

The Mitonuclear Compatibility Species Concept, Intrinsic Essentialism, and Natural Kinds

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Abstract

This essay introduces, develops, and appraises the mitonuclear compatibility species concept (MCSC), identifying advantages and limitations with respect to alternative species concepts. While the consensus amongst most philosophers of biology is that (kind) essentialism about species is mistaken, and that species at most have relational essences, we appeal to the MCSC to defend a thoroughgoing intrinsic essentialism. Namely, the doctrine that species have fully intrinsic essences and, thus, are natural kinds (of sorts), while allowing that species aren't categorically distinct.

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1. Introduction

Species are the fundamental taxonomic unit of evolutionary biology. However, how to best think about species is controversial in both the biological and philosophical literature, and different characterizations of species results both in different ways of understanding the nature of species and in how species are counted (Coyne and Orr 2009; Hey 2001; Zachos 2016). Disputes over how best to think of species spill over into whether species are natural kinds, individuals, historical entities, etc. (Ereshefsky 2022; Bird and Tobin 2023). In this essay, we contribute to this discussion by emphasizing the role of mitonuclear ecology in speciation, which is rarely considered in the biological and philosophical literature.² We introduce, develop, and appraise the mitonuclear compatibility species concept (MCSC)—roughly, the view that species should be individuated in virtue of mitonuclear compatibilities—and showcase philosophical consequences by reconsidering whether species have intrinsic essences. Specifically,

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² Notable exceptions include Hill (2016, 2017, 2019a, 2019b, 2019c, 2020), Heine and Hood (2020), and Heine and Shech (2021).

although the consensus amongst philosophers of biology is that (kind) essentialism about species is wrong, so that species at most have relational essences (e.g., Griffiths 1999; Okasha 2002), some arguing that species have partly intrinsic essences (viz., Devitt 2008, 2021, 2023), we appeal to the MCSC to defend a thoroughgoing intrinsic essentialism; namely, the doctrine that species have essences that are fully intrinsic and, thus, are natural kinds (of sorts). Nevertheless, we maintain that species aren't categorically distinct (or, alternatively, that species-membership is sometimes indeterminate), nor will typical phenotypic characteristics be determined solely by a species essence. Hence, the view we defend is *not* a traditional essentialist view.

The structure of the paper is as follows. Section 2 outlines the MCSC, while Section 3 reviews other prominent species concepts and compares them to the MCSC. Section 4 presents advantages and limitations of the MCSC. In Section 5, we present our argument for thoroughgoing intrinsic essentialism about species. As such, we distinguish our brand of essentialism from traditional, relational, and Devitt's (partly) intrinsic essentialism. Although entering the debate about natural kinds is beyond our scope, we conclude in Section 6 by explaining in what sense the MCSC suggests that species are natural kinds.

Ultimately, our aim is not to settle the debate about species essentialism. Rather, we show that the MCSC has both important philosophical consequences and serious advantages over other ways of understanding species. Consequently, it ought to be taken seriously by philosophers. Reflecting on Leslie's (2013, 132) claim, that with intrinsic (kind) essentialism about species "there is a degree of consensus among philosophers of biology (and indeed biologists) that is almost unprecedented in philosophy at large," we submit that such a consensus should be abandoned.³ Instead, we suggest enlarging the conceptual possibility-space regarding species to include thoroughgoing intrinsic essentialism.

2. Overview of the MCSC

Mitochondrial ecology is a field of evolutionary ecology that emphasizes coadaptation and, therefore, co-function between the mitochondrial (mt) and nuclear (N) genomes of eukaryotes. All eukaryotic organisms must have efficiently coadapted mt and N genomes to survive and reproduce successfully (Lane 2005; Hill 2017). This intimate co-function of mt and N genes directly influences oxidative phosphorylation (OXPHOS), viz., cellular respiration, and thus, the ability of eukaryotes to consume oxygen and produce adenosine triphosphate (ATP, or energetic currency) efficiently. This is because mt and N proteins function side-by-side within complexes of the electron transport system (ETS) and as ribonucleic acids (RNAs) during the translation of proteins. If these gene products do not function well together—that is, if they are not coadapted—then ATP will not be produced efficiently, impeding the essential processes that lead to survival and reproductive success. Although mitochondrial compatibility isn't the only mechanism underlying isolation between populations, it is, arguably, the most important aspect of eukaryotic function and, hence, speciation. Biological research has largely focused on the N genome and assumed that mt genes are static within and between populations. Yet, recent work on hybridization and mt genetics has revealed varying levels of heterogeneity in mt genotypes. Thus, mitochondrial ecology has underlined the importance of the mt genome in efficient mitochondrial and organism performance.

The mt genome of eukaryotes contains only 37 genes, whereas the N genome contains approximately 20,000 genes. The 37 genes in the mt genome code for 13 mt proteins, 22 transfer RNAs,

³ We omit reference to "kind" essentialism as opposed to "individual" essentialism—so by intrinsic essentialism, we mean intrinsic kind essentialism.

and two ribosomal RNAs (Rand et al. 2004; Kuhlbrandt 2015). The 13 mt proteins function in close association with N-encoded proteins within complexes I, III, IV, and V of the ETS. The remaining 24 gene products are involved in the replication of mt genes that influence OXPHOS in alternative ways. Additionally, there are 73 N-encoded proteins that form the ETS complexes alongside the 13 mt-encoded proteins. In total, approximately 1,500 N-encoded proteins function in the mitochondrion (N-mt genes), of which, roughly 180 co-function closely with mt genes (N_o -mt genes) (see **Figure 1**).

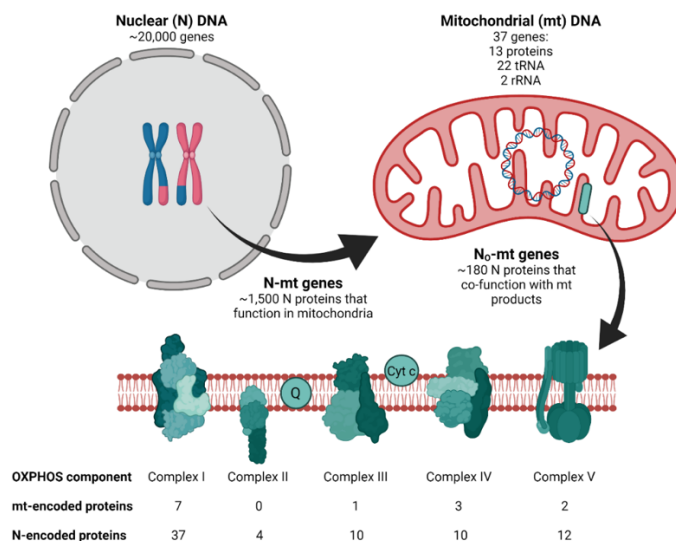


Figure 1. Illustration of mitonuclear interactions between gene products of the mt and N genomes. tRNA – transfer RNA; rRNA – ribosomal RNA; Q – ubiquinone; Cyt c – cytochrome c. Modified from Hill (2017, 395) Figure 1.

