologists classify organisms, so it’s not clear what theory he might be invoking here.

A moderate reading of Dupré’s account suggests that he rejects Ereshefsky’s claim that all post-Darwinian species concepts must import evolutionary theory to explain what makes a species a species. Ignoring what Dupré has to say about the legitimacy of folk taxonomy, this means that other areas of biological inquiry may provide equally legitimate frameworks for conceptualizing species. The most promising area that he discusses is ecology (see Kitcher, 1984b, 309-310).

3.2.3 Cross-Cutting Pluralism

Most pluralists argue for a plurality of species concepts that ‘cross-classify’ one another. This is taken to be self-explanatory. It isn’t. Different pluralists use it in different ways. In this section I will explicate the ways in which pluralists might understand this metaphor.

Pluralists use the terms ‘cross-cutting’ or ‘cross-classification’ to suggest an important modification of the ‘carve nature at its joints’ metaphor used to describe whatever natural kinds are supposed to be.¹¹ This terminology is even used by Aristotelian scholars to explain his pluralism, but even there it is not clear what is cross-classifying what.¹² Pluralists, as far as the metaphor goes, make bad butchers. As far as I have been able to discern, minimally cross-classification means that an organism can belong to more than one un-nested group. Monists can allow organisms to belong to multiple groups, but these groups must be nested, and/or form some sort of hierarchy (e.g., Burt is both a beaver and a rodent, because all beavers are rodents). Cross-classification of organisms is not uncommon in biology. For example, a particular bacterium can belong to the species *Bacteroides fragilis* and the ecological community that resides in some particular human colon. A monist can allow for this, but could interpret belonging to *Bacteroides fragilis* as more fundamental than belonging to any particular ecological community, though it isn’t exactly clear how we interpret this notion of fundamentality. It is certainly fundamental to my existence that I have organisms like this in my gut. Thus, for species concepts to cross-classify we need there to at least be different types of species, none of which are fundamental.

Due to the extant obscurity of the use of the ‘cross-classifying’ metaphor in the literature, I will maintain that a pluralist must provide answers to two related questions. First, what is it that is being cross-cut? Answers to this question range from cohesive entities/individuals, to lineages/populations, to organisms, to structural space vs. evolutionary space (the tree of life). Second, how are these things being cross-cut? If we are cross-cutting evolutionary

¹¹This latter metaphor has a long pedigree, which dates to Plato’s *Phaedrus*.

¹²See Chapter 2.

space, it is helpful to use cladistic terminology. One might ask whether we can have monophyletic, paraphyletic, and/or polyphyletic groups cross-cutting one another here. As we will see, depending on what is being cross-cut, classifications of organisms into species may occur at various levels of organization.

Evolutionists

In this section I will consider the different sorts of evolutionary species pluralism thus considered: (1) monophyletic pluralism, (2) monophyly and interbreeding, (3) plurality of evolutionary forces, (4) the general lineage species concept.

Although monophyletic pluralism is not a full-blown pluralism, because it does not entail some form of cross-classification, it is worth considering as a foil for other forms of evolutionary species pluralism. The view is in a way not a true form of pluralism, for “Mishler and Donoghue’s (1982) brand of pluralism implies that a single, optimal general-purpose classification exists for each particular situation, but that the criteria applied in each situation may well be different” (Mishler and Brandon, 1987, 403). This means there is no ‘cross-cutting’ between the different conceptions of species. Different processes are important for maintaining different species, but any given organism can belong to one, and only one species. According to monophyletic pluralism, it is a necessary condition for species taxa to be monophyletic groups, as are all super- and subspecific taxa, but there are a plurality of processes responsible for the existence of species taxa: “A species is the least inclusive taxon recognized in a classification, into which organisms are grouped because of evidence of monophyly . . . that is ranked as a species because it is the smallest “important” lineage deemed worthy of formal recognition, where “important” refers to the action of those processes that are dominant in producing and maintaining lineages in a particular case” (Mishler and Brandon, 1987, 406). Thus, this view offers a monistic approach to how we group biological taxa, but a pluralistic approach to how to rank them.

What is important to note about this form of pluralism is that species are not treated as special taxonomic units. It is not that they are suggesting that

species do not exist, they are suggesting that they are not significantly different from any other taxa, whether super- or sub-specific. However, they do argue in favour of the proposal that we “[a]pply species names at about the same level as we have in the past, and decouple the basal taxonomic unit from notions of “basic” evolutionary units”(Mishler and Donoghue, 1982, 497). This thus constitutes a form of pragmatism about the species category, since it attempts to retain most of the species names at the same level as we have had in the past, but it is modified by the requirement that species form monophyletic groups.

The key difference between de Queiroz and Donoghue’s position and monophyletic pluralism is the interpretation of the conflict between species concepts that focus on either monophyly or interbreeding. As they put the case themselves:

[T]he tension surrounding species concepts results from there being different kinds of real biological entities. Some of these entities exist as an outcome of a process conferring cohesion, while others exist as an outcome of descent from a common ancestor. And sometimes an entity that exists as the consequence of one of these processes happens to correspond exactly with one that exists as a consequence of the other (de Queiroz and Donoghue, 1988, 325).

Cases of exact correspondence between these two (and further) sorts of processes have not been followed up on in the literature on species pluralism. It is not clear from this quotation whether they are suggesting that there are two real biological entities, which sometimes overlap, or whether there are three. The point for de Queiroz and Donoghue is simply that we should abandon the attempt to achieve a single general-purpose taxonomy:

[N]either populations nor monophyletic groups are generally more real or significant than the other; instead, their relative significance varies with the particular theoretical context. We therefore agree with the tenet that “there is no unique relation which is privileged in that the species taxa it generates will answer to the needs of all

biologists and will be applicable to all organisms” (Kitcher, 1984: 309). Nevertheless, we reject the brand of pluralism that applies different criteria or even different combinations of criteria on a case by case (group by group) basis in an attempt to achieve a single, optimal, general-purpose taxonomy (de Queiroz and Donoghue, 1988, 334).

They are here exactly decrying the form of pluralism offered by Mishler et al., and also, it should be noted, rejecting pragmatism about the species category. On this account of evolutionary species pluralism, species are significant, and distinguishable from other taxa. It is just that there are (at least) two sorts of species, and that each species concept, taken by itself, will have different consequences. They unfortunately fail to explore cases where we take species concepts together.

As we have discussed, Ereshefsky’s argument for species pluralism leans heavily on the fact that different legitimate species concepts can cross-classify the Tree of Life. On his view we have “one taxonomy consisting of interbreeding units, another consisting of ecological units, and a third consisting of monophyletic taxa” (Ereshefsky, 1992, 681). Helping pick out these different lineages is what the different legitimate species concepts are in the business of doing. However, according to Ereshefsky (2001, 134), there are only two sorts of ways that these approaches can cross-classify the world’s organisms:

1. An organism may belong to two lineages with one lineage properly contained in another
2. An organism may belong to two lineages that are disjoint

This is the most explicit statement I have found of what someone means by ‘cross-classify,’ but even this is somewhat unclear. With regard to the first way, this would not be terribly different from how species and genera cut up the world. It just means that species can form nested groups. With regard to the second case, it is not exactly clear what he means by ‘disjoint,’ because in the toy example he provides to illustrate this type of case the two species have

member organisms in common. However, what I take him to mean by the second point is that we can have un-nested groups, which becomes clear from his explicit rejection of Mishler et al.'s (1982; 1987) monophyletic pluralism. As I see it, and to put this in cladistic terms, Ereshefsky is arguing that species can be either monophyletic or paraphyletic groups, and that these can be bigger and smaller than one another depending on the evolutionary process highlighted by a particular species concept. In contrast, according to Mishler et al.'s monophyletic pluralism, species must be monophyletic groups, but a species cannot be a monophyletic group that includes a smaller monophyletic group that is also a species. If I'm reading this right, this is a very important difference.

What sort of cross-cutting does Ereshefsky's account rule out? Well, to use cladistic terms again, we cannot have polyphyletic groups. This is because polyphyletic groups do not form lineages in the proper sense. They are not spatiotemporally connected. This, as we will see when we get to the extra-evolutionary species pluralists, is one way of distinguishing the two forms of species pluralism.

When it comes to cross-cutting, de Queiroz's (1998; 1999; 2005a; 2007) general lineage conception of species is far more difficult to evaluate than the other evolutionary views considered, because he is nowhere explicit about how his definition would resolve situations where there is conflict between different species concepts (what he calls species criteria).

On one reading, he comes out more permissive than even Ereshefsky, in that he will allow for monophyletic, paraphyletic and polyphyletic groups to all count as species. This is because he says that: "The fact that lineages can be paraphyletic or polyphyletic does not mean that the same is true for . . . species; some species definitions permit paraphyly and polyphyly while others require monophyly" (de Queiroz, 1998, 60). One species definition that permits paraphyly is a phenetic species concept, which just requires that members of a species be more similar to each other than they are to any members of the out group. This is probably quite rare, but depending on what metric we use this could happen by convergent evolution. However, he also states that "[A]lmost

all modern biologists have the same general concept of species” (de Queiroz, 1998, 57).¹³ Further, he does claim that the phenetic species concept is subsumable under his general lineage conception of species (de Queiroz, 1998, 63). However, he does seem to later take it that phenetic similarity should be used merely as a diagnostic criterion for picking out a lineage (de Queiroz, 2005a, 2007). Still one might ask, is it possible for a polyphyletic “lineage” to evolve separately from all other lineages? This might not satisfy the minimalist definition of the species category he provides. However, if the answer is yes, then this would allow for this sort of cross-cutting, and would thus partially grade the distinction between the evolutionary and extra-evolutionary species pluralists. If the answer is no, then we are left with a form of evolutionary species pluralism not much different than Ereshefsky’s, save their respective stances on the species category problem. If this reconstruction is obscure, the take-home point is that de Queiroz’ GLC lacks clarity in this regard.

However, on a second reading of de Queiroz’s other work on the PhyloCode, a new system of taxonomy that incorporates monophyly as a requirement for recognizable entities, his understanding of the GLC might be closer to that of monophyletic pluralism. Like them he has a variety of ranking criteria, but his grouping criteria is a separately evolving metapopulation lineage. At any rate, for him to give a complete account, we need to know what happens when species concepts conflict.

Extra-Evolutionists

I will now examine the different ways extra-evolutionary species pluralists may interpret the ‘cross-cutting’ metaphor. To save space, I take it that an extra-evolutionary species pluralist could admit all the sorts of cross-cutting that the evolutionary species pluralist might, but will go further. One way of seeing this is that the extra-evolutionary species pluralist does not rule out species concepts that pick out polyphyletic groups. But we may also see (1) a distinction between evolutionary and structural space, or (2) a distinction

¹³See also (de Queiroz, 2005b, 6602).

between the Tree of Life and the Web of Life. These are very different ways of conceiving of cross-classification.

Kitcher's account may be interpreted as offering a distinction between evolutionary and structural space. Filling in some more of the details of his account, his distinction between different types of species is based on Mayr's similar distinction between proximate and ultimate explanations. Roughly speaking, proximate explanations are structural, functional, or teleological in nature. Ultimate explanations are evolutionary explanations of the proximate explanations provided by structural, functional and teleological explanations. Kitcher removes the requirement that his structural properties are subordinate to the historical properties, though there is of course some relationship between the two. Some evolutionary path could lead to a novel structural group. For example, a monophyletic species could have developed a new type of wing, distinct in origin from the wings of bats, birds, and bugs. That is, it seems possible that a structural and a historical species concept could pick out equi-inclusive groups. However, it does not seem that in this case we would want to say we have the same sort of species, as we might in the case of two historical (evolutionary) species concepts picking out the same group. This is because, even though these groups are equi-inclusive now, it could be the case that something else also independently develops the same sort of structure (making that structure a homoplasy).

Thus, if it's right to say that even when Kitcher's structural and historical species concepts pick out the same group of organisms they do not pick out the same species, then what is it that these concepts are cross-cutting? If we keep things at the metaphorical level, the historical concepts are carving up something like the Tree of Life, or what we might call evolutionary space. Likewise, the structural concepts are carving up something like structural space. Thus, given that, for Kitcher, there are two radically different sorts of species concepts, these two sorts will correspond to two different structural spaces: evolutionary and structural.

When it comes to explicating what is meant by cross-cutting, Dupré himself gives limited suggestions. His work is mostly aimed at demonstrating and

defending what he calls “promiscuous realism”: “The realism derives from the fact that there are many sameness relations that serve to distinguish classes of organisms in ways that are relevant to various concerns; the promiscuity derives from the fact that none of these relations is privileged” (Dupré, 1981, 82). According to Dupré’s anti-reductive approach to natural kinds in general: “there are many different kinds of things in the world, from physically simple things like electrons or quarks, to very complex things such as planets, elephants, or armies. Many or all these things, in my view, have equal claims to reality” (2008, 12). All of these things are real, because they have causal powers not reducible to the powers of their constituent ‘parts.’ The details of how this form of realism applies to biology, and to species in particular, are not always clear.

When it comes to a distinction like Kitcher’s, Dupré claims that “There is no doubt at all that interesting structural or physiological properties crosscut any possible phylogenetically based classification” (Dupré, 1999, 13). However, what is clear from his discussion of folk taxonomy, the taxonomy of gastronomes (e.g., the distinction between garlic and onions), and biology proper is that different classifications are based on different interests: “Even within biology different interests call for the emphasis of different distinctions” (Dupré, 1981, 83). Further, “there is no uniquely correct way of classifying organisms: different investigative interests dictate different and often cross-cutting modes of classification” (Dupré, 2008, 17). This might suggest that what it is that is being cross-cut is, in fact, our interests, which would thus suggest that he is advocating for a sophisticated form of relativism, and not pluralism. However, he does also note that the existence of species can be seen as a map of individual organisms into clusters and bumps on a multidimensional quality space. This would suggest something more akin to reading Kitcher as suggesting that there is something like a structural space. Given Dupré’s focus on ecology, it might also be useful to employ something like the web of life metaphor as a contrast to tree of life metaphor. In fact, he says as much when discussing problems in determining the phylogenies of microbial life forms: “the genetic relations between microbes do not really form a unique tree at all, but rather

a web. It may be useful for particular purposes to represent the evolutionary relations between microbes in the form of a tree, but we must remember that this is an abstraction from a much more complex reality. The web of life and the tree of life itself would be two different ways of cutting up the world” (Dupré, 2008, 21). Species, perhaps, would correspond to either strands of the web or branches on the tree.

Another possibility that comes from considering Dupré’s more recent work on developing a process ontology for biology. Though it is difficult to distill anything useful for the matter at hand from that work, given the blurriness that a process ontology is supposed to reflect, perhaps viewing species as processes suggests that these underlying biological spaces, to use the metaphor just developed, are not as discontinuous from one another as the extra-evolutionary species pluralist might suggest. Thus, not only is it not that case that “Nothing in biology makes sense except in the light of evolutionary theory,” but what does make sense in biology is not easily compartmentalized into discrete categories like Kitcher’s structural and historical properties. We might not easily be able to separate biology itself into distinct domains governed by different theories. Developing a coherent form of extra-evolutionary species pluralism will of course require much more work than evolutionary species pluralism, this is meant only as a suggestion of how to go forward. If we are species pluralists because our best biological theories are disunified, then we need to know what sort of disunity we are talking about, and whether there would then be anything more than a common name to the different senses of ‘species.’ Evolutionary pluralists, who at least retain a certain unity of biology, can always appeal to evolutionary theory to show what is common to the different senses of ‘species.’ What should be at least clear is that it is far more intellectually fruitful to ask these sorts of questions of pluralists, questions about what concepts they rule out, about the reasons they rule them out, and questions about how the concepts they admit relate to one another, rather than asking them what their stance is on the species category.

3.3 Conclusion

In this chapter I have argued that focusing on what species pluralism implies about the species category problem drastically oversimplifies what is at stake for biological practice when it comes to the different forms of species pluralism that we have to choose from. One main distinction we need to make is between evolutionary and extra-evolutionary species pluralism. However, there are different forms of these two different kinds of species pluralism. In order to distinguish between those forms, we need to ask two questions. First, what concepts, and on what basis, does each form of species pluralism allow for? Second, how do the admissible concepts (cross-)cut up the biological world? These questions are separate from what pluralism entails about the species category, and they are separate from each other, because we can allow for multiple species concepts, but not allow for any sort of cross-classification. Failure to give explicit answers to these two questions has blurred and will continue to blur important distinctions between the different forms of species pluralism.

Further, on any resolution of the species category problem for pluralism, we also (1) still need to come to a further ontological decision about what species taxa are, and (2) a pragmatic decision about when, where, and how to use the species concepts that we accept as legitimate. These two issues are intimately connected with asking pluralists about (1) which concepts are legitimate, and (2) how these cross-cut one another, and will be dealt with in Chapters 4 and 5 respectively.

Chapter 4

Ontological Frameworks For Species Pluralism

The only biological category
possessing an undisputable
ontological significance is that of
a living individual

(Dobzhansky, 1935, 344)

Introduction

This chapter concerns the relationship between species pluralism and the species taxa problem. Species taxa are the sorts of entities that our Linnean binomials refer to, e.g., *Castor canadensis*, *Alopex lagopus*, *Branta canadensis*, etc. As we discussed in Chapter 2, the essentialism story tells us that the traditional approach treated species taxa as natural kinds with fixed essences. From the standpoint of modern evolutionary theory this approach has been widely deemed unacceptable. There are now numerous alternatives to the traditional approach: species as (1) individuals (Ghiselin, 1974; Hull, 1976), (2) natural cluster kinds (Boyd, 1999a,b), (3) some mixture of both individuals and kinds (Griffiths, 1999; Millikan, 1999; Rieppel, 2013), (4) plural particulars (Slater,

2013; Simons, 2013), (5) sets (Kitcher, 1984a,b; Valen, 1988), or (6) processes (Rieppel, 2009; Dupré, 2012). Deciding between these ontological frameworks, and getting clearer about what's at stake between them, is the species taxon problem. I will not be providing reasons for choosing one framework over the others. The purpose of this chapter is to examine the ways in which species pluralism changes the ways in which the species taxon problem is resolved.

I reconsider the two main forms of species pluralism that were developed in the last chapter: evolutionary and extra-evolutionary species pluralism. As we saw there, the various forms of species pluralism differ both in terms of what theory or theories they take to be central to species, and also in the ways they allow different species concepts to cross-classify one another. Thus, in this chapter, I evaluate what species pluralism implies about the species taxon problem by considering the following questions.

First, to what extent are forms of species pluralism and solutions to the species taxon problem emphasizing the significance of the same sorts of properties? As we saw in Chapter 3, both modern forms of species pluralism are at least partially grounded in evolutionary theory to avoid collapsing into relativism. From a pluralist perspective, this gives us reason to attribute *some* historical properties to *some* species, since both views recognize the legitimacy of species concepts that group species on the basis of their relational, historical properties, rather than on the basis of shared intrinsic similarities that obtain, for the most part, amongst the individual member organisms. I'm focusing on this aspect of species pluralism, because it tracks well with what is at stake between different ontological accounts of species, and with the essentialism story that was discussed in Chapter 2. Further, there is a growing consensus that certain ontological frameworks are better at emphasizing historical properties (e.g., Ereshefsky, 2001; Wilkins, 2003), while others are better at emphasizing the intrinsic similarities (cf. Sterelny, 1994; Dupré, 2001; Ereshefsky, 2014b). Focusing on this feature of ontological frameworks will give us some means for finding the right framework for the different forms of pluralism. This is an important move to make, because many species pluralists, as we saw in Chapter 3, have focused on what pluralism implies about the nature of the species cat-

egory, and have not always been explicit about what pluralism implies about the nature of species taxa. Here I will show that evolutionary species pluralists are going to require frameworks that emphasize historical properties, while extra-evolutionary species pluralists may be better off accepting some form of ontological framework pluralism. Second, to what extent are different solutions to the species taxon problem compatible with the cross-classification required by most forms of species pluralism? As we saw in Chapter 2 and 3, there are many ways to understand the cross-cutting metaphor endemic to pluralism. Though not all pluralists accept cross-classification, it is worth considering whether or not the different ontological frameworks that have been proposed for species can handle this demand. If they can, then there is a way to be a species pluralist, but an ontological framework monist.

This investigation will help us understand the implications species pluralism has for species ontology, and in turn help us further understand what is at stake between different forms of species pluralism. What is at issue is whether or not a particular form of species pluralism will imply a further sort of pluralism: ontological framework pluralism. In order to address this problem, I will first explain the difference between species pluralism and ontological framework pluralism.

4.1 Species Pluralism and Species Concepts

Many people have thought that the debate about species taxa and the debate about species concepts amount to the same thing, though perhaps from different angles. This thought is underwritten by a tacit assumption of species monism. Many have thought that different species concepts imply different ontological views of species, e.g., that a phenetic species concept implies that species are types and that an evolutionary or that the biological species concept implies that species are individuals. Monists assume that if we have the right species concept, we can read the ontology off it, or, alternatively, and as we saw in Chapter 2, monists can use views about the ontological status of species to argue against particular species concepts. If you are a monist, there

is one true species concept, one ideal system of biological classification, and one ontological account of species.

For a pluralist, species concepts may also be seen to have ontological implications. However, it is difficult to fully determine the implications pluralism for species because the different solutions to the species taxa problem are also trying to tell us what species are: individuals, natural kinds, sets, etc., but in a different way than the way species concepts do. Debates about species concepts, the species category and species taxa have all been caught up with about monism, pluralism and relativism. Thus, answering our question about the relationship between pluralism and the nature of species taxa requires (1) understanding the constraints different forms of pluralism place on the species concepts they take to be legitimate, and (2) an understanding of how to apply the constraints in a way that gives us a clear sense of the required ontological framework to ground the reality of species.

Species pluralists at minimum admit more than one ‘best’ concept, but there are still constraints upon which concepts get recognized. Constraints may stem from interpretations of biological theory or from understanding how concepts are used in practice. As we saw in the last chapter, accounts of species pluralism are largely informed by what we think biological theory implies about species, and that theory is usually evolutionary theory.¹ In Chapter 5 I will look at the relationship between pluralism and biological practice.

As we have seen in Chapter 3, the main factor that divides pluralists into separate camps concerns their stance on evolution. Evolutionary species pluralists interpret evolutionary theory as *fundamental* to our understanding of ‘species,’ and extra-evolutionary species pluralists believe there is more to species than their role in evolution. This means that for evolutionary species pluralists all legitimate species concepts must be compatible with evolutionary theory, though there are different ways of satisfying this demand. Some have argued that species are not special entities distinct from other taxa, and that

¹Many have argued for a long time that the ontological status of species taxa is theory-dependent (e.g., Hull, 1976). This thesis is an extended argument for the view that species pluralism depends on biological theory and practice.

all recognized entities must form monophyletic groups (Mishler and Donoghue, 1982; Mishler and Brandon, 1987, 1989). Some have argued that species are special, and that they may either be monophyletic groups or interbreeding groups (de Queiroz and Donoghue, 1988, 1990). Some have also argued that there are several types of species, some of which we may not yet recognize, and that all are shaped by the different cross-cutting forces of evolution (Ereshefsky, 1992, 2001). According to extra-evolutionary species pluralism, on the other hand, some admissible species concepts will ultimately explain what a species is by way of evolutionary theory, and some will not. Again, there are different ways of being this type of pluralist. Some have argued that we need to recognize species that share structural similarities in addition to the historical entities evolutionary theory requires us to recognize (Kitcher, 1984a,b, 1989). Some have argued that we need to recognize species that are governed by ecological, or other biological theory, in addition to those evolutionary entities that we recognize (Dupré, 1993, 1996, 1999). Since no reasonable species pluralist denies that evolutionary theory has some bearing on species, we should start by considering the implications evolutionary theory has for species ontology. This path is well-trodden.

The key implication evolutionary theory has for the species taxon debate lies in the notion of a ‘lineage,’ which is an ancestor-descendant sequence. A lineage is a spatio-temporally continuous entity (cf. Ereshefsky, 1991, 87). For evolutionists, species are special types of lineages, as many prominent species concepts suggest. Thus, species must be spatio-temporally continuous entities that are created by speciation events and destroyed by extinction. The argument for this lineage-centric view of species is referred to as the ‘evolutionary unit’ argument (Hull, 1976, 180-181). I have formulated the argument below to show how it could apply to both forms of species pluralism. The evolutionists will require all species to form spatio-temporally continuous lineages, the extra-evolutionists will only require that some species form lineages. Evolutionary monists can also accept this argument as formulated:

1. (Some) species are entities capable of evolution by natural selection
2. Entities capable of evolution by natural selection are lineages

3. Lineages are spatiotemporally continuous

∴ (Some) species are spatiotemporally continuous entities.²

Pluralists accept this argument, but argue that there are different types of lineages that ought to be recognized as species. Evolutionists must accept that all of the different types of species form different sorts of lineages, but there will be room for disagreement about whether they must all be monophyletic. Polyphyletic groups do not constitute lineages, and will not be recognized by these sorts of pluralists. If this sort of pluralist only wants to recognize monophyletic groups as species, then there is no need to worry about cross-classification, because there will still be a single, optimal classification of life into species. Extra-evolutionary species pluralists, on the other hand will accept the argument, but argue that the first premise, and thus the conclusion, is true for only some species. That is, these sorts of pluralists will recognize that some species form polyphyletic groups. The difference between these forms of species pluralism is the scope and the degree to which evolutionary theory, or other biological theory, governs which sort of species concepts we accept as legitimate.

In sum, species pluralists invoke aspects of biological theory to wade through the swamp of species concepts, but they disagree about which aspects are relevant. In this sense extra-evolutionary species pluralists have less constraints than their evolutionary counterparts, because they are willing to point out that there is more to biology than just evolution (Dupré, 1999, 13). Most pluralists use accepted biological theory to rule out, or at least reinterpret, typological and phenetic species concepts, as both fail to be grounded in evolutionary theory, or some other well-formed biological theory.³ However, in many cases, phenetic species will match other species concepts, including the **BSC**, **PSC**, and **ESC**. The upshot is that on either form of species pluralism we are going to need an ontological framework that captures the spatio-temporally continuous nature of (some) species. But a more general question we need to ask

²See Dupré (2001), Reydon (2003) and Crane (2004, 161-162) for important discussions of this argument.

³See the Introduction

before we look at the differences between solutions to the species taxon problem is how many ontological frameworks does a species pluralist need? Again, monism has been assumed in the species taxon debates just as much as it has been in the species concept debates.

4.2 Ontological Framework Pluralism

Species pluralism is most straightforwardly a view about species concepts, but it has implications for our ontological understanding of species taxa. As we will see in the following section, the species taxon debate has resolved itself into a dialectic between viewing species as individuals or natural kinds, although there are alternative views of species that attempt to get around problems with both views. Different species pluralists will require different ontological frameworks, and some pluralists will require multiple frameworks. In this section I will argue that if you are an extra-evolutionary species pluralist, then you have good reason to accept ontological framework pluralism.

Kitcher's (1984b) two-set pluralism represents a clear enough instance of ontological framework pluralism, except for the fact that all species are sets. On his account, there are two very different sorts of properties, structural and historical, which are taken to be constitutive of two very different sorts of species. Structural and historical properties are used in different sorts of explanations, and neither sort of explanation is reducible to the other. Some examples of structural explanations are: the mechanical accounts of normal and abnormal meiosis, of respiration and digestion, of details of physiological functioning. Some examples of historical explanations are: those that identify the evolutionary forces which shaped morphology, behaviour, ecology, and distribution of organisms. Species are grouped as such for explanatory reasons, but there are two distinct, non-unifiable reasons for grouping organisms together as a species.

If we disregard Kitcher's focus on sets⁴, but retain the general notion that there are two very different sorts of species, historical and structural, we may

⁴See Sober (1984) and Brogaard (2004) for some problems with viewing species as sets.

want to have one ontological framework for each. This would be an instance of ontological framework pluralism. There are many ways we could combine ontological frameworks. For example, we might hold that some species are individuals, some are processes, some are pluralities, and some something else. But what justifies, or stands in the way of, the inference from species pluralism to ontological framework pluralism? Hull, a staunch supporter of the view that species are individuals (**SAI**), a view we will see more of shortly, has objected to ontological framework pluralism on the grounds that it would violate the unity of science:

From the point of view of some other theory or from a future version of evolutionary theory, anything is possible. However, I believe sufficiently in the unity of science to maintain that eventually all scientific theories must be compatible. If one theory requires that species be spatiotemporally restricted and another that they be spatiotemporally unrestricted, at least one of these theories must be false (1976, 189-190).

If Hull is correct about this, then reading extra-evolutionary species pluralism as implying ontological framework pluralism means that we must deny such a ‘unity of science’ thesis. This, however, is exactly what extra-evolutionary species pluralists are arguing for! Thus, holding a unity thesis about the theory that governs species will stand in the way of ontological framework pluralism.

But does holding onto Hull’s unity of science thesis imply species monism? As we will see, evolutionary species pluralism can be made compatible with ontological framework monism. Aristotle, as we saw in Chapter 2, is a pluralist about species, but a monist about frameworks, as he allows for a certain type of cross-classification and holds a version of species essentialism. Many forms of species pluralism do not conflict with Hull’s thesis. In the next section I will also consider whether one can be an ontological framework monist while denying Hull’s thesis.

4.3 Species Pluralism and Species Taxa

The species taxon problem has been framed by the essentialism story in a way similar to the way debates about species concepts were. In both cases we have widespread agreement that the traditional approach to species has failed. For species concepts, the story tells us that the typological species concept fails to fit with evolution. For species taxa, species can no longer be thought of as paradigmatic natural kinds with fixed essences, because species evolve. The dialectic that has ensued in the species taxon debate was largely set by Hull who presented us with a disjunction, species are either classes or individuals: “By “individuals” I mean spatiotemporally localized cohesive and continuous entities (historical entities). By “classes” I intend spatiotemporal unrestricted classes, the sorts of things which can function in traditionally-defined laws of nature” (Hull, 1978, 336). For example, an organism, a chunk of gold, and the CN tower, are all individuals. Gold, water, and electron, are all classes. As we will see, much has been disputed about the status of Hull’s disjunction and the “true” status of species.