The MCSC says that “a species is a population that is genetically isolated from other populations by incompatibilities in uniquely coadapted mt and N_o -mt genes” (Hill 2017, 397).⁴ As stated, the MCSC merely tells us what species (instead of, say, genera) are. It gives us an answer to what Devitt (2008, 357), following Mayr (1982, 253-254), calls the category problem/question: In virtue of what is a species S a species (and not a subspecies, a genus, etc.)? However, reflecting on how biologists determine species membership for organisms in mitonuclear ecology, we propose the following constitutive condition for species membership and individuation as an extension of the MCSC: Necessarily, organism O is a member of species S if and only if (iff) its (particular) mt and N_o -mt genes are uniquely coadapted to function well together to promote efficient OXPHOS.⁵ As such, this gives an answer to the taxon problem/question: In virtue of what is an organism O a member of species S (and not some other species)

⁴ See also Hill (2016, 2018, 2019a). For pioneering work on the MCSC, see Levin (2003), Lane (2009), Gershoni et al. (2009), Chou and Leu (2010), Bar Yaacov et al. (2012), and Burton and Barreto (2012).

⁵ Precisely: For any organism O, species S, and gene pairing G_s such that G_s represents the mt and N_o -mt genes that are uniquely coadapted to function well together to promote efficient OXPHOS in S, necessarily, O is an S iff O has G_s . We follow the norm of using a biconditional to give a definition and add “necessarily” to emphasize our specifying what *constitutes* the kind essence of an O, i.e., of what it is for an O to be a particular S, and we propose that it is *in virtue of* having G_s that O is an S. However, the modal strength of the MCSC’s answer to both the category and taxon questions depends on the notion of possibility under consideration. If by “possible” we mean “biologically possible worlds” with mutation and selection, that is, possible worlds according to our best biological theories—including mitonuclear ecology—then the MCSC’s answers to the category and taxon questions extend to all possible worlds. But the MCSC will likely not apply in merely conceivable or logically possible worlds where evolution works differently or isn’t at play at all. We remain neutral about such worlds.

(Devitt (2008, 357), Mayr (1982, 253-254))?⁶ Thus, as we are characterizing the MCSC, it affords answers to both the category and taxon questions. It is worthwhile to emphasize that our proposed characterization is assumed implicitly when mitonuclear ecologists like Hill determine species membership for organisms, and it fits well with the spirit of mitonuclear ecology which, places “the coadaptation of mt and N_O-mt genes at the center of the speciation process” with the goal of “understanding the fundamental nature of species” (Hill 2019a, 143).⁷

To clarify, although mitochondrial function as it relates to mitonuclear compatibilities is a trait that is shared across all eukaryotes, this doesn't mean that all eukaryotes are members of the same species. The reason is that *specific* and *unique combinations* of mt and N_O-mt genotypes lead to efficient mitochondrial function. These combinations are exclusive to and different for distinct species. This contrasts with other traits or N genotypes which, alone, are inevitably shared by organisms across species boundaries. So, the mitonuclear coevolution and amino acid substitutions that have come about in, say, humans will not exist in other primates, such as orangutans. For example, humans and other primates have weakly deleterious mutations that accumulate in the mt-encoded subunits of the cytochrome *c* oxidase (COX)⁸ complex in the ETS. Occasionally, compensatory coevolution occurs, where adaptive substitutions in N-encoded mitochondrial proteins counteract these deleterious effects and prevent fitness decline (Osada and Akashi, 2012).

An outcome of the MCSC is that parents between populations incur a cost of mating through possible decreases in OXPHOS efficiency in hybrids when said parents have incompatible mt and N_O-mt genes. As such, the concept doesn't focus on whether hybridization *can* occur, as is the case with the Biological Species Concept (BSC), but it focuses on the *function* of hybrid offspring, wherein said function exists along a continuum. Consequently, belonging to a species is a matter of degree under the MCSC. Combinations of poorly coadapted gene sets result in hybrid offspring that are either inviable or contain mitochondria with inefficient OXPHOS. We can determine species membership by assessing mitochondrial performance (i.e., ETS function)⁹ in hybrids compared to parental lines (e.g., Ellison and Burton 2006). Hence, we can know whether O is a member of S because mitonuclear incompatibilities will result in decreased mitochondrial efficiency in hybrids of diverged populations, whereas mitochondrial function in hybrids from parental populations with coadapted mt and N_O-mt genes will not differ significantly from parental lines.

Allopatric, mitonuclear speciation is thought to begin when a population splits, and the two allopatric daughter populations first develop unique mt genotypes. The two populations then develop uniquely coadapted N_O-mt genes that maintain mitonuclear compatibilities. If the two populations come into secondary contact at a later time, the uniquely coadapted sets of mt and N_O-mt genes between the two populations may be incompatible when the daughter populations interbreed to form hybrids (see **Figure 2**).¹⁰ Taxonomically, O is a member of some species S1 and not S2 because it satisfies the necessary and sufficient condition of species membership noted above. With respect to S2, interbreeding with O would lead to hybrids that are either inviable or contain poorly-coadapted sets of mt and N_O-mt genes that lead to decreased efficiency of OXPHOS.

⁶ We selectively focus on species, but Devitt takes the distinction to apply to any biological taxon.

⁷ Hence, if one takes the MCSC as an answer merely to the category question, while adopting, say, an organism's evolutionary history as an answer to the taxon question, then many advantages (noted in Section 4) for adopting the MCSC would be negated, e.g., objective and explicit predictions, wide application. It would lead to ambiguous outcomes for identifying species boundaries and inconsistent explanations regarding the process of speciation across taxa.

⁸ COX reduces oxygen to water in the mitochondrial matrix, a critical step in OXPHOS.

⁹ In addition to OXPHOS, other processes will also be affected such as the production of reactive oxygen species, oxidative damage, and the many downstream processes that rely on efficient ATP production.

¹⁰ For how the MCSC can be applied to sympatric speciation, see Hill (2016).

Before continuing, it is worthwhile to consider two potential concerns to further clarify the MCSC. First, since there are many different clusters of organisms in the world (e.g., reproductive communities, demes, populations and metapopulations, phenotypically similar organisms, ancestor-descendant lineages), it may be tempting to conclude that we have given no argument for why the MCSC should be thought of as a species concept, rather than a concept that identifies other biologically important groups. In reply, mitonuclear coevolution is crucial to mitochondrial function and, therefore, to all of the energetically demanding processes related to survival and reproductive success. Since organisms must survive and reproduce successfully to evolve, mitonuclear ecology lies at the center of *speciation* and any legitimate *species* concept. In contrast, the clusters listed above don't lie at the center of speciation, and, hence, shouldn't underly species concepts because such groups don't have a *direct* influence on survival and reproduction across eukaryotes as a whole. Further, the MCSC is a species concept—and not a general guide to grouping organisms—because it makes specific predictions about the function and hybridization of organisms. Additionally, the proof is in the pudding. Below, we identify advantages that the MCSC—if taken as a species concept instead of an identification of merely biologically important groups—has over other species concepts. Last, in our view, the philosophy should follow the science. So, if biologists seriously consider the MCSC as a species concept, it seems fair for philosophers to do so as well and, therefore, enquire into the advantages/disadvantages of adopting the MCSC as a species concept (Sections 3 and 4) and the philosophical consequences that may follow (Section 5 and 6).

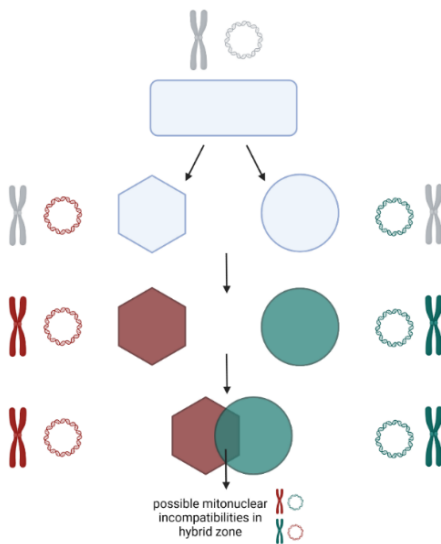


Figure 2. Illustration of speciation via the Mitonuclear Compatibility Species Concept. Modified from Hill (2019a, 152) Figure 7.3.

Second, one may worry that the MCSC gives a circular definition for species membership since it identifies those properties that determine species membership in relation to a particular species (*vis-à-vis* the notion of uniqueness). The worry, we believe, is misplaced since ultimately those properties that determine species membership will be *a particular set of genes*. Consider the following: take any two eukaryotes on the planet, call them O1 and O2, and allow them to mate to produce an offspring. Based on compatibility of their mt and N_O-mt genes, the resulting offspring will either be viable or not. Of those that are viable, their mitochondrial function will exist on a continuum based on how well their mt and N_O-mt genes co-function to promote efficient OXPHOS. Members of the same species, then, will be formed based on what offspring are able to survive and reproduce. *This is a direct product of efficient mitochondrial function that results from mitonuclear compatibilities.* Alternatively, we can carry out

cybrid¹¹ studies to assess mitochondrial function based on varying levels of mitonuclear compatibility. Said function declines when the genomes of more distantly related organisms are combined. Different levels of coadaptation between the mt and N genomes of two cell lines lead to variance in mitochondrial performance and, therefore, varying levels of relatedness (i.e., different species; see Section 4 for more on cybrid studies). Therefore, we need not have a prior determination of what species O1 and O2 belong to in order to determine species membership. Importantly, if we want to provide necessary and sufficient conditions for species membership, what we are looking for is a set of properties $\{p_1\}$ that, should some organism O possess said properties, it is a member of species S1, $\{p_2\}$ for S2, and so on. On the MCSC, the properties $\{p_1\}$ that determine that O1 belongs to S1 (and not S2 or any other species) is the above mentioned set of mt and N_0 -mt genes.

3. Varieties of Species Concepts and Their Relation to the MCSC

Biologists have developed many diverse species concepts, of which the BSC and the Phylogenetic Species Concept (PSC) are most widely adopted in practice today. The BSC states that a species is a population which is reproductively isolated from other populations (Mayr 1940). Under this concept, gene flow is the primary determinant of speciation, with a focus on N genes and the ability of organisms to form hybrids. The PSC states a species is a monophyletic group of common ancestry (de Queiroz and Donoghue 1988). Here, the focus is on evolutionary history, where a species stems from a shared line of descent among organisms, in reference to one or more traits.¹²

The MCSC is related to and expounds upon both the BSC and PSC, while settling disagreements and elaborating on details surrounding hybridization and the role of genetics in speciation. The BSC focuses on the exchange of N genes, whereas the MCSC focuses on the exchange of mt and N_0 -mt genes that are unique to populations and directly influence OXPHOS through coadaptation. Here, the MCSC provides a narrower focus on which genetic compatibilities are important and unambiguously makes predictions surrounding incompatibilities that result from hybridization. The BSC focuses on speciation that results from cessation of N geneflow and the inability to form hybrids. The MCSC, in contrast, allows for the exchange of N genes and hybridization between species but requires that such species retain distinct, coadapted sets of mt and N_0 -mt genes. Although the MCSC is a novel, independent species concept, it does share a limited number of characteristics with preceding concepts, such as breeding and the formation of hybrids, as outlined in the BSC.

Under the PSC, populations have a unique evolutionary history but retain coadapted sets of mt and N_0 -mt genes. Hence, a group of organisms may be a separate species under the PSC but not under the MCSC, depending on whether the phylogenetic assessment is of a genetic origin. Again, the MCSC provides a more detailed explanation of what is a “unique” evolutionary history, with emphasis on

¹¹ Cybrid cell lines are generated by combining nucleated and enucleated cells, fusing the mtDNA from one cell with the N DNA of another cell. This differs from hybrids which combine nucleated cells.

¹² Although there are several versions of various species concepts, such as the monophyly and diagnosability versions of the PSC, we compare the MCSC to other concepts *generally speaking* to outline how the MCSC is an important species concept that should be taken seriously by both biologists and philosophers, and which implies intrinsic essentialism. For instance, the diagnosability version of the PSC focuses on “a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind” (Eldredge and Cracraft 1980). Irrespective of these variations, our thesis that the MCSC implies intrinsic essentialism holds, and it is beyond our scope to address such variation within alternative species concepts.

coadaptation and co-function between specific genotypes. It is important to note, however, that in most cases, species identified under the PSC are maintained under the MCSC (Hill 2017).

The Ecological Species Concept (ESC) defines a species as a “lineage 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). The Genotypic Cluster Species Concept (GCSC) states a species is a “morphologically or genetically distinguishable group of individuals that has few or no intermediates when in contact with other such clusters” (Mallet 1995; Coyne and Orr 2009, 273). Both the ESC and GCSC are perhaps more distantly related to the MCSC than the BSC and PSC. The ESC focuses on adaptive zones within an environment, which are defined regardless of the organisms present (Van Valen 1976). Problems with the ESC arise, though, when organisms change their environment to influence their survival and reproductive success, and different organisms inhabit the same environment without gene flow (e.g., temporal variations as seen in periodical cicadas; Coyne and Orr 2009). Unlike the MCSC, sympatric taxa that exchange genes to form viable hybrids with efficient mitochondrial function but inhabit different niches would be considered different taxa under the ESC. This issue doesn’t arise with the MCSC. Irrespective of whether organisms inhabit similar or different environments in space or time, the exchange of incompatible mt and No-mt genes can influence mitochondrial function and, therefore, organism performance.

Issues with the GCSC arise because there is no specification of how many, or what, genes or traits must be different to define a species. Additionally, it isn’t clear what level of organization determines a cluster (e.g., species, genus, family). One advantage of the GCSC, however, is its application to asexual taxa, given that it doesn’t rely on hybridization. The MCSC doesn’t rely on hybridization either but on how hybrids *function* (i.e., the diffusion of mt genes). In the following section, we note further details on the advantages and limitations of the MCSC.

4. Advantages and Limitations of the MCSC

We believe the MCSC is an improvement upon other species concepts, but this does not preclude the MCSC from having limitations. Specifically, the MCSC is advantageous and builds on previous concepts in at least four ways: (1) it is a unifying species concept since it is widely applicable, (2) it is objective, in that we can make clear predictions and precise, unambiguous empirical measurements, (3) it is explanatorily superior (in certain respects) and (4) it exists on a continuum. Nonetheless, limitations exist regarding its inability to provide insights into speciation for bacteria and archaea, and it doesn’t specify what is considered “dysfunction” among hybrids.