Species pluralists recognize the need to incorporate evolutionary understandings of species. Thus, some of the species concepts requiring an ontological framework will involve recognizing lineages, which are spatio-temporally continuous entities. These sorts of species concepts will differ in whether they specify that organisms of the same species must share a common niche, evolutionary fate, geographic location, etc., If a species pluralist wants to be an ontological framework monist, the so-called traditional approach will be ruled out, e.g., a full-blown intrinsic essentialism, where species are solely constituted by their intrinsic properties (their genetic makeup), regardless of what historical properties they may bear. I will now review some of the remaining frameworks that pluralists have available to them.

4.3.1 Species as Individuals

Species as individuals (SAI) is the view that species are concrete, spatio-temporally restricted objects, namely lineages, which have organisms for parts

(Ghiselin, 1966, 1969, 1974, 1987, 1989, 1995, 1997, 1999; Hull, 1974, 1975, 1976, 1978, 1980, 1981, 1989b). One way of understanding this view comes from considering species as analogous to individual organisms. As a mosquito's wing is part of its body, so is the mosquito biting my arm part of *Culex tarsalis* (Hull, 1976, 181). The analogy isn't perfect, individual organisms still possess a fixed genetic makeup that doesn't change much over the course of their existence, whereas the genetic makeup of a species is not like this. This is presented as the first novel approach to species, and is argued for as an alternative to the traditional approach: the view that species are spatiotemporally unrestricted classes of organisms. **SAI** is perhaps the most popular framework among biologists (e.g., Mayr, 1978, 52) and the received view in philosophy of biology. It is a testament to its popularity that some have even argued that compatibility with **SAI** is a means of ruling out illegitimate species concepts (Mayden, 1999, 97). This itself goes to show how well people believe **SAI** fits with evolutionary theory, and the historical properties it requires.

Hull's disjunction, species are either spatiotemporally unrestricted classes (e.g., gold, water) or they are spatiotemporally restricted individuals (e.g., organisms, organs), has set a certain dialectic. One argues for one view on the basis of the other being false, or having arguments against it. Typically **SAI** is argued for on the basis of species not being classes, because they are spatiotemporally restricted, and can be formulated roughly as follows:

1. If species were spatio-temporally unrestricted classes, then species could be historically disconnected
 2. No species can be historically disconnected
- ∴ Species are not spatio-temporally unrestricted classes (cf. Kitcher, 1984b)

Evolutionary theory is brought in to support the second premise, since it demands a certain spatio-temporal connection between organisms that belong to the same species. **SAI** is offered as a viable alternative that succeeds in capturing this connection where the traditional view fails. This argument isn't the only one for **SAI**, there are of course some positive reasons in favour of the view. Friends of **SAI** have argued that their view explains why species are named ostensively. In practice, biologists provide definitions of species in the

form of type specimens, but this is not meant to be a real definition. A type specimen can actually be quite a typical in comparison with its conspecifics. A type specimen is more of a reference to which the name is anchored. Defenders of **SAI** suggest that this should be thought of as ostensibly pointing to a part of the species, i.e., that type specimen of *Lynx canadensis* there in the museum, in order to define the group to which it belongs. Advocates of **SAI** have argued that their view also explains why a particular species do not figure in any laws of nature. These are some of the points in favour of the view. Many have disputed the reasons in favour of **SAI**, but the way this argument for **SAI** sets the dialectic for debates about species taxa is important for us to grasp.

For our purposes, it is sufficient to point out the most important part of evolutionary theory that the **SAI** thesis is designed to capture. On this view, a certain sort of spatio-temporal connectivity is necessary for a group of organisms to be considered a species. A certain cohesiveness is required (cf. Brogaard, 2004), one that is due to causal relations between the organisms (e.g., Ereshefsky and Pedroso, 2013). The main ontological implication of **SAI** seems to be that two organisms may be very similar in many respects, but unless they belong to the same spatio-temporally continuous lineage, they are not of the same species. These properties are extrinsic to each organism, and they determine which species an organism belongs to independently of the intrinsic differences that organisms of the same species may have. The genetic makeup of individual members of *L. canadensis* may vary a great deal over the history of that species's existence, but each lynx will be part of the same spatio-temporally continuous lineage. This means that a polyphyletic lineage cannot form a species.

4.3.2 Species as Natural Kinds

Even if we accept Hull's dichotomy and the same essentialism story, we might reach a different conclusion from the one he reached. That is, we might conclude that the fact that species evolve does not imply that species are not natural kinds. All it implies is that we must rethink what it means to be a

natural kind. We might hold that species are still natural kinds, but they lack fixed essences. On this view, there is no set of necessary and sufficient conditions for species membership. The most promising view is that species are cluster kinds defined by the common possession of some range of theoretically important property or set of properties. Organisms are still members of species, not parts of species, but it can be indeterminate whether an organism belongs to a particular species. This view is designed to explain why we still make generalizations about particular species, e.g., all lynx have white fur on their chest. This sort of view can also be made consistent with the denial that there are laws in the sense of spatio-temporally unrestricted, true generalizations that apply to particular species, e.g., something could be a lynx and white fur on its chest, but if we had to bet whether or not some arbitrary lynx had white fur, it would be a good bet to make. This doesn't mean it is impossible for a typical lynx to have chest hair of another colour, just that it is improbable. Even though species lack fixed essences, belonging to a species plays an important explanatory role, and thus species should still be thought of as natural kinds. Knowing that Banjo is a cat, gives me good reason to think that she is a pet and that she has cat-like reflexes. I could be wrong about this, Smudge is also a cat who is a pet, but he lacks cat-like reflexes. There are many further reasons for viewing species as natural kinds, but the way proponents of this view have responded to negative argument for **SAI** is what is crucial.

Consider the evolutionary objection to viewing species as natural kinds: "Organisms are members of natural kinds, not in virtue of heredity relations, but in virtue of intrinsic properties. But the evolution of a species taxon requires that hereditary relations join together the organisms of the taxon" (Brogaard, 2004, 224). That is, species are not natural kinds, because grounding the "essence" of a species in intrinsic properties is incompatible with the evolutionary explanation of how a species came to be historically and how it will change over time. In response to this sort of objection, natural kind theorists have tried to accommodate these properties into the kind's definition. On this view, belonging to a species is partially determined by the histori-

cal relations that obtain amongst the individual member organisms, and not wholly by whatever cluster of intrinsic properties the individual members of a species have (e.g., Millikan, 1999). However, viewing species as natural kinds is still primarily a similarity approach to species ontology, because these sorts of views focus on the mechanisms responsible for different similarities that obtain amongst members of the same species, e.g., stability, homeostasis, or common descent. Common descent is not taken as a primary defining property of species, since it is just one of many causes of similarity.

Again, just because traditional “intrinsic species essentialism” fails, we are not forced to adopt **SAI**, we can also reconsider the way we think of similarity. Essentialism is one way of spelling out why the members of a species are similar, because they share intrinsic essences, but there are alternatives. An important view to consider is Boyd’s (1989; 1991; 1999a; 1999b; 2010) homeostatic property cluster kinds (HPC-kinds) approach. This account of natural kinds has undergone numerous changes over the years, and not everyone who advocates it has the same thing in mind. Here I will briefly go over those which pertain to species.

According to the HPC-kinds approach, species still have something like an ‘essence.’ That is, a discoverable, causally important objective set of properties that distinguishes a particular species from other species and other taxa. However, the way we define this underlying ‘essence’ is rather loose and fluid. On this view, homeostatic mechanisms bring about the co-occurrence of the properties in the cluster that defines a species. According to Boyd,

The appropriateness of any particular biological species for induction and explanation in biology depends upon the imperfectly shared and homeostatically related morphological, physiological and behavioral features which characterize its members. The definitional role of mechanisms of homeostasis is reflected in the role of interbreeding in the modern species concept; for sexually reproducing species, the exchange of genetic material between populations is thought to be essential to the homeostatic unity of the other properties characteristic of the species and it is thus reflected in

species definitions (1991, 142).

As initially formulated, this account of species taxa appears biased in favour of the biological species concept, which is only one of the concepts that most pluralists accept. Interbreeding should thus be construed as only one sort of homeostatic mechanism. Indeed, as the HPC-kind view has developed, Boyd and others have hedged their bets about which homeostatic mechanisms are crucial to our understanding of species. This is partly due to the fact that HPC-kind theory is developing against a certain backdrop: the essentialism story. This means that most explications of this view focus on how it can capture what we may want from the so-called traditional approach, by having a more nuanced understanding of natural kinds. Though, the vagueness about which mechanisms are relevant also constitutes a wariness about making an explicit decision about which species concepts are legitimate. As we saw in Chapter 1, many species concepts are fairly explicit about what makes a species come into and go out of existence. The important point here is that species on this view are apt for induction. We can predict with better than chance accuracy that a particular cat will have cat-like reflexes, yet this does not require that there are necessary and sufficient properties for being a cat. But how does this sort of view account for the spatio-temporal restrictedness that many think evolution forces upon our understanding of species, the requirement that species form continuous lineages?

According to Millikan's (1999) account, HPC-kinds should be thought of as historical kinds. Millikan points out that for species the reference to interbreeding, which Boyd accepts, restricts particular species to some actual historical location. Historical properties are an important part of what the biological species concept and similar species concepts capture. In a similar fashion, the reference to 'lineage' in many other species concepts (e.g., the ecological, phylogenetic or evolutionary species concept) also should incline us toward explicitly historicizing HPC-kinds. Though if we were using only a phenetic species concept, a concept she seems to reject, we would not require that the kind be historicized. Thus, Millikan concludes: "Biological kinds are defined by reference to historical relations among the members, not, in the first

instance, by reference to properties. Biological kinds are, as such, historical kinds” (1999, 54). On her account, there is a certain historical link between the members of the kind that causes them to resemble one another. Two sorts of things function to preserve this link. First, something akin to reproduction or copying has produced all the various kind members from one another or from the same models. This way of stating the case doesn’t rely solely on the biological species concept, which, as we saw in the first two chapters, refuses to recognize asexual species as real species. Second, the various kind members have been produced in or in response to the very same ongoing historical environment.⁵

In a response to Millikan (1999), Boyd agrees with her that HPC-kinds are always historical kinds, and argues that the members of some given species:

1. are like one another, not because of a shared eternal essences, but because of historical relations between them;
2. exhibit the properties of the kind because the other members exhibit them;
3. support induction because such inductions are ‘grounded’ because there is a certain kind of historical link between the members, for which reason the members are like one another; and
4. are modally, spatially and historically delimited so that, for example, *Homo sapiens* could not occur on Twin Earth. (Boyd, 1999b, 68)

With this development in view, HPC-kind theory looks a lot more like the **SAI** thesis, aside from the emphasis on the HPC-kind being explanatory, or supporting inductive inferences. Of course some differences remain to be explored. According to **SAI** we ought to think of organisms as parts of species,

⁵She also has some objections to Hull’s claim that because **SAI** is true, species do not function in scientific laws. On her view, a valid scientific law is just a true, well-grounded generalization. However, these historical kinds are unlikely to ground true exceptionless generalizations, which, for what it’s worth, is what Hull takes a law of nature to be.

and on the HPC view organisms are still members of species. Though there is a lot of debate about the differences between these views, it is not clear what is at stake here. For our purposes, differences like this aren't really telling in favour of one view over another, especially when both seemingly accept the same sorts of historical claims about species, e.g., that *Homo sapiens* cannot occur on Twin Earth.

In my view, as this dialectic has progressed, the two sides have become closer and closer to one another. On the difference between **SAI** and his own view, Boyd says that "Once we get the metaphysics and epistemology of natural kinds right, we can see that, even if biological species are, in the relevant sense, historical individuals, their constituent populations constitute natural kinds nonetheless. So much for analytic metaphysics!" (Boyd, 1999b, 72). Boyd has also stated that "the distinction between kinds and individuals is much less important than it might seem" (Boyd, 1999b, 73). It is these sorts of statements that make the species taxon debate seem like a frustrating waste of intellectual resources.

I will argue that species pluralists can avail themselves of either ontological framework, **SAI** or species as HPC-kinds, but that they need a framework that places the same restrictions on species as those made by their particular brand of pluralism. Evolutionary species pluralists range from allowing only monophyletic groups to also including paraphyletic groups as species. Extra-evolutionary species pluralists accept polyphyletic groups as species. **SAI** can fit with evolutionary species pluralism, because these sorts of pluralists rule out polyphyletic groups and so does the **SAI** thesis. But what does the HPC-kind view have to say about such restrictions?

Ereshefsky (2007, 296) argues against viewing species as HPC-kinds, because doing so emphasizes similarity to the detriment of phylogenetic approaches to taxonomy. I show that this objection is not raised against the HPC-kind approach *per se*, but against Boyd's formulation of it. Phylogenetic approaches to taxonomy prohibit taxa, species included, from being paraphyletic or polyphyletic groups. As we've seen in Chapter 3, Ereshefsky advocates a form of evolutionary species pluralism that restricts species to

lineages, but he allows species to be paraphyletic and monophyletic lineages. Boyd suggests that species do not need to form continuous lineages, albeit on the basis of cases where species formed by hybridization events evolve, go extinct, and then re-evolve again. Thus, he allows even polyphyletic groups to constitute HPC-kinds (1999b, 80; 82). When it comes to his own interpretation of HPC-kind theory, Boyd himself says: “I do not, for better or worse, hold that HPC kinds are defined by reference to historical relations among members, rather than by reference to shared properties” (1999b, 80). Boyd’s view of HPC-kinds then allows similarities to win out over historical properties. Ereshefsky, I think, puts the point a bit too strongly by suggesting that HPC-theory “allows taxa to be nongenealogical and hence non-historical entities” (2007, 296). The point is rather that if we let this version of HPC-theory rule the day, we will be allowing for more species concepts than what a certain evolutionary understanding of species concepts (especially phylogenetic theory) dictates. There are many other approaches to classification in biology. However, we shouldn’t accept an ontological framework more permissive than is warranted by a particular brand of species pluralism. The constraints on species concepts should match.

In sum, an evolutionary species pluralist can accept either **SAI** or something like Millikan’s account of HPC-kinds, because these frameworks impose the same restrictions as evolutionary species pluralism, but not Boyd’s account of HPC-kinds which accepts polyphyletic groups as species. Millikan’s account, on the other hand, does not accept that such groups may form species. According to **SAI**, species are restricted so that they cannot go in and out of existence. For the HPC-kind account to fit with evolutionary species pluralism, given that it overcomes the other problems with a traditional essentialist approach to species, a similar restriction needs to be adopted. This however doesn’t mean that Boyd’s version of HPC-kinds wouldn’t fit with a version of extra-evolutionary species pluralism. But before we determine whether or not this would work, we need to look at some other solutions to the species taxon problem.