Virtually all eukaryotes contain mitochondria¹³, including asexual¹⁴ organisms such as plants, fungi, and protists. As such, a species concept such as the MCSC, which is applicable to many organisms (including facultative asexual organisms), is advantageous in comparison to concepts that have a narrower scope with respect to the range of organisms to which they apply. In other words, since the need for mitonuclear coadaptation is universal among eukaryotes, the emphasis on mitonuclear interaction affords a *unifying* species concept—the MCSC—that is applicable across distantly related eukaryotes, where compatibilities between mt and N genes (and mitochondrial performance) can be compared directly and

¹³ For an exceedingly rare exception, see Karnkowska et al. (2016), which outlines the existence of a eukaryotic microorganism containing no mitochondria.

¹⁴ See Hill’s *Mitonuclear Ecology* (2019a) for how mitonuclear compatibilities are relevant to the evolution of sex, as well as how mitonuclear ecology differs between sexual and asexual eukaryotes.

widely. For instance, if we want to use behavior to build a phylogeny of mammalian taxa, it would be difficult in most respects to compare, say, the behavior of dolphins to the behavior of humans in a meaningful way. However, such an approach is not only possible but practical using the coevolution and cofunction of mt and N genes. Even if we can find similarities in behavior between organisms such as dolphins and humans, such commonalities become non-existent at the extreme ends of eukaryotic speciation. Still, the cofunction of mt and N genes, and their importance in animal performance, is present across Eukarya.

One limitation is that the MCSC doesn't work for organisms without mitochondria like bacteria or archaea. Yet, it is worth considering whether prokaryotes warrant being organized via species concepts comparable to eukaryotic species concepts, due to lateral gene transfer as seen in bacteria. Here, the consideration is not whether prokaryotes exchange genes but how they do so. According to Hill (2019a), prokaryotes may not warrant such a consideration because they exchange genes in a way that doesn't rely on vertical gene transfer via recombination (sex), but on horizontal gene transfer (lateral transfer) which isn't dependent on the transfer of genes from parents to offspring. If this is the case, then the MCSC covers virtually all relevant organisms (i.e., eukaryotes) for which it needs to explain species-level organization. At least those with comparable mechanisms of gene transfer.

Furthermore, as an approach to species and speciation, the MCSC is *objective* since it affords clear *predictions*, utilizing precise, unambiguous measurements to delineating species' identities provided mitochondrial function can be measured in comparison to that of parental lines. This differs from species concepts that are more subjective, such as the GCSC, which doesn't specify what or how many genes, or traits, are needed to diagnose species boundaries. Simply stating that a species is "morphologically or genetically distinguishable" from other groups without explaining the specific traits or genotypes that are relevant is perhaps problematically subjective, provided researchers can determine this based on their research program and preferences. Likewise, the ESC doesn't specify the precise qualifications by which an adaptive zone is "minimally different" or what constitutes a lineage to "evolve separately." Additionally, the PSC doesn't specify the criteria in deciding which organisms constitute the "smallest monophyletic group." It doesn't say whether taxonomic decisions regarding relatedness are based on genetics, morphology, breeding, fossils, etc. Instead, the MCSC is based on the evolution and coadaptation of specific mt and N_O-mt genes that *must* cofunction well to achieve efficient OXPHOS; therefore, researchers can make detailed predictions as to the requirements of speciation by predicting exactly which genes function together and how they influence OXPHOS. One could argue, however, that no objective boundary exists for what is considered hybrid "dysfunction," provided mitochondrial function exists along a continuum. Although, researchers can correlate mitochondrial function to whole-animal performance including survival, reproductive success, and whole-organism respiration.

Moreover, the MCSC is explanatorily superior to said approaches since it largely explains variation in survival and reproductive success (both of which are energetically demanding), where other approaches don't. For example, recent work suggests a direct functional connection between the unique combinations of mt and N_O-mt genes of house finches and, thus, their mitochondrial performance, and the process of carotenoid oxidation and feather pigmentation which, in turn, relates to various phenotypic traits such as the plumage color of house finches. Such a connection further "provides a novel *mechanistic explanation* for why carotenoid coloration relates to a range of aspects of individual performance and why females use plumage redness as a key criterion in choosing mates" (Hill et al. 2019c, 8; our emphasis). In general, although it is beyond our scope here to get into details, by "elevating the interaction of mt and N genes to a central process in discussions of speciation" the MCSC "leads to novel explanations for some of the most interesting and perplexing characteristics of species including

Haldane’s rule, asymmetrical outcomes of hybrid crosses, and the tendency for N genes to diffuse across species boundaries while mt and Z-linked genes typically show discrete transitions” (Hill 2019a, 178). That said, an additional limitation of the MCSC is that it doesn’t afford historical explanations a la Devitt (2023, Ch. 3) (see Section 5).

Additionally, the MCSC operates on a *continuum* of mitochondrial function and, hence, speciation is to some extent a *matter of degree*. That is, the MCSC states that speciation doesn’t revolve around whether hybrids can form (as with the BSC). Instead, what matters is hybrid function with respect to mitochondrial performance. Parents from different populations risk having offspring with mitochondrial dysfunction if the mt and N_o-mt genes from the populations are incompatible. For instance, if we take cybrid studies such as Kenyon and Moraes (1997), we observe that when the mtDNA of primates closely related to humans is combined with the N background of humans, respiratory function decreases by 20%, 34%, and 27%, for common chimpanzee, pigmy chimpanzee, and gorilla, respectively, but is functional in comparison to human cell lines. Nevertheless, when the mtDNA of more distantly related primates, e.g., orangutan, old-world monkey, new-world monkey, lemur, is set against the N background of humans, mitochondrial performance isn’t restored to a functional state. As such, the key to understanding and defining species’ boundaries may not rely on whether two populations can interbreed but the extent to which hybrids can function to survive and reproduce successfully, which is directly and largely dependent upon mitochondrial performance (Heine and Hood 2020; Heine 2021).

Thus, a consequence of the MCSC is that it gives rise to what we call a “gray zone” for determining the extension of a species, provided hybrid function exists along a continuum. For example, two populations with highly diverged mt genotypes may both be able to function against similar N backgrounds (functioning hybrids), or alternatively, two populations with diverged mt genotypes may function poorly against N backgrounds that are also highly diverged (dysfunctional hybrids). These scenarios create various circumstances that lead to a continuum of greater or lesser mitochondrial function and, therefore, organism performance. This is because the mt genome of two populations can diverge without requiring an equal level of divergence in the N genome. Put differently, the MCSC is consistent with a scenario where, hypothetically, an organism O belongs to two different species S1 and S2, but the criterion of mitochondrial performance allows for the determination of the species, S1 or S2, that O resides in *to a greater degree*. Accordingly, under the MCSC, *species are not categorically distinct*. In our view, this is a feature of the account, not a bug. That said, in cases of hybridization between species in the gray zone, one could also hold that it is indeterminate whether the hybrid belongs to one or another species. In any case, for practicing biologists, pragmatic decisions are made as to which species organism O belongs (such as S1 over S2, for our example). Moreover, DNA barcoding suggests that gray zones are rare. Mt genotype identifies species in agreement with pre-existing concepts ~95% of the time. This indicates that abrupt shifts in speciation¹⁵ might occur more often than expected under mitonuclear theory (Hill 2020). Nonetheless, evolution occurs continuously and, thus, doesn’t fit well into a discontinuous, binary mold. Therefore, species accounts that imply a discontinuous boundary are in some sense artificial since evolution implies there ought to be vague cases of speciation.

As an anonymous reviewer notes, the MCSC has the counterintuitive implication that were a “tiger” to evolve completely independently on a different planet, assuming it is intrinsically and genetically identical to tigers on Earth, it would still be a tiger according to the MCSC. Generally, if two

¹⁵ See Hill (2019b) for a discussion on the rampant introgression of mt genomes between species, which can lead to the erasure of species under the MCSC. The introgression of mt genomes between species can have two potential benefits: better adaptation to a local environment over the native mt genotype, and overcoming a high mutational load of the mt genome in the recipient taxon. Both circumstances may lead to an increase in fitness.

groups of organisms independently evolve the same mt/No system, then they are the same species under the MCSC—even if found in outer space. Moreover, if the offspring of two conspecific parents, through mutation, exhibit a very different mt/No-mt coadapted system, then they are a different species under the MCSC (unless they fall into the gray zone noted above). Conversely, species concepts like the PSC that emphasize evolutionary history don't have these counterintuitive implications. In response, we make three points. First, perhaps these scenarios are counterintuitive, but they are also extreme and unrealistic, so it seems permissible for there to be counterintuitive implications. After all, these implications also hold for the BSC. Second, other such thought experiments count in favor of the MCSC and against the PSC. Consider three such scenarios (from Devitt (2023, 102; original emphasis)):

Twin-Earth Tigers: Suppose that there was a Twin Earth with a qualitatively identical tree of life to that on Earth. So, there would be a species on Twin Earth that would be intrinsically identical to our tigers and would have evolved from ancestors and a founder population that were intrinsically identical to the ancestors of our tigers...

Engineered-Tigers: Suppose that we genetically engineered new organisms “from scratch”, organisms bearing no lineal relationship to existing tigers yet which are genetically and phenotypically indistinguishable from those existing tigers and capable of interbreeding with them to produce fertile offspring...

Semi-Engineered-Tigers: Not only *can* these engineered-tigers interbreed with existing tigers, many of them *do*. The result is a population made of three groups, indistinguishable except by their origins: (a) descendants solely of historical tigers; (b) descendants solely of engineered tigers; (c) descendants of both, “semi-engineered-tigers”...

While according to the MCSC twin-Earth tigers, engineered-tigers, and “tigers” in groups (b) and (c) are all tigers, the PSC (and other species concepts that emphasize actual evolutionary history) holds that such organisms are not tigers. This seems to us highly counterintuitive, also given that the tree of life on twin Earth would be identical to that on Earth. In our view, the take-home message here is that not much can be concluded about the viability of a serious species concept considered by biologist from reflecting on unrealistic thought experiments. Different folks will have different intuitions and counterintuitive scenarios will have counterintuitive implications.

5. Intrinsic Essentialism, Relational Essentialism, and Natural Kinds

Our goal in this section is to argue that the MCSC implies that species have fully intrinsic essences and, thus, suggests that species are natural kinds (of sorts). Section 5.1 reviews the received view of “relational essentialism” and Devitt’s new (partly) intrinsic essentialism, while Section 5.2 argues for our brand of thoroughgoing intrinsic essentialism and distinguishes it from other types. We will assume metaphysical monism about species; namely, that there is a “single correct species concept” (Ereshefsky 2022). Before starting in earnest, it is worthwhile to get clear on what we mean by a species “essence” and how the idea that O is an S *in virtue of* an essence may be fleshed out.

Traditionally, species essences are *explanatory*, so that it is *because* an organism is a member of some species that it has certain phenotypic characteristics typical of that species.¹⁶ Devitt (2023, 58-59)

¹⁶ Also see Austin (2019).

calls this “the Sober demand:” an essence “must be explanatory... A species essence will be a causal mechanism that acts on each member of the species, making it the kind of thing that it is” (Sober 1980, 25) (quoted in Devitt (2023, 58-59). However, while in what follows we will inquire into whether and to what extent a proposed species essence is causal-explanatory, this is *not* the notion of essence that we are working with. Instead, we adopt a *classificatory* notion of essence as discussed in, say, Okasha (2002, 202): “[The] essence of a kind is ... that set of properties which are jointly sufficient and individually necessary for being a member of the kind...” As we elaborate below, this allows that said set of properties are intrinsic (intrinsic essentialism), partly intrinsic and partly relational (partly intrinsic essentialism), or relational properties (relational essentialism).¹⁷

5.1 Intrinsic Versus Relational Essentialism

The default view about species, the view we would have if we did not think we have good reason to think otherwise, is that species are natural kinds with intrinsic essences. One way to think about essentialism is articulated by David Hull (1994, 313): “each species is distinguished by one set of essential characteristics. The possession of each essential character is necessary for membership in the species, and the possession of all the essential characters sufficient.” Two prominent problems with this conception concern biologists’ inability to find a common essence that all and only the members of a species share (Sober 1980; Ereshefsky 2001; Okasha 2002), and that evolutionary theory itself implies there are no sharp boundaries between species (Hull 1965; Okasha 2002; Ereshefsky 2022). In other words, evolutionary mechanisms including mutation, gene flow, genetic drift, and natural selection can cause the disappearance of traits in subsequent generations of a species. To see that a trait is not essential, note that it can disappear from a population after occurring in all members of a species. Yet, different species often share common characteristics; therefore, the natural processes of evolution work against the idea that a trait is unique to a species and only members of that species.

Accordingly, there is a consensus amongst philosophers of biology that intrinsic essentialism “about species is today a dead issue” (Sober 1980, 249) and that it is “both false and fundamentally inconsistent with the Darwinian view of species” (Griffiths 2002, 72). For instance, Elliot Sober holds that “biologists do not think that species are defined in terms of phenotypic or genetic similarities... Similarities and differences among organisms are *evidence* about whether they are conspecific, but a species is not *defined* by a set of traits” (Sober 2000, 151; original emphasis). Samir Okasha (2002, 196) concurs: “Virtually all philosophers of biology agree that... species are not individuated by essential characters...” He continues: “Empirically, it simply is not true that the groups of organisms that working biologists treat as con-specific share a set of common morphological, physiological or genetic traits which set them off from other species.” Likewise, Sarah-Jane Leslie (2013, 132) explains that there “is no such thing as ‘lemon DNA,’ no common genetic code that makes for membership in the kind *Panthera tigris*.” Similar views are held by Barker (2010), Dupré (1999), Ereshefsky (2001), Ghiselin (1974), Griffiths (1999), La Porte (2004), Lewens (2012), Matthen (1998), Rosenberg (1985), Slater (2013), and Sterelny and Griffiths (1999), among others.