4.3.3 Some Alternatives

As we have seen, there is a fairly worn-out dialectic between friends of **SAI** and friends of species as natural kinds, especially the **HPC**-kind view. In this section I will examine some views that attempt to escape certain aspects of this debate by denying the dichotomy. Some have held that species are both individuals and natural kinds, or that species are neither individuals nor natural kinds, but something else. I argue here that the only alternative to accepting one side or the other of the disjunction worth considering is ontological framework pluralism, and that this is the main upshot of looking at the species taxon debate from the perspective of species pluralism. Species pluralists either restrict species to continuous lineages, or they do not. If a pluralist restricts some species to continuous lineages, but allows some others to be unrestricted, then this should be understood as ontological framework pluralism.

One way of denying the dichotomy is to hold that each species is both an individual and a natural kind. Rieppel's (2007; 2013) 'one of a kind' view, tries to combine **SAI** with the **HPC** view of natural kinds (cf. Boyd, 1999b; LaPorte, 2004; Brigandt, 2009; Reydon, 2009). On this view a species is an individual with organisms for parts, but it is also a 'one of a kind' natural kind. The problem with Rieppel's one of a kind view, is that it is unclear what is instantiating the kind. Is it the species as a whole or the organisms that constitute the whole that instantiate the natural kind? For species to be natural kinds there must be a certain degree of explanatory power that being a member of a kind carries. If I say to you that you are one of a kind, I might as well be saying that you are unique. If I say to you that you are a human being, then I am implying that you are not unique, and that you share certain characteristics with other human beings. One would think, that on any version of species as natural kinds it should be the member organisms that each individually instantiate the kind to a greater or lesser degree. Rieppel himself claims that "species are spatiotemporally located complex wholes (individuals), that are composed of (i.e., include) causally interdependent parts, which collectively also instantiate a homeostatic property cluster (**HPC**) nat-

ural kind” (Rieppel, 2013). It’s not really clear what explanatory power this sort of one of a kind natural kind would carry. This view is in a way saying what Boyd already said earlier about there being no real difference between viewing species as kinds or individuals. In short, this particular way of blurring the lines between individuals and classes, and getting around the disjunction seems unprofitable.

However, there are other ways of holding that species are individuals and natural kinds (or classes in Hull’s sense, rather than according to the HPC-kind view). For example, one could hold that some species are individuals, some natural kinds, but no species is both a natural kind and an individual. Perhaps the species according to the **BSC** are natural kinds, and all the asexual species are individuals. Kitcher’s (1984b; 1984a; 1989) “two-set” pluralism is worth considering in this context. People often argue against viewing species as sets, classes or kinds on the grounds that these views of species do not preserve the historical or genealogical criterion that evolutionary theory places on species ontology (see Crane, 2004). In response to this sort of argument, Kitcher argues that claims about species as individuals can be translated into talk about sets. We just need to specify some sort of historical or genealogical connection as our criterion for set inclusion.⁶ As we saw in Chapter 3, Kitcher (1984b; 1984a) argues for a form of extra-evolutionary species pluralism where species can be either historical or structural sets of organisms. Thus, species are sets, but, as we noted above, there are just two radically different kinds of sets. On his view it is not whether species are individuals or natural kinds. Species are sets that can be grouped on the basis of shared history, or on the basis of shared structure. However, one might think that this translation move between individuals and sets cannot be made so easily:

The problem with historical sets, as with all sets, is that sets are abstractions. Sets do not preserve the order and location their members have outside the set. In Kitcher’s case historical/genealogical relations are used as a criterion to determine which organisms are

⁶See Hull (1978, 336-337) for a similar discussion.

members of the same set. But the set does not represent or capture these historical/genealogical relations (Brogaard, 2004, 229).

This might be a very weak objection to viewing species as sets, if we allow that sets can preserve some of the structure. Sets, according to Brogaard, just ‘represent’ the concrete aggregation of organisms, but they are not the same things as the concrete aggregation of organisms. But if we are going to be such sticklers about sets, one might also wonder whether or not species as individuals, where individuals are interpreted as mereological sums, as they are in the dark corners of analytic metaphysics, suffers a similar problem. On this view of individuals, a sum may preserve order and location, but not the causal relations between the organisms. As we’ve seen, this is not what Hull, or anyone else means by **SAI**. What is clear from this debate is that it is not a question about whether individuals, or sets, or classes, are the best ontological frameworks for species, it’s whether they support the requisite historical properties. And these properties, as far as pluralists are concerned are varying degrees of restrictions on what sort of historical connectivity is required for a group to be a species or not. The key thing about Kitcher’s view is that he recognizes this and tries to keep the two different sorts of species distinct. Thus, although this view holds that all species are sets, it is still a form of ontological framework pluralism.

Another way of denying the dichotomy is to accept a view of species as belonging to an ontological category distinct from individuals and classes, e.g., the view that species are processes (Dupré, 2012; Rieppel, 2009). The implications of a process ontology for species have yet to be fully worked out, but this view does seem to capture the contingent, historical nature of species that evolutionary accounts of species focus on. Further, process ontologies are often associated with the standard metaphysical accounts of **SAI**, where species are understood as perduring, four-dimensional objects, or “space-time worms” (cf. Reydon, 2008). Boyd, however, interestingly says about his own view that “the property cluster and homeostatic mechanisms which define a species must be individuated non-extensionally as a process-like historical entity” (1989, 18). This raises the same suggestion that viewing the distinction between kinds and

individuals as merely syntactic does. That is, from some ways of looking at it, different ontological frameworks all seem to blend into one another.⁷ But as we've seen with Boyd's account, the key difference concerns the sorts of historical groups he is willing to recognize as species (paraphyletic and polyphyletic). An advocate of **SAI** would not recognize polyphyletic groups. The debate is not about the name by which one should call the correct ontological framework for species. Similar to what we saw in Chapter 3, this is an issue of how evolutionary theory bears on species, and this is what is at stake between different forms of species pluralism. Further, viewing species as processes seems to fit with either side of the individuals versus natural kinds controversy on what sort of groups can be recognized as species.

However, as Dupré develops the process account of species, it is perhaps not limited by a certain evolutionary understanding of species that fits both with species as individuals and evolutionary species pluralism. Dupré argues that the thesis that species are individuals: "is linked to the idea that species are branches of the evolutionary tree and therefore inherits the limitations of that idea" (Dupré, 2008, 23). By this, he means the requirement that species form continuous lineages. Dupré, as we have seen in Chapter 3, has argued that it may be useful to think of species not just as branches in the evolutionary process, but also as strands in the web of life. This is all very metaphorical. However, if we want to view species as playing different roles in both of these metaphors for the structure of life, then perhaps it is better to think of species as processes, rather than as individuals. Would this work? One could argue that there would still be radically different kinds of processes, one akin to *SAI*, which fits the evolutionary tree understanding of species, and one not so strictly limited by space and time. As I understand it, viewing

⁷Thanks to Matt Barker for this suggestion. There are many views here I'm glossing over. A more recent contender is species as plural particulars (SPP), which is the view that a species is just a plurality of organisms (Slater, 2013; Simons, 2013). Simons's even refers to **SPP** as a "thorough-going nominalist" stance, where the base entities are organisms. Slater's (2013) defense of **SPP** also involves an attempt to break down the realism-antirealism dichotomy about species. Reydon (2015) quite rightly calls this a 'very light sort' of realism, one that comes dangerously close to nominalism. As it stands, **SPP** seems a rather dubious ontological framework for species.

species as processes has yet to be developed fully. Most of Dupré’s work on developing a process ontology for biology has been done on whether or not this a viable ontology for other biological ‘individuals,’ like cells, organisms and viruses. If viewing species as processes is going to be a viable solution to the species taxon problem, it will have to be on grounds other than those used to argue for species pluralism. The restriction that species pluralism puts on this solution to the species taxon problem is the same as that placed on **SAI** or the HPC-kind view. If a pluralist restricts species to continuous lineages, then this restriction needs to be placed on species as processes. As I see it, the constraints coming from viewing species as processes are unclear.

In sum, the way of denying the dichotomy that works, the way that fits with extra-evolutionary species pluralism, is ontological framework pluralism. The other ways of denying the dichotomy either fail to make sense, like Rieppel’s “one of a kind” view, or collapse into **SAI** or something like the HPC-kind view. Species monists have only so many options when they engage in the species taxon debate. They must choose one side. Holding species pluralism adds another option to the debate: ontological framework pluralism. But does a species pluralist need to be committed to ontological framework pluralism, or can she be an ontological framework monist?

4.4 Cross-Classification

If species pluralism is to be made compatible with ontological framework monism, we need a framework that can make sense of cross-classification. This is a further way of spelling out the varying degrees of spatiotemporal restrictedness that different species pluralists accept. Most accounts of species pluralism, save monophyletic pluralism (Mishler and Donoghue, 1982; Mishler and Brandon, 1987), and sophisticated forms of quasi-pluralistic monism (de Queiroz, 1998, 1999, 2005a,c, 2007; Mayden, 1997, 1999; Shun-Ichiro, 2011; Kendig, 2014), require an ontological framework(s) that will allow for some overlap between species. But there are different restrictions on what sort of overlap is permissible. As we saw in Chapter 2, evolutionary species pluralists

minimize how much cross-classification occurs by restricting species to different sorts of continuous lineages. On this view, one organism can belong to multiple sorts of lineage, but no polyphyletic groups would be recognized as species. A particular tree could belong to one species that is a monophyletic group, but could also belong to another species that is a more or less inclusive polyphyletic group. Extra-evolutionists, on the other hand, are much less restrictive in the ways species can overlap one another. Here we might see even different biological spaces, e.g., historical vs. structural space, cross-classifying one another. On the evolutionary view, we could map this on to one messy branching Tree of Life. According to the extra-evolutionary view, we can't settle with one messy map, we need something more than the Tree of Life. This, in many ways is similar to Aristotle's pluralistic approach, as discussed in Chapter 2, though extra-evolutionary species pluralists are mainly concerned with the basal group, species, being explanatory, and not all biological groups. How can the different solutions to the species taxon problem accommodate these restrictions on cross-classification?

One way of accommodating cross-classification would be to have a different framework for every species concept, e.g., ecospecies could be individuals, phenospecies could be natural kinds with fixed essences, and biospecies could be Millikan-style HPC-kinds. This is interesting because many people think that certain species concepts entail certain resolutions to the species taxon problem. Some have argued that there are differences between modern species concepts, in that some entail **SAI**, while others entail that species are natural kinds (Reydon, 2003; Crane, 2004). Once we determine what sort of species concepts a pluralist will allow for, we can then read the ontological framework(s) right off those species concepts. If there are straightforward ways of interpreting what species concepts entail for species ontology, this approach would make things easy. However, the level of abstraction that solutions to the species taxon problem operate on is far too general to favour singular species concepts. The different solutions to the species taxon problem all fit with multiple species concepts. For **SAI**, differences in species concepts can correspond to differences in understanding how the parts of an individual

species causally interact. That is, **SAI** as an ontological framework allows for a plurality of ways of understanding how species causally interact. For the HPC-kind view, differences in species concepts correspond to differences in understanding which homeostatic mechanisms are relevant in which particular case. Here there is also an implicit pluralism about homeostatic mechanisms. Thus, for the most part solutions to the species taxon problem don't pick a winner to the species concept debate. From a pluralist perspective this is a good thing, because there is no single winner to the species concept debate. For our purposes we need to look at cross-classification through the way we developed it in Chapter 3, according to what types of cross-classification are permitted by different forms of species pluralism. If a solution to the species taxon problem permits the cross-classification required by a particular form of species pluralism, then that form of species pluralism is compatible with ontological framework monism.

Now before we talk about cross-classification any further, let's consider an actual example that would fit with the demands of evolutionary species pluralism. Consider some Canadian oaks like *Quercus macrocarpa* and *Quercus bicolor*. Given the biological species concept, and the fact that there is a good deal of gene flow between members of these groups form hybrids where they occur together in the wild, these would be considered one species, because they are not reproductively isolated from one another. Given the ecological species concept, and the fact that these groups occupy different niches, and have done so for a very long time, they would be considered two species. In this case the two species concepts fail to pick out the same groups. Now let's consider what solutions to the species taxon problem would say about such a case.

Can **SAI** accommodate this form of cross-classification? According to **SAI**, some given oak may be both part of the individual *Quercus macrocarpa*, and the individual composed of *Quercus macrocarpa* and *Quercus bicolor*. Thus, species pluralism seems perfectly and easily interpretable in terms of individuals. In fact, some have even argued that **SAI** entails a form of species pluralism (Brogaard, 2004, 236-240). This is because there are many processes,

not just gene-flow as in the biological species concept, that may preserve or cause species to have cohesion (see Ereshefsky's Forces Argument in Chapter 3). The crude notion of **SAI** fits with multiple lineage based species concepts, and these fail to yield a single, unified classification of organisms in to species. Rather, they will yield multiple overlapping mereological sums. This, however, rests on the back of an assumption that viewing species as natural kinds would yield a single, unified classification of organisms, but as we have seen this is not true even for someone as anti-evolutionary thinking as Aristotle.

Can species as natural kinds accommodate the cross-classification demands of evolutionary species pluralism? Natural kind theory seems highly amenable to the monist assumption that there is one true system of classification. This comes from reflecting on the 'carve nature at its joints' metaphor endemic to natural kind literature. Brogaard, for example, argues that viewing species as natural kinds wouldn't fit with species pluralism (Brogaard, 2004, 236), because it cannot accommodate cross-classification. However, on the basis of the essentialism story, most modern natural kind theorists are more than willing to be a little flexible in how well-defined these 'joints' are. It may take some work to develop an account of natural kinds that 'butchers nature' in the appropriate sense, and so this account, though compatible with species pluralism, may be harder to develop and motivate. One might argue that we are discovering that nature itself has way more joints than we thought. As we have discussed in Chapter 2 we have a cross-classifying theory of natural kinds that goes back as far as Aristotle, and is tied to his rejection of Platonic bifurcating division. But do we have an account of natural kinds that allows us to say that a given oak may be a member of the **EcSC**-kind *Quercus macrocarpa*, and the **BSC**-kind composed of *Quercus macrocarpa* and *Quercus bicolor*? On the HPC-kind account, the differences between these sorts of overlapping species would amount to differences in homeostatic mechanisms, like gene-flow and selection pressures, but the general overlap would be explained by way of common descent.

What about the cross-classification demands of extra-evolutionary species pluralists? As I argued in Chapter 3, for these to be successful they need to be

grounded in biological theory that does not reduce to evolutionary theory. The cross-classificatory demands of evolutionary species pluralists can be grounded in differing conceptions of how to divide up segments of the tree of life, but those of extra-evolutionary species pluralism will require a different, separate structure, and this underlying structure is what constitutes ontological framework pluralism.