An alternative view of species essentialism, which can be called “relational essentialism” (Ereshefsky 2022), has been suggested by, e.g., Griffiths (1999), Sterelny and Griffiths (1999), Okasha (2002), and LaPorte (2004). According to relational essentialism, relational properties among organisms, or between organisms and their environment, are the essence of a species. For example, Kim Sterelny and Paul Griffiths (1999, 8) explain: “Contemporary views on species are close to a consensus in thinking that species are identified by their histories. According to these views, Charles Darwin was a human being...

¹⁷ Strictly: there are intrinsic and extrinsic (non-intrinsic) properties, and a relation is intrinsic/extrinsic/partly intrinsic and partly extrinsic just in case it supervenes on the intrinsic/extrinsic/partly intrinsic and partly extrinsic properties of its relata (Okasha 2023, 8-9).

in view of his membership in a population with a specific evolutionary history.” Consequently, “the essential properties that make a particular organism a platypus, for example, are historical or relational” (186). Similarly, according to Okasha (2002, 202) “...Darwinism shows the essential properties of species to be relational rather than intrinsic” and Sober (2000, 153) suggests that “species are historical entities; this means that two organisms are conspecific in virtue of their historical connection to each other, not in virtue of their similarity.”

These authors hold that species essences are relational (instead of intrinsic) properties because, “in fact, on the most popular accounts of the species concept found in contemporary evolutionary biology, organisms are assigned to species on the basis of relational properties” (Okasha 2002, 199). For example, with the BSC and also Paterson’s (1985) related “mate recognition” species concept, which concentrates on recognizing potential mates, it’s an organism’s relation to other organisms—viz., via the ability to breed with or recognize potential mates—in virtue of which an organism belongs to a species. Under the PSC, for instance, an organism is a member of a species in virtue of its evolutionary history; two organisms are of the same species since they share an evolutionary line of descent. Similarly, under the ESC, species are also delineated via their location in evolutionary history through occupying an adaptive zone or ecological niche—environmental resources and habits—of the right kind. In sum, most species concepts seem to imply relational essentialism.

Importantly, “relational essentialism” about kinds is different from how “essentialism” is historically characterized in more ways than merely the shift from intrinsic to relational properties. Following Okasha (2002) on this point, Locke (1689) distinguished between the nominal and real essence of a kind. Nominal essence concerns how we come to know kind membership, for instance, by associating properties like shiny, malleable, yellow, and metallic, with the kind gold. The real essence of a kind, in contrast, are those intrinsic properties in virtue of which a kind has its nominal essence. Additionally, the real essence *explains* why, say, being a shiny malleable yellow metal is associated with being gold. Although Locke believed that real essences weren’t discoverable, Putnam (1975) and Kripke (1980) argued otherwise. They held that the intrinsic essence of a kind—the genetic code for species (Putnam 1975, 240) and something’s hidden structure more generally speaking (Kripke 1980, 121)—serves both *semantic* and *causal/explanatory* roles. For instance, having atomic number 79 is causally responsible for and explains why the kind gold is associated with being a shiny malleable yellow metal, and also what users of the natural kind term ‘gold’ are really referring to, i.e., intrinsic essences determine semantic extension. While relational essentialism maintains that essences determine semantic extension by replacing intrinsic properties with relational ones, the view abandons the causal/explanatory role that essences are meant to serve:

[If] we apply the Kripke/Putnam model to biological species ... by replacing Kripke’s and Putnam’s “hidden structure” with whatever relational property we think determines species membership – we *do* sever the semantic and causal/explanatory roles. To see this, suppose we adopt [the BSC] and we use morphological similarity as a fallible indicator of that ability. Now clearly, the causal explanation of why an organism has the particular morphological traits it does will cite its genotype and its developmental environment, not its ability to interbreed with certain other organisms. Morphology is indicative of that ability, but not the causal outcome of it. [Similarly, other species concepts] only play the semantic role that Kripke and Putnam attribute to “hidden structure,” not the causal/explanatory role... (Okasha 2002, 203-204; original emphasis)

In short, although kind essences are traditionally intrinsic and play both semantic and causal-explanatory roles, relational essentialism involves relational properties, and such essences only play a semantic role. We return to this issue in the following subsection.

In contrast to the consensus, Michael Devitt (2008, 2021, 2023) has argued for “intrinsic biological essentialism,” where species and other biological taxa have *partly* intrinsic essences. Devitt’s argument may be summarized in four steps. First, following Mayr (1961) and Kitcher (1984), he distinguishes between “historical” and “structural” explanations, focusing on the latter: Structural explanations “explain the properties of organisms by means of underlying structures and mechanisms” (121). Second, he notes that biology has generalizations such as grouping organism together under a species and that such generalizations are both informative and provide structural explanations. Third, he submits that such generalizations cannot be brute facts and must be explained (Devitt 2021, 70). Fourth, he appeals to inference to the best explanation (IBE) to conclude that what is required are intrinsic properties: there is some “intrinsic underlying, probably largely genetic, property that is part of the essence of the group” (Devitt 2008, 253). Since we aren’t concerned with appraising Devitt’s argument, we only engage with parts of his account, insofar as these are related to essentialism as implied by the MCSC, a topic we turn to next.

5.2 The MCSC, Species, and Essentialism

Our argument for intrinsic essentialism is outlined as follows:

- P1) The MCSC has significant advantages over other species concepts.
- P2) The MCSC implies intrinsic essentialism about species.
- C) Therefore, species have intrinsic essences.

The evidence supporting P1 has been given in Sections 3-4. There is, though, a weaker and stronger reading of the premise, with corresponding conclusions. On the stronger reading, advantages of the MCSC over other species concepts suggest that biologists and philosophers of biology adopt the MCSC. The conclusion, then, is that species have intrinsic essences. Nonetheless, a more tenable interpretation that we support concerns a weaker reading. Namely, we have shown that the MCSC has significant advantages over other species concepts. This implies that biologists and philosophers of biology take the MCSC seriously. Perhaps, then, species have relational essences under other species concepts, but species may have intrinsic essences under the MCSC. Consequently, we submit, the unprecedented degree of consensus amongst philosophers of biology in rejecting intrinsic essences must be abandoned.

Regarding P2, recall that according to the MCSC, necessarily, an organism *O* is a member of species *S* iff its mt and $N_{O\text{-mt}}$ genes are uniquely coadapted to function well together to promote efficient OXPPOS (viz., concerning the taxon question), and a species is a population that is genetically isolated from other populations by incompatibilities in uniquely coadapted mt and $N_{O\text{-mt}}$ genes (viz., concerning the category question). Since having a set of genes is an intrinsic and non-relational property of an organism, the MCSC implies intrinsic essentialism: those properties that determine that *O* is a member of *S* are intrinsic to *O*. Similarly, the answer that the MCSC gives to the category question holds that the species-making property (that is, the property in virtue of which a collection of organisms counts as a species) is a combination of genes, so it is an intrinsic answer. This satisfies a constraint recently argued for by Okasha (2023, 17), viz., that “the Taxon question has an intrinsic answer if and only if the Category question has an intrinsic answer...” However, an immediate worry comes to mind since one tenet of kind essentialism is that “all and only the members of a kind have a common essence” (Ereshefsky 2022), but evolutionary theory entails a type of variation and change that is at odds with this tenet and, hence, with essentialism. Relatedly, another worry is that evolution is a gradual process. But if “species *A* gradually evolves into species *B*, where in this lineage should one draw the line that marks

where *A* ends and *B* begins? Any line will be arbitrary. Essentialism, it is alleged, requires precise and nonarbitrary boundaries between natural kinds” (Sober 1993, 147). In reply, we note three points.