Dupré (2001) has suggested that his form of extra-evolutionary species pluralism is compatible with viewing species as a certain sort of natural kind. However, he hasn't been precise about the nature of these sorts of natural kinds. Dupré's form of pluralism involves divorcing the units of biological classification from the units of evolution. He agrees that the units of evolution are lineages: "Lineages in general are sequences of entities related by ancestry and descent. The relevant entities in this case are populations, or groups of interconnected populations. Populations are themselves, I take it, individuals, and they are the temporal parts of other individuals, lineages" (Dupré, 2001, 213). He thus allows Hull's evolutionary unit argument to go through, but maintains that *only* units of evolution are individuals. The term 'species,' according to this view, should not merely refer to a sort of evolutionary unit. The term 'species' should be used as a classificatory unit, and thus, evolution does not require that all species must be individuals. We should note that Dupré, for the most part, holds that natural kinds can't evolve, and claims that if we are focusing on the lineages, or individuals, that evolve, then this won't be good enough to meet all of our taxonomic needs: "many different concerns, both theoretical and practical, generate an interest in the classification of organisms. But unlike the situation generally supposed to obtain in chemistry, there is no uniform theoretical perspective that will generate such a classification" (2001, 215-216). Thus on this view, "some species are real natural kinds, but many are not" (2001, 217). In a footnote he suggests that Boyd's HPC-kind theory may be able to support the sorts of kinds required by his promiscuous realism. However, given that he recognizes the theoretical, but non-fundamental, importance of understanding species as individuals, it seems that his view would profit from making this distinction explicit at

an ontological level. Given that extra-evolutionary species pluralism is based in theoretical pluralism, ontological framework pluralism seems like the way to go here. This doesn't mean that an extra-evolutionary species pluralist is forced to accept **SAI** in even the limited sense that Dupré does here, but that they must accept an ontological framework that is restricted in the way evolutionary theory demands, and one that is not. Both frameworks could be versions of the HPC-kind account, both could be versions of species as processes, but given the clear separation of restrictions on species coming from extra-evolutionary species pluralism, this view implies ontological framework pluralism. But, given that **SAI** is clearly developed to meet the restrictions of evolutionary theory only, it won't be sufficient to meet the cross-classificatory demands of extra-evolutionary species pluralism.

In sum, all of these ontological frameworks seem at least partly compatible with cross-classification. That is, they can be developed so as to allow for cross-classification, even though here I've only suggested how this may work. It may not be as easy for some ontological frameworks as it is for others. For natural kinds, it seems difficult, due to the way that these are tied to the 'carve nature at its joints' metaphor many have taken natural kind theory to be consistent with monism, and not pluralism. However, for a natural kind theorist to admit of cross-classification, a more relaxed account of kinds may allow some overlap, because this is a different sort of cross-classification than what an essentialist like Aristotle admits. For **SAI** cross-classification at first seems less problematic, but this is partly due to the much looser and scattered cohesion that species are thought to have, if interpreted as individuals, over something even more cohesive, like an individual organism. However, given the similar spatio-temporal restrictions that evolutionary species pluralism and **SAI** put on species, **SAI** is a poor choice for the cross-classificatory demands of extra-evolutionary species pluralism. Thus, there is nothing about cross-classification in and of itself that leads us to ontological framework pluralism. The theoretical pluralism advocated by extra-evolutionary species pluralists requires ontological framework pluralism.

4.5 Conclusion

In this chapter I have examined the relationship between species pluralism and the species taxon problem. The short version is that species pluralism does not resolve the debate. But given that species pluralism doesn't tell us that *one* species concept is correct (it tells us that *some* are) this isn't surprising. In similar fashion, some ontological frameworks may be suitable from a pluralist perspective. This is not uninformative, because monism tells us absolutely nothing about what species are, only that we need to seek a unified concept and ontological framework for species. Species pluralism, however is compatible with multiple species concepts, but in order to be distinct from relativism, pluralism must be tied to biological theory. It is this tie to theory that is important. Extra-evolutionary species pluralism fits with ontological frameworks that can capture both 'intrinsic' and historical properties. Evolutionary species pluralism minimally requires an ontological framework that captures historical properties. However, we still need to be clear about the nature of these historical properties, for example, if species are path-dependent entities, rather than entities with merely essential origins, then this will have implications for the sorts of ontological frameworks suitable for species pluralism (Ereshefsky, 2014b). On this view, it is not the origin that is important to species, but the entire path they follow as they evolve from other species until their extinction or speciation into new species. I will leave this for another time. In the next and final chapter, I will put species pluralism into practice.

Chapter 5

Species Concepts as Tools

Classis et ordo est sapientiae,
species naturae opus

Linnaeus

Introduction

On the basis of the forms of species pluralism discussed in the last two chapters, I develop species pluralism so that it can explain and guide biological practice. Hitherto the focus for pluralists and many monists has largely been on conceptual and ontological issues. This chapter makes a novel contribution to the literature by putting species pluralism into practice. I offer an approach to what we may call the ‘species concept application’ problem, which I argue is distinct from the so-called ‘species-taxon’ and ‘species-category’ problems. I sharpen the different forms of species pluralism by exploring the ‘species concepts as tools’ metaphor on the basis of a case study in yeast systematics. As shown in Chapter 3, a pluralist may rule out certain species concepts as unsuitable tools for systematic work by the lights of biological theory, but my aim is to be more discerning. Pluralists have suggested that different concepts work well for different areas of biology, but what this means remains under-explored. Rather than ask on what grounds a concept is legitimate by the

lights of biological theory, one can ask on what grounds concepts are legitimately applied. As we saw in Chapter 2, part of the reason species pluralism has become defensible is that there are so many different species concepts currently in use. Pluralists need to develop an account of how a species concept can be used well or misused, which remains an under-explored topic. The aim of this present Chapter is to explore how different concepts can be applied adequately in a given context of inquiry.

Pluralists are in some sense splitters. They wish to split up the concept ‘species’ or the species category into many, related and similarly governed sub-concepts (e.g., *ecospecies*, *biospecies*, etc.). But they are not relativists, and do not want to go on splitting indefinitely or arbitrarily. Partly because of this felt need for constraints, most pluralists have allowed for overlap between different sorts of species concepts.¹ The different types of permissible overlap are spoken of generically, as we have seen in previous chapters, by the term “cross-classification.” When it comes to application, being explicit about what sort of cross-classification are permissible helps us learn about when a particular species concept is appropriate. There may be domains where a certain sort of species concept is always inappropriate, for example, the traditional account of the biological species concept, where species are reproductively isolated populations, seems wholly inappropriate for talking about groups of any asexual form of life. A monist who noted such a failure of universality in their preferred concept, could accept that asexual forms of life fail to form species. A pluralist can note this as a limitation in the applicability of one concept among many. Each concept has its limitations, for there are many different ways of producing and maintaining species.

Most species pluralists often stress the separation of legitimate species concepts, rather than the extent to which they might be integrated. This non-integrative approach to pluralism suggests that each species concept will present us with a different classification of life that is suited for an entirely different purpose. Separating species concepts in this way might give us multiple

¹Though as we saw in Chapter 3 monophyletic pluralism is not a form of pluralism that allows for overlap.

true trees of life. This implies a one-to-one correspondence between successful applications of a species concept and a species, which means we cannot use two or more species concepts together to delineate one species. However, close attention to the way concepts are applied in the midst of the conceptual pluralism suggests otherwise.

Even though multiple species concepts are often used together to delineate a single species, it is still true that in general these species concepts sometimes do not isolate the same groups. Delineating a new species involves a diverse array of data, molecular, biogeographical, morphological, etc. (e.g., Lachance and Fedor, 2014). And different species concepts will make use of this data in different ways. A form of pluralism that allows species concepts to be used together as *tools* to extract taxonomic information from such data is called for. Given this sort of research, a pluralist will need a rationale to determine whether or not a species concept is being used well or not in a particular area. In order to elucidate the species as tools metaphor, I provide a case study on how concepts are used by yeast taxonomists studying the large-spored *Metschnikowia* clade. On the basis of this study, I argue that: (1) there can be a many-to-one correspondence between species concepts and species; (2) despite two sorts of arguments from consilience for species monism (Ruse, 1987; Richards, 2010), this fact is acceptable to the species pluralist.

As we have seen in Chapter 3, most accounts of species pluralism that focus on reading pluralism off of biological theory do not say much about how species concepts interact. On an uncharitable reading, this means that even when different species concepts pick out equi-inclusive groups of organisms by way of different biological properties, we have two different co-located entities. For example, if I use a biological species concept on some birds and pick out the black-capped chickadees from the Carolina chickadees because they don't interbreed, and I also separate them from each other according to a morphological species concept by the greyness of their napes, I don't thereby have four different species! Ruse is correct in this case, where these features align we have more reason to mark these populations as two separate species. This is a puzzle that pluralists need to address. I will address this puzzle by

applying toolbox theorizing to species pluralism, and by looking at how species concepts are used by biologists attempting to discover new species.

5.1 Toolbox Theorizing

The toolbox metaphor has floated around for a while in discussions of scientific pluralism. Chang, for example notes that “pluralism in science is just as natural as wanting to have various types of tools in our toolbox, or having different types of shoes in our cabinet to suit different occasions” (2012, 273). This way of talking about the toolbox is largely put to a pedagogical use in explaining what pluralism is. Though this aspect is important, it offers us very little guidance for how pluralism fits with scientific practice. Brigandt (Brigandt, 2006, 2011, 2012) has developed a nuanced account of scientific concepts as tools in terms of their reference, inferential role, and the epistemic goal pursued by a concept’s use. Brigandt’s framework has been applied to concepts like homology, gene, and evolutionary novelty, though his framework has yet to be applied in detail to species. I will develop the toolbox metaphor for species further by examining Waters’ (2011) account of toolbox theorizing for the Price Equation, and then Stanford’s use of the toolbox metaphor in evaluating Kitcher’s brand of extra-evolutionary species pluralism.

Waters’ (2011) account of toolbox theorizing offers perhaps the most useful way to interpret the purposes to which we put theories, concepts and models. The basic idea comes from a distinction he makes between two different sorts of realists: fundamentalists and toolbox theorists. For fundamentalists the world is made up of natural kinds of processes, and there is a one-to-one correspondence between a token process and its true model. For toolbox theorists there is a possibly messy world, because for a given token process, some concepts and models might be useful for constructing correct accounts of some aspects of this process, others for other aspects. For species pluralists however, the same entities, *species*, will often be accounted for using different models, *species concepts*.

In order to elucidate what he means by toolbox theorizing, Waters argues

that different versions of the Price equation (a covariance equation that determines the change in allele frequency of a population), or ‘tools in a box,’ are needed. Neither version is fundamentally correct. Rather, the appropriateness of the ‘tool’ depends on the question. If biologists want to know what would happen if selection were eliminated by changing the environment, one version will suffice. If we want to know what would happen if transmission bias were increased, another version will suffice. Both versions provide informative, partial causal decompositions. The causal landscape is complex, and there are many legitimate ways of providing a ‘parsing of causes.’ However, applying Waters’ strategy here to species concepts is not a straightforward procedure. I will now make some suggestions about how to apply Waters’ strategy in the case of species.

One problem with applying toolbox theorizing to species concerns the notion of a ‘parsing of causes’ (cf. Kellert et al., 2006). This comes about in the context of the Price equation for good reason, but with species we might be more concerned to talk about a ‘parsing of objects.’ Most pluralists (and even some monists) will accept that certain aspects of our classificatory practices do not attempt to uncover the causal structure of the world (e.g., consider the use of a phenetic species concept as discussed in Chapter 1). Thus, we are going to need an account of toolbox theorizing that fits with the fact that we have species concepts in our toolbox that are not (directly) in the business of getting at the causal structure of the world. Having these species concepts in our toolbox might then lend some credence to a form of extra-evolutionary species pluralism (though not necessarily Dupré or Kitcher’s version). Let me further spell out three related reasons why having a causal restriction on what gets to go in the toolbox will be inadequate.

First, taxonomists often distinguish between different stages of taxonomy, for example, α , β , and γ -taxonomy (e.g., Mayr et al., 1953, 17-19), or we might take to be a discovery and justification stage of taxonomy (Colless, 2006). The idea behind these distinctions, is that different stages of taxonomy require different sorts of tools, that is, different sorts of species concepts. The first stage, α -taxonomy, or the discovery stage of taxonomy, does not involve

parsing any causes. This stage requires the use of a species concept, which was once typically based on morphological criteria (Mayr, 1969b, 15). Thus, we might use morphology to tell the black and blue butterflies apart from all the other butterflies. Further stages of taxonomy will use this initial classification to go further. For example, we might use DNA analysis to tell the different types of black and blue butterflies apart from each other. In response to this practice, one might argue that these preliminary classifications are ultimately going to be discarded, and that the real tools of systematics only come in during later stages of taxonomy. That is, perhaps we have two drastically different toolboxes in play here. However, as the case study below will show, taxonomy doesn't always proceed from one stage to the next. It is hard to make a clear-cut distinction between a discovery and justification stage of taxonomy, because the same species concepts can be used in both stages.

Second, phenetic, morphological, or typological species concepts can play an important role in many areas of systematics, even if they are not the ultimate arbiters of what gets to count as a species. These species concepts are non-causal, the information used by these concepts to delineate species does not get used to explain why a species is the way it is. That is, there is not a direct connection between the species concept and how we understand speciation. The biological species concept, on the other hand, is causal, because gene-flow and reproductive isolation explain, at least to a certain extent, why species are distinct from each other. A biological species has at some point acquired reproductive isolation mechanisms that maintain, to a certain extent, its separation from other species. Now, not only do non-causal species concepts get used in the preliminary stages of taxonomy, but they get used to help justify the claims being made in the later stages. That is, there is a sort of back and forth here that would make the notion of two different toolboxes seem inadequate. This is especially clear when we consider how such a concept is used to corroborate the hypotheses of other species concepts when they pick out equi-inclusive groups. However, when they do not, as in the case of cryptic or sibling species (species that look the same, but have significant genetic differences, or are reproductively isolated from one another, or occupy

significantly different niches), we need a different rationale. This may spawn further research into why something like morphology and other biologically significant properties come apart in a given study. When they come together, generally one should say that the same species has been delineated through two methods, or species concepts, and when they come apart, one may want to suggest that one is a real species and that the other is perhaps an artifact of speciation. Thus, we will need to make use of these sorts of non-causal species concepts, or those that pick out the pattern and not the process to justify our claims about the process.

Third, if we adopt some form of extra-evolutionary species pluralism, this may allow for non-causal species concepts to pick out genuine groups, even if we think these groups are not tied together by the forces of evolution. As it stands, how this would work is for the moment unclear. There are no extant species concepts that are quite like the ones that Kitcher and Dupré advocate for. The point is merely that a species concept based on Kitcher's structural properties or Dupré's notion of a systematic ecology may not always involve the use of species concepts that say anything about the causes that contribute to speciation.

Another problem, already partially broached, comes from considering when we might want to use different tools to do the same job. This pertains to how two different causal concepts work together. Given pluralism, it does not seem correct to say that when two species concepts make the same delineation that we have two different species. As my case study shows, this is not how species concepts are applied. Further, Waters' 'Toolbox Theorizing' does not account for this because there is still a one-to-one correspondence between different formulations of the Price Equation and different causal parsings. Even though many pluralists admit of cross-classification, this doesn't mean that every species concept they recognize will always cross-classify every other species concept.