First, on the MCSC it is *roughly* true that “all and only” members of a species will have a common essence since the focus isn’t on any phenotypic or genetic trait but on the right *combination* of genes, namely, sharing uniquely coadapted sets of mt and N_O-mt genes that don’t exist in the same combinations in other eukaryotes. Second, we say “roughly” because, as noted above, it’s true that under the MCSC species boundaries will not be sharp; they will be somewhat vague and indeterminate. We called this the gray zone at the end of the last section, and it arises since hybrid function can exist along a continuum. Again, we see this as a merit of our account instead of a fault since it accords well with evolutionary theory. Yet, the worry may be interpreted as one specific to essentialism. In reply, we can only repeat what Devitt (2008) has successfully argued for in this regard: First, essentialism “does *not* require sharp boundaries between species... Essences are a bit indeterminate” (373). Second, the indeterminacy that stems from evolutionary theory isn’t a special problem for intrinsic essentialism (neither ours nor Devitt’s). Last, recall that the MCSC is consistent with a scenario where an organism *O* belongs to two different species *S*₁ and *S*₂, but the criterion of mitochondrial functions allows for the determination of which species *O* resides in to a greater degree. This means that the decision of whether *O* belongs to *S*₁ or *S*₂ isn’t entirely arbitrary but depends on mitochondrial function and the nature of what researchers deem relevant—for example, what is considered “statistically significant” or whether genotypes are “significantly” diverged.

To elaborate further on our MCSC-motivated intrinsic essentialism, it’s worthwhile to reflect on the role that our essentialism plays in comparison to relational essentialism and Devitt’s (partly) intrinsic essentialism. Starting with relational essentialism, we noted that the view maintains the semantic role of natural kind essence while abandoning the causal/explanatory role so that it’s an extra step removed from the historical characterization of kind essentialism. Our intrinsic essentialism maintains a *partial* causal/explanatory role for essences. To see this, recall that according to Kripke and Putnam, science discovered that having atomic number 79 is the (real) intrinsic essence of gold, and “this is the underlying microstructural property which explains why all samples of gold are shiny, yellow and malleable” (Okasha 2002, 194). Furthermore, Okasha (2002, 203) says, “‘hidden structure’ is meant to be causally responsible for the presence of those superficial characteristics... ‘having atomic no. 79’ is both the true criterion for something’s being gold, i.e., it is what the term ‘gold’ really refers to, and is *also* what explains why all samples of gold have the superficial characteristics – yellowness, malleability etc. – that they do.” But if we substitute “gold” for “eukaryotic species,” “shiny, yellow, and malleable” for “mitochondrial function,” and “hidden structure” for “unique combinations of mt and N_O-mt genes,” it follows that under the MCSC biology is, in fact, attempting to *both* seek causal generalizations to explain organism survival and reproductive success via efficient mitochondrial function, *and* to identify “units that play a fundamental role in the evolutionary process.” In drawing said analogy, substituting “gold” for “species,” we can refer to eukaryotes as a whole or individual eukaryotic species. In both circumstances, mitochondrial function is unique, provided prokaryotes don’t contain mitochondria *and* each eukaryotic species contains uniquely coadapted sets of mt and N_O-mt genes that are *causally* related to mitochondrial performance.

In other words, the MCSC implies that, *contra* Okasha, it *is true* that “the groups of organisms that working biologists treat as con-specific share a set of common... genetic traits which set them off from other species” (Okasha 2002, 196). Significantly, it’s not “genetic traits” that are important, but *combinations* of genetic traits—particularly, the mt and N_O-mt genomes collectively. Conspecifics don’t share the exact same genes, however, they do share uniquely coadapted sets of mt and N_O-mt genes that don’t exist in the same combinations among other eukaryotic groups. For example, under the BSC and PSC, blue- and golden-winged warblers (*Vermivora cyanoptera* and *Vermivora chrysoptera*, respectively) are not considered distinct species; the populations are able to hybridize, and they do not have unique evolutionary histories. Furthermore, their N genomes are 99.97% identical. However, when these two

birds mate, their hybrid offspring have low fitness, and their mtDNA is 3% diverged (enough for sister species classification). Therefore, under the MCSC, blue- and golden-winged warblers are distinct species (Hill 2017). This conclusion—along with the case of red coloration in house finches mentioned in Section 4—shows that our intrinsic essentialism about species maintains a partial causal-explanatory role. Although it is no doubt different from the historical notion of kind essentialism, it is also closer to such a notion than “relational essentialism” and, thus, worthy of the name.

Nevertheless, an anonymous reviewer notes two worries. First, if the intrinsic essences of the MCSC are only partially explanatory, doesn't it follow that there are some other properties (e.g., other genes, environment, evolutionary history) that explain the phenotypic traits typically associated with an organism that is a member of a species? If so, shouldn't these other properties also count as part of the essence? Our reply is that on the *classificatory* notion of essence that we are working with, the answer (to the second question) is “no.” But we admit that on a *casual-explanatory* notion of essence we must, by the very definition of “essence,” answer in the affirmative and this means that while the MCSC may capture part of species essences, it is incomplete. Second, Devitt (2023, Ch. 3) argues that an organism's relational essence, e.g., their evolutionary history, provides a historical (instead of structural) explanation. Namely, it explains why organisms of that sort evolved in the first place: “For objects to be polar bears, they must have a certain history and that history brought it about that these objects have the phenotype properties that they have” (Devitt 2023, 92). Thus, our claim (following Okasha (2002)) that relational essences aren't explanatory is too quick. In response, we admit that relational properties provide explanations not had by intrinsic properties, and perhaps this counts against the MCSC. This also suggests that relational essentialism severs the semantic and *structural* causal/explanatory role, while maintaining a *historical* causal/explanatory role.

Next, reflecting on our view in comparison to Devitt's (partly) intrinsic essentialism, our essentialism is both weaker and stronger than Devitt's account. It is *weaker* because it applies only to species and not to other biological taxa, while Devitt's essentialism applies to all (or most) biological taxa. The MCSC doesn't apply to higher taxa beyond the species level, provided mitochondrial function ceases entirely once mitonuclear incompatibilities lead to inviable offspring. The result of incompatibilities between two genera may lead to complete hybrid dysfunction in the same manner that incompatibilities between distantly related families may lead to complete hybrid dysfunction.