Despite these two difficulties, 'Toolbox Theorizing' can be sufficiently modified so that it reflects the ways biologists use multiple species concepts. What I hope to make clear through this case study is the sort of complex tool that

species concepts are, and the sort of messy world that these tools attempt to work with. A particular species concept is not going to play the same role in every investigation. What I do want to retain from Waters' account is the distinction between toolbox theorizing and fundamentalism. Before we get to this, I first want to look at how the toolbox metaphor has been used in relation to species concepts.

Stanford (1995) uses the metaphor in arguing for a pluralist, but anti-realist stance toward species. This comes out when he characterizes Kitcher's version of species pluralism. According to Stanford, we should reflect on whether or not there is redundancy in the different tools we put in our box. As he puts it, "The question is whether Kitcher's tool box is filled with various wrenches, pliers, and screwdrivers or merely with nine hammers" (1995, 72). In the end, Stanford concludes that "While his toolbox might turn out to contain a spare wrench or pliers, Kitcher's tools are plausibly heterogeneous and his demand for pluralism well-founded" (1995, 76). Stanford may be viewed as suggesting that we should not have tools that are redundant. Although redundancy is a concern when it comes to distinguishing pluralism from relativism, this might not be a problem for Stanford, since he argues for a relativistic form of pluralism. The problem with this way of understanding the toolbox metaphor though is that it still suggests that different concepts are used for different jobs. A hammer will be used for nails, a screwdriver for screws, etc. However, to continue with the metaphor, the thing about tools like pliers, wrenches, screwdrivers, and hammers is that they can sometimes work together to do one and the same job. If I want to remove an old nail from a board I may end up using a hammer, flat screw driver, and a pair of pliers. Stanford is still right that having two hammers in such a situation won't do me any better than having just one. The picture I want to paint using the toolbox metaphor, is that what goes into the toolbox is a theoretical matter, i.e., determined by what biological theory we think governs the use of 'species.' However, the ways in which the tools are used is a local one, varying from investigation to investigation.

5.2 Yeast Systematics

In this section I will examine how different species concepts are used to delineate novel species mainly within the large-spored clade of the *Metschnikowia* genus, but also in some related genera. This is not a well-known genus of yeast, apart from the fact that one species in this genus, *M. pulcherrima*, has been investigated for use in wine-making. Nonetheless, for our purposes, investigating the way systematists demarcate the boundaries between species in this genus will prove illuminating. Before I begin, I will motivate why focusing on such an area of systematics provides a worthwhile case study for species pluralism, rather than say looking at how the boundaries between the eleven species of the bird genus *Agelaius* were adjudicated.

First off, we are still finding new species in *Metschnikowia*. This means we don't have to worry too much about the reasons for pragmatism about the species category, which stem from revising pre-existing classifications that are used ubiquitously. When it comes to birds, most of the work on species has already been done, even during Mayr's original formation of the biological species concept in the 1940s, and of course many species still have the names given to them by Linnaeus well before our development of modern species concepts. This doesn't mean that there won't be any further disputes in these well-trodden areas. Consider for example Cracraft's (1992) analysis of the birds of paradise (Paradisaeidae). The point is just that we are at a stage with many macroscopic organisms where enough data has been collected so that we can be fairly sure about our classification schemes.

Second, the area of yeast systematics we are about to consider provides an interesting example for pluralism, because multiple species concepts are often used to delineate one species. This is important because species pluralists assume that each species concept, when appropriately applied, will yield only one species. That is, that there is still a one-to-one correspondence between successful applications of species concepts and species. However, this is not in keeping with an important way biologists use species concepts. Delineating new species is a complicated procedure. Though species concepts play a role,

species are not delineated through a straightforward application of a concept. Nor, as already noted, are some species concepts even straightforwardly applicable. How does someone actually apply the evolutionary species concept (see Chapter 1) or the general lineage conception of species (see Chapter 3)? Another problem is that systematists are rarely explicit about what their species concept(s) is (are), so we need to take any rational reconstruction, as always, with a grain of salt. However, there are many areas of systematics where multiple concepts are used in particular situations. Yeast systematics is not the only case out there.

We encounter a similar case with viruses. We have yet to discover all the viruses, or even have a good sense of how many are out there, and we have to use multiple species concepts in order to distinguish the real boundaries between species. The International Committee on Taxonomy of Viruses (ICTV) in 1991 accepted the following definition of viral species: “A virus species is a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche” (Van Regenmortel 1990). The ICTV also accepted the use of the usual categories of species, genus and family for viruses. The definition is important because: “The classification of viruses should not be confused with the classification of viral genome sequences. Viruses are biological entities and the notion of ecological niche is a crucial component for demarcating individual viral species” (Regenmortel, 1997, 18). Van Regenmortel stresses the fact that this definition emphasizes the “polythetic” nature of viral species. By using the term “polythetic” here, we have the acceptance that multiple species concepts will be used to recognize viruses. Viral species ought to be considered as explicitly polythetic because biological species concepts, ecological species concepts, and phylogenetic species concepts give us either clear-cut breeding discontinuities or boundaries in time that are impossible to demarcate.

A further case comes from considering how cultivable bacteria is classified. For this area of systematics, a phenotypic species concept has often been used, but given extensive studies of the family *Enterobacteriaceae*, a genetic species concept (based on DNA:DNA relatedness) has proved more useful for

defining the boundaries between different species. Part of this may be because many estimate that the number of species described so far represent only a tiny portion of what's still out there (Bull et al 1992; Embley & Stackebrandt 1997: Ch. 4). For cultivable bacteria, Goodfellow et al. (1997) suggest what they call a polyphasic species concept that makes integrated use of genotypic and phenotypic characters. To this end they consider examples of organisms of medical and industrial importance. They claim that given the small size, asexual reproduction, and lack of knowledge on the genetics of bacterial populations (and Archaea), we should adopt a more pragmatic approach to a bacterial species concept. They argue that: "It is the pattern of distinctive properties shown by bacteria not the process which gave rise to them which is currently seen to be paramount in bacterial systematics" (Goodfellow et al., 1997, 26). That is, we have good reason to use a non-causal species concept for classifying bacterial species.

Which species concepts will be relevant for the yeast systematist? In some cases a biological species concept (BSC) is not relevant because there are asexual forms of yeast, e.g., *Kodamaea transpacificca* (Lachance et al., 2012; Freitas et al., 2013; Groenewald and Smith, 2013). But the BSC can be relevant because, though strains of yeast are often haploid (they have one set of chromosomes), they can be heterothallic (they have sexes that reside in different individuals), so species ought to be delineated on the basis of reproductive discontinuity (Lachance and Fedor, 2014, 541). But in practice species assignment can be based on the **BSC** and DNA sequencing (Lachance and Fedor, 2014, 542), which reflects the use of a different concept, a genetic species concept (GSC), that marks out species on the basis of an empirically determined degree of genetic difference. When it comes to DNA sequencing, it depends how the sequences are analyzed. A **GSC** would be used if one is taking into consideration the proportion of divergent nucleotides, but a **PSC** would be used if one used the tree inferred from the sequences. This, I take to be a limited form of classificatory consilience. Often mating success is determined by the sort of spores produced, or even the presence or absence of spores, which can be interpreted as a morphological species concept (MSC) tailored

to a particular group, but also as a phylogenetic species concept (PSC) based on synapomorphies (shared derived traits). However, there is a very limited sense of spore morphology being used more in tandem with the **BSC**, that is, to show whether or not some individuals share a common gene pool. Spore morphology is more useful for delineating yeast genera and higher taxa. With yeast there can also be quite a bit of interspecific mating that can lead to introgression (the introduction of genes from one species into the gene pool of another species), and this can obscure how we interpret genetic information. Thus, an ecological species concept (ESC) is also relevant, because, for example, the different sorts of flowers or beetles is important for distinguishing it from other strains. And further, despite those that invoke the ‘Everything is Everywhere’ model of microbial dispersal, there are plenty of cases to be made for strong endemism (e.g., in the genera *Kodamaea*, *Metschnikowia*, and *Wickerhamiella*). Yeast systematists working in this area have a sophisticated understanding both of the limitations of these concepts for delineating new species, and of the ways that these concepts can supplement one another. This sophistication needs to be accounted for if pluralism is to make sense of how ‘species’ is used in biology. In the remainder of this section I will go into more detail, and consider some examples of the way these different species concepts are used to delineate new species of yeast.

5.2.1 The Morphological Species Concept

Consider how a morphological species concept (**MSC**) is used by yeast systematists. According to a **MSC**, we are basically trying to capture the different ways things look. Upon close inspection, if two groups of organisms look different enough, they belong to different species. Consider the following dated, but still relevant characterization of the **MSC**:

(MSC) The Morphological Species Concept: “Species may be defined as the easily recognized kinds of organisms, and in the case of macroscopic plants and animals their recognition should rest on simple gross observation such as any intelligent person can make

with the aid only, let us say, of a good hand-lens” (Shull, 1923, 221).

In the case of the yeast systematist, a good phase-contrast microscope will have to substitute for a good hand-lens. Unfortunately, merely looking through a microscope is not much help when it comes to yeast. As a general rule of thumb, morphology may help distinguish different genera, but is not much good at the species level. Like many uses of the **MSC** it also depends upon which portion of the life-cycle we are looking at. For example, characteristic asci (the sexual spore-bearing cell produced in ascomycete fungi) and ascospores helped place *M. cubensis* in its genus (Fidalgo-Jiménez et al., 2008). Lachance et al. (2005), however, describe three new species of yeast in the large-spored *Metschnikowia* clade. According to an **MSC** these three species (*M. hamakuensis* sp. nov., *M. kamakouana* sp. nov. and *M. mawinuiana* sp. nov.) are similar to another, already described species, *M. hawaiiensis*, but according to other species concepts they should not be lumped together. We should note that there isn’t always one morpho-type associated with a species. For example, *M. drakensbergensis* sp. nov. is noted to be polymorphic according to some growth tests results, often termed “phenotype,” though phenotypic polymorphism can sometimes correspond to a genetic polymorphism (de Vega et al., 2014).

From this preliminary analysis, a **MSC** is useful to a yeast systematist, but not very. Like in many areas of systematics, the **MSC** is used in the beginning stages of analysis, α -taxonomy or the discovery stage. For this area of biodiversity, this concept would pick out groups that are too big, and would underestimate biodiversity by an order of magnitude.

An extra-evolutionary species pluralist might wish to hold that such morphological distinctions between microbial species are important in their own right, even if they fail to track the true evolutionary origins of each species. A **MSC** might be put to the use of bridging the gap between the important groups that extra-evolutionary species pluralists argue that we should be in the business of classifying. How this would work however is unclear, but the point is that if we need a separate non-evolutionary classification involving

non-evolutionary species concepts as Dupré and Kitcher have suggested, then the **MSC** might be useful in integrating this sort of classificatory scheme with an evolutionary classification scheme.

5.2.2 The Ecological Species Concept

Let's consider how an ecological species concept (**EcSC**) is used by a yeast systematist. The classic definition of the **EcSC** characterizes species as follows

(EcSC) A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range (Van Valen, 1976, 233).

According to this concept, a species is a lineage of organisms that share a distinct ecological niche. The **EcSC** often cross-classifies with the **BSC** as is evident from its initial formulation involving the study of North American oaks (*Quercus*).

How would one apply such a species concept to yeast and other microorganisms? Some hold a cosmopolitan view of microbial ecology: the view that everything is everywhere (Fenchel and Finlay, 2004). However, typically species in the *Metschnikowia* clade are found on islands though not always. For example, what has now been delineated as *M. (Candida) ipomoeae* is unusual in its ecology in that it ranges across the hemispheres, i.e., from Brazil to Tennessee, and occurs mostly in the asexual state (Wardlaw et al. 2009). Depending on the larger group we are investigating, geographic distribution can be quite important, and might tell us something about the particular local ecological niche a yeast occupies. Currently, we do not know much about the relationship *Metschnikowia* species have with their vector organisms, the beetles (and other floricolous insects) they are found on. However, one important case to consider is that *M. locheadii* and *M. hawaiiensis* co-exist in the same locality, and even on the same flowers, but are found in different beetle species (Lachance et al., 2003). Thus, it seems worth pursuing the relationship further between the yeast and their vector beetles.

Before closing the section on ecology, it's worth considering how Dupré's in principle argument for extra-evolutionary species pluralism may apply here. Recall that this argument involves divorcing the use of 'species' from its role in evolution, to focus on its role as a unit of classification (which of course reflects its historical use). Dupré argues that ecology may in principle have recourse to finer grained classifications of organisms. Is there anything like a trend here in yeast systematics? Though making an argument for a trend would require a much broader survey, I want to briefly consider what ecological concepts that survey might encompass.

Consider for example the ecological distinction between what are called generalist and specialist yeast. A generalist yeast has the ability to utilize diverse carbon compounds and due to this they can survive and grow in different environments. Specialist yeasts have a simple physiologic profile and obtain energy solely from few carbon compounds and this limitation restricts their habitat amplitude (Pimenta et al., 2009, 206-207). Some other examples of important ecological distinctions are that between cosmopolitan/endemic, fundamental/realized niche, and commensal/pathogenic. Translating Dupré's idea here would involve the creation of a potential taxonomy of yeast that factors in these distinctions.

First, it is not clear how much finer-grained a taxonomy we could develop on the basis of such distinctions. At best these concepts are often relative to various scales of inquiry, from the local population in a pond, to a group of organisms spread across an entire continent. Some of the distinctions will also tend to grade in to one another, though this may be no more problematic than the ways different evolutionary species concepts allow for gradation between species. However, it is of a different sort of gradation, there is not necessarily a historical explanation for some of these distinctions. For example, the fact that a yeast is cosmopolitan will not tell you much about its phylogeny. In fact, the knowledge that a yeast is cosmopolitan rests on the knowledge of phylogeny. Though, if a yeast is known to belong to a particular clade, it might be reasonable to guess at whether or not it is endemic.

Second, if the extra-evolutionary species pluralists are right, then this separate taxonomy must be explanatorily distinct from evolutionary accounts of species. Neither approach is explanatorily fundamental. However, I take it that this doesn't mean that there wouldn't be something informative to be gained from comparing and understanding the relationships between these two radically different classification schemes. Knowing which clades evolved which ecological traits, and how such ecological traits affect evolution are important avenues of research.

5.2.3 The Biological Species Concept

Let's consider how a biological species concept (**BSC**) is used by yeast systematists. According to a **BSC**, the boundaries between species are determined by an array of mechanisms that allow genes to circulate among members of the same species, and a further set of mechanisms that keep a species' gene pool isolated from those of other species in same environment. An often cited definition of the BSC is as follows:

(BSC) **The Biological Species Concept**: “species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups” (Mayr, 1942, 120)²

According to the **BSC** gene flow, the transfer of alleles or genes from one population to another, keeps species together, and reproductive isolating mechanisms³ restrict gene flow and keep species apart.⁴ The **BSC**, thus puts a great deal of emphasis on sexual reproduction. So how does this work for yeast?

²Mayr offers this definition after quoting an earlier definition he gives “A species consists of groups of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade or interbreed wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers” (1940, 256).

³Mayr (1942, 247-248) gives a taxonomy of four sorts of isolating mechanisms: ecological, ethological, mechanical, and genetic or physiological.

⁴See Beurton (1995) for some potential concerns with the standard way of understanding gene flow associated with the **BSC**.

Yeast come in sexual and asexual forms, so in order for a taxonomist to make use of a **BSC**, they need to consider yeast that take sexual forms. In practice this means that they need to first be able to isolate both mating types. If both mating types are not isolated, this can lead to an erroneous classification, because another sort of conception of species will be used in this case. For example, de Oliveira Santos et al. (2015) discovered the second mating type of what was once referred to as *Candida ipomoeae*, and so renamed it *Metschnikowia ipomoeae*, thus classifying it in an entirely different genus. This species was initially classified as *C. ipomoeae*, because it was thought to be asexual. Thus, the good thing with the **BSC** is that it can pick up where the **MSC** left off, moving from something like α - to β -taxonomy. For example, the same three *Metschnikowia* species deemed conspecific with *M. hawaiiensis* according to the **MSC**, were shown to be distinct species as based on **BSC**, that is, according to mating compatibility and ascospore formation (Lachance et al., 2005). Asexual reproduction occurs in yeasts by budding, by fission, and by the production of conidia on short stalks called sterigmata (Yarrow, 1998, 80). Mating experiments involve the mixture in pairs of active cultures, often including authentic strains of previously described, and tested species. These mixtures are examined periodically for zygote, asci, or ascospore formation. Lachance et al. (2005) assigned strains to the same species only when compatible crosses gave rise to the formation of abundant asci that contained pairs of ascospores after 3 days at 18°C. The groups classified as *M. hamakouensis*, *M. kamakouana*, *M. mauinuiana*, and *M. hawaiiensis* failed to mate with each other, and were thus classified as separate species (Lachance et al., 2005). Mating experiments are not always conclusive and need to be supplemented “Any questionable identification was verified by rDNA sequencing and then reconfirmed by mating” (Lachance et al., 2005, 1370). Thus, some yeast taxonomists don’t just make use of the **BSC**, and **MSC**, they also use a genetic species concept.

5.2.4 The Genetic Species Concept

Let's consider how a genetic species concept **GSC** is used by a yeast-systematist. This is loosely speaking a geneticist's equivalent to the **PhSC**. According to a **GSC**, individuals with different genetic material are different species. The boundaries between species are thus set by a degree of genetic difference, which can vary from species to species. Typically, researchers focus on specific regions of genetic data that they find to be more indicative of species boundaries, though there is nothing but practical constraints limiting the sequencing of entire genomes.

When yeast systematists apply something like a **GSC** they have tended to focus on the number of substitutions in the D1/D2 variable domains of the large subunit rDNA (roughly 600 bases in size) to yield species boundaries (Kurtzman and Robnett, 1998). According to this version of the **GSC**, conspecific strains are separated by less than 1% nucleotide substitutions, but different species are separated by more than 1%. However, this generalization concerning the degree of genetic difference required for distinct species is often supplemented by considering differences between other genetic material, clade structure, or mating experiments. This measure of genetic difference is also used as a way of telling when two different isolates are of the same species, and can also tell us how polytypic, genetically speaking, a species is, relevant to other related species.

For example, Lachance et al. (2005, 1374-1375) found this to correspond to their own argument for the species delineation of three new large-spored *Metschnikowia* species. However, there was one exception, the sequence-based separation of *M. hamakuensis* from *M. hawaiiensis* differed by only one substitution and one gap in the D1/D2 region, though their ITS1 regions differed by 5 substitutions and 3 gaps. There was a polymorphism for *M. hamakuensis* in the ITS1 region: one strain differed from others by two substitutions and a five-position gap. When it came to *M. mauiensis* and *M. hawaiiensis* they were found to differ by 5 substitutions and 2 gaps in the D1/D2 region, but there was only one gap in their ITS regions. Another use of a **GSC** is as a supplement to mating experiments: "Any questionable identification was veri-

fied by rDNA sequencing and then reconfirmed by mating” (2005, 1370). This is a clear case of two species concepts being used together to do the same job.

The **GSC** is important, but we should be clear that it’s not blind allegiance to a fixed degree of genetic difference that allows these systematists to delineate a new species. Genetic difference should be considered in relation to the factors picked out by other species concepts.

5.2.5 The Phylogenetic Species Concept

Consider how a phylogenetic species concept **PSC** is used to determine the boundaries of yeast species. According to one version of this concept species should form monophyletic groups. This of course only works for currently existing species that have not themselves speciated. Organisms that belong to ancestral populations would not belong to any species, making this concept entirely useless for paleontology. Unfortunately, there is no yeast paleontology.

Let’s consider how the **PSC** and **GSC** can work together. At the level of genera, clade structure is important, as is noted by the reference to part of the *Metschnikowia* genus as the large-spored *Metschnikowia* clade (a group of organisms that consists of a common ancestor and all its lineal descendants, those things with large-spores). Now, recall again that many yeast species descriptions are based on generalizations made by Kurtzman and Robnett (1998). According to their generalizations, the D1/D2 domains of the large subunit rRNA gene normally exhibit a polymorphism of three or fewer substitutions, and good species differ by 1% or more substitutions. This is the degree of genetic difference used when applying a **GSC** to yeast. Thus, based strictly on this, there would only be marginal support for making these isolates distinct from *M. locheadii*. Generalizing from this, de Oliveira Santos et al. claim that: “Although sequence divergence can inform species delineation, phylogenetic relatedness is measured not in units of sequence distance, but rather in terms of clade structure” (2015). Figuring out clade structure involves considering the different possible cladograms, which represent the different possible past histories for some group of organisms, and checking for monophyletic groups.

Given their analysis, they found that we would get monophyletic groups taking either of the isolates by themselves, both of them together, and with both of them and *M. locheadii*. This sort of structure is seen as a requirement for species membership (de Oliveira Santos et al., 2015).

But, *M. bowlesiae* is possibly an intermediate stage in a succession of peripatric speciation events between *M. dekortorum* and *M. similis*, and may even hybridize with these two separate species (Lachance and Fedor, 2014). This is an important case: “In spite of the systematist’s common aversion for paraphyletic taxa, during early stages of peripatric speciation, the stem ancestral (stem) (sic) species is bound to remain paraphyletic with respect to the new, emerging species. The present case is to our knowledge the first suggestion in yeasts of such a three-species succession” (Lachance and Fedor, 2014, 545). In this case, descent and reproductive isolation are telling us different stories. Though these systematists have chosen to pick what they believe to be the best, a pluralist perspective would allow one to pick both in this instance.

5.3 Whither Consilience?

What are we to make of the ways which the yeast systematists we surveyed above use species concepts? In this section I will consider whether or not the way species concepts are used in practice provides evidence for monism. Many have suggested there is something like ‘consilience’ occurring in the way different species concepts are used. Consilience in general means reaching the same conclusion by different approaches. By consilience here I mean the basic idea that as we refine our understanding of species concepts further and further, we see that they are approaching the same classificatory goals from different angles. This consilience has been taken as evidence for monism, but as we will see, this need not be the case.

In this section I examine Ruse’s (1987) argument for classificatory consilience, and Richard’s (2010) argument theoretical consilience, and consider Ereshefsky’s (2014a) criticisms of both arguments. I want to show that despite the soundness of his criticisms, there still is something to the notion of con-

silience worth adding to our pluralist toolkit. Generally speaking, consilience between different ways of classifying species has been used as a reason for an *in principle*, rather than an *actual* monism. Even though things look grim now, a small minority of thinkers believe that the different species concepts will eventually pick out exactly the same groups.⁵ Conceptual pluralism will one day resolve itself into conceptual monism. One would think that if this is the case, then we should see some signs that we are working towards this brighter monistic future. Thus, pluralists have responded by denying that the trend is real, pointing out both the legitimacy of different species concepts, and the fact that different species concepts often pick out overlapping groups, that is, they cross-classify, and further, that as we investigate more and more, this cross-classification will be seen as ever more widespread. In response to this, monists have either sought consilience at some other level, or have stuck to their guns and have used cross-classification as a reason why competing concepts are illegitimate.

Ruse has been the biggest advocate of what Ereshefsky refers to as classificatory consilience: “There are different ways of breaking organisms into groups, and they coincide! The genetic species is the morphological species is the reproductively isolated species is the group with common ancestors” (1987, 238). According to him, consilience is a mark of reality. Thus, if we have multiple species concepts picking out the same taxa by way of different biological properties, then we have good reason to believe that those are real species. Ruse believes that eventually the different classifications of species according to different species concepts will coincide. They will pick out the same groups, but by different means. Ruse’s suggestion has been dismissed by many because it is simply not the case that the different species concepts he discusses are leading us to the very same classification of organisms. However, as critics fail to make explicit, this doesn’t mean that there is absolutely no relationship between the different ways of breaking organisms into groups. Even

⁵Most biologists are certainly aware that biology is the science of exceptions to the rule. With this in mind, when someone has obtained exactly the same results from different approaches might be best interpreted as a sign that some of the data has been made up.

though they do cross-classify, they also can often classify in compatible ways, as we have seen in our discussion of the large-spored *Metschnikowia* clade.

Richards (2010) has argued that there is a different sort of consilience that pertains to species, what Ereshefsky dubs theoretical consilience. His approach is developed as an interpretation of the hierarchical approaches to species concepts offered by de Queiroz (1998; 1999; 2005a; 2005c; 2007) and Mayden (1997; 1999). As we have seen in Chapter 2, these sorts of approaches end up reducing species concepts to some version of an evolutionary species concept, which, as Richards notes, coheres well with accepting **SAI** as our ontological framework. On this approach the evolutionary species concept lies at a higher theoretical level in our conceptual framework, while the various other species concepts are accepted as mere operational variants of it. As argued for in Chapter 2, this view ends up being a form of quasi-evolutionary species pluralism, since these hierarchical approaches choose what I call a minimalist solution to the species category problem. Due to the focus on that problem the view suffers, because advocates of the hierarchical approach are unclear or silent about whether or not the different subordinate, operational species concepts cross-classify one another. Both de Queiroz and Mayden focus on solving the species category problem to the detriment of determining the relationship between the different “operational concepts.” On Richards’ account, though, consilience comes not from the different species concepts aligning (or at least some day aligning), but from considering the history of systematics, and how over time biologists have generally restricted species to lineages. That is, numerical taxonomy and the phenetic species concept have gradually moved out of the picture. This is of course something an evolutionary species pluralist can accept, but not an extra-evolutionary species pluralist. To put the point another way, the extra-evolutionary species pluralist is denying the reduction to, or the fundamentality of the evolutionary species concept.

Ereshefsky (2001; 2014a), however argues against understanding what is happening in these hierarchical approaches to species concepts as a form of consilience. We cannot re-frame some species concepts as simply operational, for they all contain a theoretical component: “Biologists do not think that

all genealogical lineages are species; they hold that species are a particular type of genealogical lineage. Moreover, they disagree on which type of lineage constitutes a species. Consequently, there is no theoretical consilience concerning ‘species’ ” (2014a, 78). The distinction between a theoretical and an operational concept is not illegitimate, though concepts like the evolutionary species concept still have no obvious operational consequences. This, again, is the exact same criticism he has levied against de Queiroz’s general lineage conception of species (Chapter 2). This is an important criticism of such views. However, if we abstract from this sort of disagreement, which is one over how to define the species category, we see that there is much in common between Ereshefsky, Richards, de Queiroz and Mayden. All are (quasi-)evolutionary species pluralists who recognize roughly the same sorts of species concepts, and restrict species to lineages (even though, as Ereshefsky is clear to point out, not all lineages are species). Thus, the disagreement is about two things. First, how are we to accommodate the cross-classification that often occurs between different lineage based species concepts? This is something de Queiroz and Mayden both fail to give a clear answer to. Second, what is the nature of the genealogical restriction? Following updated cladistic terminology, there are two sorts of continuous genealogical entities that may or may not fit the bill as species: monophyletic and paraphyletic groups. Even if there is some agreement that species are genealogical entities, we need to know more about their status.

However, if the extra-evolutionary species pluralists are right about the state of biology, then Richards is just plain wrong. That is, his argument for theoretical consilience presupposes some sort of conceptual unification within biology, but according to extra-evolutionary species pluralism, this conceptual unification is missing. From this perspective, there is more to biology than just evolution, and considering species as genealogical units. Unfortunately for our purposes, seeing how this form of pluralism can make sense of the work of practicing yeast taxonomists is difficult. Extra-evolutionary species pluralism stands or falls mainly with *in principle* arguments that are grounded in the explanatory demands of other areas of biology. Most practicing biologists

use species concepts that are grounded in some interpretation of species as evolutionary units, though they often use non-evolutionary species concepts in a more secondary fashion. Although there are often no explicit consequences drawn from arguments for extra-evolutionary species pluralism, it is through the use of these sorts of species concepts that there may be a place for this form of pluralism in contemporary biological practice.

Now, despite the problems with these forms of consilience, there is something to seeking points of agreement between competing species concepts that is readily seen from an examination of the way species concepts are used by systematists. This is what we might call local classificatory consilience, as distinct from Ruse's global classificatory consilience. The global view is that the different species concepts (will someday) line up and give us the same global classification scheme: there is one true Tree of Life waiting out there for us to discover. Unfortunately, as many have pointed out, this doesn't seem to be the case, nor does it seem like it might become the case, on account of the fact that there is just too much cross-classification between competing species concepts. As opposed to this global view about where things are headed, the local view comes from focusing on the significance of the cases where species concepts line-up. In the next section I will show that local classificatory consilience is a more profitable understanding of biological practice.

5.3.1 The Toolbox View of Species

Species delineation is not a simple application of species concepts to a data set. Many species concepts are used to varying degrees and in different capacities, and the multifaceted inferences drawn from these uses are supported by the complex relationships between the applications of these concepts.

If species concepts are tools, which of these tools are required for delineating new species of yeast? As we have seen above, sometimes different species concepts pick out the same groups, and sometimes they do not. First, what is the status of the morphological species concept (MSC)? The **MSC** is a way of distinguishing between organisms based on their different phenotypic

forms. The **MSC** is not very useful in making a final distinction between different species of yeast, because many “species” according to other species concepts of yeast look the same. However, this concept is useful to begin an initial investigation. It says something about relatedness, and we can use this information to narrow down what a species is by looking at other factors. However, to a certain extent, we need to study morphological features in a very limited sense (e.g., the presence or absence of spores) to know whether a mating experiment is successful.

Second, what about the ecological species concept **ESC**? The **ESC** distinguishes species on the basis of their status as a lineage occupying an ecological niche different from any other lineage in its range and evolving separately from others outside its range. In this particular area of yeast systematics (the large-spored *Metschnikowia* clade), the **ESC** is far more informative than the **MSC**. Focusing more on this concept may involve uncovering more about the relationship between different yeast species and their vector insects. Ecology is also important at a higher level, but in many ways the biogeography of endemic yeast is something we work towards by looking at a number of different factors that are tied to other species concepts.