Our essentialism is also *stronger* than Devitt's since it implies that species have solely intrinsic essences, while Devitt's essentialism holds that biological taxa have *partly* intrinsic and partly relational essences. That is, the MCSC implies a *thoroughgoing* intrinsic essentialism about species. Moreover, *methodologically*, while both relational essentialism and our thoroughgoing intrinsic essentialism are motivated by considering species concepts, Devitt's essentialism is motivated by an IBE. To evade the objection that his essentialism doesn't do justice to species concepts, Devitt (2008, 357) appeals to the distinction between the category and taxon questions/problems (noted in Section 2). He then argues that while the focus of essentialism ought to concern the taxon problem, most species concepts are primarily concerned with the category problem and “throw little light” on the taxon problem (Devitt 2008, 358). Here, we don't wish to enter this debate, nor do we scrutinize Devitt's arguments. Nonetheless, we must tackle a potential objection, viz., that the MCSC also throws little light on the taxon problem. In reply, it seems clear to us that the MCSC answers *both* the taxon and category problems/questions.

Regarding the latter, what makes a population S a species and not a subspecies, a genus, etc., is the level of genetic isolation of S in comparison to other populations by incompatibilities in uniquely coadapted mt and N_o-mt genes. If we want to extend our approach to higher taxa, we can estimate the percent divergence in mt and N genotypes, however, such an assessment will not address mitochondrial performance, as such high levels of divergence will all lead to complete mitochondrial dysfunction. It is important to note that evolution is occurring at the population/species level and not between phyla, classes, etc. per se. Higher taxa are also the result of evolution, but evolutionary mechanisms occur at the

population level between breeding individuals. For example, gene flow between two interbreeding populations can alter genotype frequencies within each population but will not determine whether phylum A mates with phylum B.

Regarding the former, in defining the MCSC to incorporate the constitutive condition noted above, species membership and individuation is included: the MCSC tells us that O is a member of S (and not some other species) in virtue of having the right combination of genes; namely, mt and N_O-mt genes that are uniquely coadapted to promote efficient OXPHOS. Such gene combinations will not be shared with other species and are specific to OXPHOS. Yet, one may object that the MCSC's answer to the taxon question only gives an operational criterion for determining species membership and is, thus, "metaphysically hopeless" (Devitt 2008, 362). In other words, the MCSC is similar to operational species concepts such as those referring to S16 RNA in bacteria. The S16 RNA properties unique to one bacterial species help distinguish it from other species. But they don't say much about what it is *to be* this particular bacterial species. Generally, one ought to explain how those properties that determine species membership are related to typical distinguishing features of said species.

Our reply comes in three parts. First, operationally-epistemically speaking, we can *know* that O belongs to S based on downstream, relational effects, such as comparing the genetics and mitochondrial function of parents and offspring. Metaphysically-ontologically speaking, what *makes* O an S—on the classificatory notion of essence that we have adopted—are the particular mt and N_O-mt gene combinations that we have discussed. Crucially, Hill (2019a, 157) considers concrete proposals for characterizing the MCSC operationally that "make mt genotypes good predictors of species boundaries even if mitonuclear coadaptation plays no direct role in the speciation process"—call this "neutral theory." He then shows that several predictions of neutral theory contradict the evidence, thereby further dispelling the charge that the MCSC is merely an operational criterion for classifying organisms according to species. Second, by requiring that those properties that determine species membership tell us about typical distinguishing features of said species in the same way that, say, "having atomic number 79" is causally-explanatorily related to being "shiny, malleable, yellow, and metallic," the objector is begging the question against anyone who looks to give a non-traditional essentialist account of species. Coadapted mt and N_O-mt genes unique to S1 (and not S2) are intrinsic properties that *partly* explain features typical of S1 (and not of S2) such as oxygen consumption, ATP production, oxidative damage, etc. But they don't determine all typical phenotypic traits characteristic of S1 in the same way that atomic number of 79 ostensibly determines most observable characteristics of gold. To us, this suggests that evolutionary biology is different from chemistry and quantum mechanics. Still, if we want essences to abide by the "Sober demand," then Devitt (2008, 2023) is likely correct to hold that biological essences are partly intrinsic and partly relational/historical.

Third, Devitt (2008, 361) holds that his essentialism "*partly explains* why the members of a species have the characteristics ... [that] make them a species: it is partly because those members have a certain essential intrinsic properties that, in the given environment, they interbreed and occupy a niche." However, he says little in terms of what said intrinsic properties amount to except that they are "probably largely genetic." The MCSC, then, can fill in the details on some of the largely genetic properties to which Devitt may be referring. Moreover, as noted above, the MCSC partly explains the causal generalizations underlying organism survival and reproductive success, and the units that play a fundamental role in the evolutionary process. Specifically, the *unique combinations* of genes linked to mitochondrial function explain both organismal function that leads to the propagation of genes in subsequent generations (survival and reproduction) and the fundamental units (here, the genes) of eukaryotic evolution as a process.

6. Conclusion

We argued that the MCSC implies a thoroughgoing intrinsic essentialism about species, and that philosophers of biology ought to take seriously the MCSC and its consequences. Our essentialism is thoroughgoing in the sense that, first, properties that determine species membership are fully intrinsic (in contrast with relational and Devitt's essentialism). Second, we maintain both a semantic role and a partial causal/explanatory role for species essences and, in contrast with Devitt's essentialism, the MCSC only applies to species. Crucially, our goal was not to give a knock-down argument against alternative species concepts or philosophical accounts of species. Rather, we argued for enlarging the conceptual possibility-space regarding species—considering the MCSC—to include thoroughgoing intrinsic essentialism.

We conclude with two final points. First, we assumed monism about species. If, instead, pluralism about species concepts holds, and the correct concepts include one that is intrinsic in character, such as the MCSC, and another that is relational, such as the PSC, this suggests a hybrid view of essentialism about species (like Devitt's): qua the MCSC, intrinsic kind essentialism holds, qua the (say) PSC, relational kind essentialism holds, so that species' essences are partly intrinsic and partly relational. Second, there is a debate in the literature concerning the question of whether species are natural kinds with essences, individuals (e.g., Ghiselin (1974) and Hull (1978)), natural kinds via the notion of a Homeostatic Property Cluster (e.g., Boyd (1999)), etc., with some exciting new contributions such as Slater (2013)—who defends an “adjectival stance,” wherein natural kindness is a status attributed to groups of real organisms—and Austin (2019)—who argues for kind essentialism through a neo-Aristotelian metaphysics in which natural kinds are distinguished by their capacities and propensities. Unfortunately, it is beyond our scope to enter these debates. Instead, we adopt a neutral stance since, as Okasha (2002) notes: “...it is largely a matter of convention whether species are conceptualized as individuals, kinds or historical entities... [Thus,] the issues about [intrinsic versus relational] essentialism do not depend on which view of the ontological status of species we favour” (193-194). Still, wish to briefly outline in what manner the MCSC suggests that species are natural kinds “of sorts.”

On the one hand, MCSC-motivated species-as-natural kinds seem to satisfy some common desiderata in the literature (e.g., Bird and Tobin (2023)): members of a natural kind should have some (natural) properties in common, natural kinds should permit inductive inferences, and members of a natural kind should form a kind. But other criteria aren't met: species, on the MCSC, aren't categorically distinct, they don't form a hierarchy, and they don't participate in laws of nature. To us, this suggests that characterizations of “natural kinds” ought to be tailored to and motivated by particular sciences instead of decided by pre-theoretic intuitions, a priori means, or other sciences. In any case, an MCSC-motivated analysis of such issues must await another occasion.

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