Third, let’s consider the **BSC**. The **BSC** is a concept that distinguishes species on the basis of their status as reproductively isolated populations. For yeast systematics, this concept proves to be an interesting limit case. This concept is useless for asexual forms of yeast. The **BSC** is very useful for sexual yeast, but even there it is not always the most important, or relevant species concept. This is shown by how it is often supplemented by a genetic species concept, given that many asexual forms of yeast are delineated by a certain degree of genetic difference from related sexual and asexual groups of yeast.

Fourth, what about the genetic species concept **GSC**, which differentiates species on the basis of their genetic material? For yeast systematists, the **GSC** as applied to the D1/D2 region is a very useful surrogate for delineating species, but this method is not foolproof. This is shown by how it can be supplemented by BSC, or by a different degree of genetic difference.

Fifth, let's review the phylogenetic species concept (**PSC**). The **PSC** is useful, but is best seen as a supplement to the **BSC** and **GSC**. Though many evolutionary trees are given, these are not the ultimate arbiters of what is and what is not a species. Phylogeny is much more important at higher levels of organization, when we compare the relationships between the species already delineated by way of other concepts. This though in turn may have effects on the way those concepts are applied in the future, especially when a relationship between phylogeny and geography is established.

This review of how species concepts are applied in yeast systematics is not meant to be the final word, and of course focuses largely on the large-spored *Metschnikowia* clade. Things of course may change somewhat as more and more yeast species are discovered and methods change, but given the way current practice is going, how other related areas of systematics are going, it seems likely that multiple species concepts will continue to be required to judge the boundaries between species. These concepts come apart in many instances, and this is well known by biologists, but still some yeast systematists often argue that they have made a delineation on the basis of cases where multiple species concepts align. How can current versions of species pluralism account for this sort of local classificatory consilience? What does a pluralist say about situations where lineage concepts like the **BSC**, **ESC**, and **PSC** align?

Before we answer these questions, there are two caveats we need to address from the basis of each major form of species pluralism. First, as we have seen in previous chapters, an evolutionary species pluralist might wish to rule out the **MSC** and **GSC** as non-evolutionary species concepts. These concepts are both 'typological' in the Mayrian sense. Someone who applies these concepts is searching for discrete patterns of morphology or discrete clusters of genetic information, and using these in the absence of any notion of an evolutionary lineage. Thus, these two concepts simply wouldn't be considered as proper tools for making decisions about what is and what is not a species. However, ruling them out this way doesn't explain their continued use.

Second, a general problem with trying to see how extra-evolutionary species pluralism would fit into practice, is that none of the candidate species concepts

proposed by Kitcher or Dupré that fall on the extra side of the pluralism are actually used by practicing biologists. This is because, especially for Dupré's pluralism, these concepts are best interpreted as in principle additions to the already existing array of species concepts. But these additions are importantly different in that they don't pertain to an evolutionary understanding of species. I have here and there given some thoughts about how this sort of pluralism might be put into practice, but this form of pluralism remains under-explored. Concepts like the **MSC** and **GSC**, while used in connection with evolutionarily informed species concepts, may also be, in principle, used in connection with concepts informed by an understanding of structural, or perhaps ecological space.

Despite these two caveats, pluralists need to explain why biologists continually look for consilience between different species concepts. They don't always find consilience, as we saw with *M. dektorum*, but using multiple species concepts is part of a good general strategy for delineating new species. As this case study has shown, a pluralist simply cannot relegate only one species concept per some particular area of taxonomy, for example, using the **BSC** for sexually reproducing species, and something else for asexual organisms. There are many areas of taxonomy where one concept is not enough. Investigators working on the large-spored *Metschnikowia* clade provide a good example of this. Pluralism can help here by giving us further options when local classificatory consilience is not found. However, biological practice is also partly limited by some pragmatic constraints, which I will now turn to.

Perhaps the yeast systematists we've surveyed are looking to avoid instability in their classifications, rather than actively seeking out consilience. This is an important objection to consider, because systematists often are explicit in following prudence and erring on the side of what they have grounds to perceive as the more stable classification. Thus, one might argue that using multiple species concepts to make a delineation can be viewed as a forward-thinking pragmatic decision that biologists make, which is independent of pluralism or monism. Given uncertainty about the state of biology, having more than one way of justifying the delineation of a new species means that when we do

settle on a classification, it will be more likely to remain stable, even if say, some of the species concepts used in a particular area fall out of favour. This connects with similar motivations that lead many to pragmatism about the species category, which is the idea that we should accept pluralism, but still retain more or less the traditional divisions of organisms into species because revising them would be too costly (see Chapter 3).

A further case can be made for a pragmatic classification scheme of yeast on the basis of estimates about how many species remain to be discovered. Most research estimates this number as quite high in comparison with those we have discovered (cf. Lachance, 2006). The reverse would be the case for birds. A classification based on the use of the **PSC**, or cladistic methods more generally, is more stable, the more taxa are analyzed and compared. This is akin to Hennig's (1966) notion of 'reciprocal illumination.' For this reason, as more yeasts are discovered this might change the stability level of the larger classification.

Another way of considering this objection is to think that perhaps "the yeast species concept," if there truly is such a thing, is in a transitional phase, as some have argued of fungi more generally (Brasier, 1997). One, final quasi-disjunctive species concept for all yeast is on the way! This might suggest that we could have a classificatory consilience for all yeast, somewhere in between my local and Ruse's global classificatory consilience. That is, it could be the case that Ruse is wrong about all uses of species concepts, but he would be right about the way species concepts are used in certain areas of classification.

In response to these pragmatic worries, let's first note that there is nothing wrong with interpreting biological practice as both aiming at avoiding instability and at a certain kind of consilience. There is nothing obviously incompatible about these two aims, in fact, they complement one another. However, interpreting current practice as transitional, and in search of a monistic, or quasi-disjunctive yeast species concept is not warranted. This interpretation of current practice is problematic for several reasons. First of all, in the face of all the work that species pluralists have done, it suggests that there is a such thing as a single optimal species concept, though just one for yeast, as

opposed to other areas of the Tree or Web of Life. Given that there is no global consensus in nature or theory about what a species is, there is no reason to think that there would be a consensus just for yeast. If it's messy globally, then there is reason to believe that it would be messy locally. Further, as the case study shows, it is in fact somewhat messy in the case of the large-spored *Metschnikowia* clade (and this probably the least messy clade among all ascomycetous yeasts). Second, this is the wrong way to think of species concepts. In many ways it is arbitrary where yeast is divided off from fungi, plants from animals, etc. Thus, there is no reason to expect that since we have delineated higher taxa, there will then be one set of criteria for differentiating species beneath them. Note for example the difference between how species concepts are applied for *Candida* and *Metschnikowia*. In addition to this point about the vagueness of biological domains, this is not the concern of species concepts, but what kingdom concepts, phyla concepts, etc., are about. Species concepts are attempts at demarcating the species from subspecific taxa, and superspecific taxa in general, not in particular cases. Species pluralism is thus a claim at *this* global level: for all of systematic biology, though whether or not every organism belongs to a species is a slightly different issue. Thus, for species pluralists, species concepts should be thought of as tools so that they can be as widely used as possible, across many different types of genera, phyla, and so on, but then only possibly restricted by the local demands of a particular genus, clade, and so on.

One last concern about how species pluralism is applied in practice concerns the relationship between pluralism and relativism. As argued for in earlier chapters, distinguishing pluralism from monism has led us to discuss the conceptual issues that surround the species category problem. However, distinguishing pluralism from relativism, will allow us to ask questions about which sorts of concepts are admissible and how they interact with one another, that is, how they cross-classify one another and the world. What is clear from this case is that there is another layer of interaction between concepts that comes from practice. Focusing on this layer adds a further dimension to the distinction between relativism and pluralism. As is clear from this case, the

use of different species concepts is highly context-dependent. However, this does not mean that species concept use is arbitrary. The choice of a species concept depends on the case at hand, and the territory already mapped out. Further, how species concepts are used cannot simply be determined in a top-down fashion, e.g., by reading off which species concepts are legitimate by the lights of evolutionary theory.

5.4 Conclusion

As we have seen in this Chapter, there is more to species pluralism than just making it suitable for biological theory. Pluralists need to account for the way species concepts are used in practice. The suggestions offered hitherto fail to account for the sophisticated way that researchers often use different species concepts together. This doesn't mean that there is any global concilience happening amongst our theoretical tools, i.e., that these tools will in the end delineate the same species. The lesson pluralism tells us is to mitigate our search for agreement among species concepts, and to pause when species concepts lead to conflicting classifications. Even if the world is the way pluralists think it is, we do not need to use whatever species concepts we allow for independently of one another. There are important lessons to learn from using them together. What remains to be done in future work is to determine in more detail the ways in which species concepts interact. It is clear from this case study that there is a certain degree of going back and forth between different concepts, for example between the **MSC** and **BSC**. However, determining how species concepts interact in global terms is a much more sophisticated task. One could of course continue the piece-meal approach taken here, but a rigorous survey of taxonomic guidelines and practice are called for.

General Conclusion

The purpose of this dissertation was to provide a multidimensional analysis of species pluralism along historical, conceptual, ontological, and practical lines. The ultimate goal of the dissertation that species pluralism is a view not just about the species category and the ontological status of species, but also a debate about which species concepts are admissible, and where and how different species concepts are to be legitimately applied. I ultimately argue that species pluralism can be further distinguished by determining what degree of interaction may occur between different species concepts for a particular case.

In Chapter 2 I examined the relationship between species pluralism and the history of systematics by drawing connections to two interrelated cases: the relationship between the essentialism story, and the study of Aristotle's theory of classification. I raised four points of comparison: (1) the explanatory power of taxonomic ranks, (2) the importance of the species category problem, (3) the question of intrinsicism, and (4) how to interpret the "cross-cutting" metaphor endemic to the pluralist literature. The purpose of this chapter was to provide a foil for comparing the different pluralist solutions to the species category problem and the species taxon problem.

In Chapter 3 I took a critical stance to what pluralism implies about the species category problem: eliminativism, disjunctivism, minimalism, and pragmatism, by showing that there is not a great deal at stake between many of these views. However, in Chapter 5 I argued against a form of eliminativism. My purpose in Chapter 2 is to show that pluralism is more than a definitional problem. One further distinction we need to make is between evolutionary and extra-evolutionary species pluralism. These aren't strictly defined views, because there are different forms of these two different kinds of species pluralism. In order to distinguish between them even further, we need to ask two questions. First, which concepts, and on what basis, does each form of species pluralism allow for? Second, how do the admissible concepts (cross-)cut up the biological world? These questions are separate from what pluralism entails about the species category, and they are separate from each other, be-

cause we can allow for multiple species concepts, but not allow for any sort of cross-classification. I argued that failure to give explicit answers to these two questions blurs important distinctions between different forms of species pluralism.

In Chapter 4 I examined the relationship between species pluralism and the species taxon problem. Adopting species pluralism does not resolve the debate, but given that pluralism doesn't tell us that *one* species concept is correct (it tells us that *some* are) this isn't surprising. In similar fashion, some ontological frameworks may be suitable from a pluralist perspective. This is not uninformative, because monism tells us absolutely nothing about what species are, simply that we need to seek a unified concept and ontological framework for species. Species pluralism, on the other hand, is compatible with multiple species concepts, but in order to be distinct from relativism, pluralism must be tied to biological theory. It is this tie to theory that is important. I showed that extra-evolutionary species pluralism fits with ontological frameworks that can capture both 'intrinsic' and historical properties, and that evolutionary species pluralism minimally requires an ontological framework that captures historical properties.

In Chapter 5 I argued that pluralists need to account for the way species concepts are used in practice. Pluralism needs to be developed to account for the sophisticated way that researchers often use different species concepts together. This doesn't mean that there is any global consilience happening amongst our theoretical tools, i.e., that these tools will in the end delineate the same species. The general lesson pluralism tells us is to mitigate our search for agreement among species concepts, and to pause when species concepts lead to conflicting classifications. Even if the world is the way pluralists think it is, we do not need to use whatever species concepts we allow for independently of one another. There are important lessons to learn from using them together. What remains to be done in future work is to determine in more detail the ways in which species concepts interact. The case study I provided and analyzed on the *Metschnikowia* genus is only one area of systematics, and one way species concepts are used together to delineate species, though it is an important area

to show that pluralists need to account for interaction between concepts.

To some, pluralism seems like giving up, for it seems as if our scientific practice and theories have become so garbled that we finally throw our hands up and blame the world for what might be our own conceptual confusions. But to a pluralist it is even more puzzling to look back on history. Why did we never question these monistic assumptions, that there should be one single definition of species, before? This is just as puzzling as the fact that the Earth's immovability wasn't questioned, that the fixity of species wasn't questioned. However, only once we truly ask a question for ourselves can we begin to see the earlier questioners: Aristarchus, Empedocles, and oddly enough in this case Aristotle. Tracing the development of species pluralism in our era has an impact on how we look at the past. Just as post-Linnaeans attempted to force a taxonomic understanding of *genos* and *eidos* on Aristotle, so too have we forced a monistic understanding of classification on him.

Looking at the history of systematics with pluralism in mind can help shed light on what it is that different pluralists are attempting to achieve today. It is not a simple matter of giving up. Sorting through the many operational and theoretical challenges that a systematic understanding of life presents us with from a pluralistic perspective is an important task. Accepting pluralism doesn't mean that anything goes, it just means that the world is a much messier place than we assumed it to be. It is naive to think that 'species' can have a simple, unified and workable definition, just as it is for many important theoretical concepts in many different fields. This doesn't mean that our work is merely to identify and eliminate these concepts from our theoretical and practical discourse, for in this too there is a trace of unwarranted monistic assumptions. There is no need to break down 'species,' or any other pluralistic concept into a fixed hierarchy of sub-concepts, for this will not help us use these concepts to do the work we need to do. We must strive to be more sophisticated in our understanding of key concepts in the sciences, as sophisticated as those who apply the concepts are themselves on a daily basis.

From a philosophical perspective this means that simple-minded arguments about how concepts are used won't be nearly enough to determine a workable

ontology for practicing pluralists. We need to consider not only the theoretical state of a discipline, but also the sophisticated ways researchers understand and apply concepts in different situations before we can draw conclusions about ontology. Philosophical arguments play a role, but these arguments aren't separable from what biologists themselves do. If anything this thesis has showcased the philosophical acumen of the biological field.

However, it is also clear that scientists and philosophers both have been drawn to unwarranted monistic assumptions. It is only through working on the philosophical problems and implications that surround pluralism that we can begin to make progress on old problems in the philosophy of science. This thesis is one of many first steps down new paths. There is definitely more to say about the history of pluralism in biology, not just with respect to 'species,' but with respect to many other key concepts. Now that we know what to look for, when has pluralism been used before, and why has it been used? As looking at Aristotle can help us frame some of the contemporary debates with regard to species pluralism, so can looking at other figures from the history of biology help us shed light on other forms of pluralism. Further, progress on species pluralism can feedback into progress on other forms of pluralism within contemporary biology and other areas within the philosophy of science. This piecemeal approach could even help us even rethink the complicated development of pluralism within the history of the philosophy of science from the Vienna Circle and before to today. We tend to think pluralism developed because reductionism and unification failed, but perhaps there is more to this story if we got back and look at things more closely now that some distance has been established.

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