A Critique of Relational Essentialism in Biology

Abstract

Okasha (2002) and others (Sterelny and Griffiths, 1999; Wilson, 1999) argue that biological species have relational essences. Okasha's argument for relational essences is based on definitions of species from biology called 'species concepts.' Okasha's argument hinges on two premises: species concepts define species in terms of relational properties, and these relational properties are biological essences. I show that these two premises are false and, accordingly, that relational essentialism is not justified by the modern species concepts. Whereas some of the modern species concepts define species in terms of non-relational properties, other species concepts define species via relational properties without these properties being species essences. Despite what Okasha and others suggest, the modern species concepts do not warrant relational essentialism.

Keywords essentialism – species – species concepts – natural kinds – hybrid zones – introgression.

This paper is about the membership conditions for species taxa. An account of species membership should specify which feature I share with other humans that make me a member of *Homo sapiens* rather than, say, *Pan troglodytes* (chimpanzees). To that end, accounts of species membership use distinct *types* of features, such as overall similarity and common ancestry (see e.g., Ereshefsky, 1992). This paper evaluates an account of species membership advanced by Okasha (2002). According to Okasha, I am a member of *Homo sapiens* because I share a *relational essence* with other humans but not with chimpanzees. The goal of this paper is to show that Okasha's essentialism is incorrect (section 2). Okasha's argument hinges on two premises: species concepts define species in terms of relational properties, and these relational properties are biological essences. I show that these two premises are false and, accordingly, that relational essentialism is not justified by the modern species concepts. But before I move to my criticisms, let me introduce Okasha's relational essentialism first.

1 Okasha on species membership

The received view within philosophy of biology is that species essentialism is false. Species essentialism is the view that all and only members of a species must share a certain property, that species essence. In other words, essentialists believe that interspecific variation is confined to *accidental* features, leaving *essential* features invariant during a species' lifetime. Promoters of the received view maintain that the distinction between essential and accidental properties is biologically unfounded (Hull, 1965; Mayr, 1982, 1991; Sober, 1980). As opposed to the received view, Okasha (2002) claims that species essentialism is not only consistent with but also justified in current biology.

Okasha's (2002) argument against the received view relies on the distinction between *intrinsic* and *relational* properties. Intrinsic properties are features that something has regardless of what is happening outside of itself. A paradigmatic example of an intrinsic property is an object's mass. As opposed to intrinsic properties, certain properties of an object depend on the relation of an object to something else. For instance, an object's weight varies depending on whether it is on the Earth's or on the Moon's surface. In the case of biology, having a certain genotype (or phenotype) is an example of an intrinsic property whereas the property of being an ancestral taxon is a relational property. Having introduced the distinction between intrinsic and relational properties, let me discuss how Okasha's (2002) employs this distinction to articulate his version of essentialism.

Okasha (2002) claims that, although species do not have 'intrinsic' essences, species have 'relational' essences. According to Okasha, the arguments for the received view shows that intrinsic features of organisms (e.g., genotype) are not essential to species (ibid., p. 199).

Once we characterize species essences as relational properties, Okasha claims, Kripke's and Putnam's versions of essentialism can apply to species (Okasha, 2002, p. 202). Like Kripke and Putnam, Okasha thinks that "superficial morphological traits" are fallible indicators for species membership. But whereas Kripke and Putnam think that 'intrinsic' properties ultimately determine species membership, Okasha contends that 'relational' properties are what ultimately fix the extension of species taxa.[1]

As with Kripke and Putnam, Okasha believes that the essence of a kind is an empirical matter, determined by the relevant scientific theory rather than by a priori intuitions (ibid., p. 193). Okasha's argument for relational essentialism is based on species definitions from biology called *species concepts*. According to him, the current species concepts warrant the view that species contain relational essences. Like Okasha, other philosophers of biology also endorse this view. For instance, Sterelny and Griffiths say that, according to the current species concepts:

> No intrinsic genotypic or phenotypic property is essential to being a member of a species. People born with the wrong number of chromosomes, eyes, or arms are still human beings. *So the essential properties that make a particular organism a platypus, for example, are historical or relational* (Sterelny and Griffiths, 1999, p. 186, emphasis added).

Similarly, Wilson says:

> In contrast with the traditional view that essences are sets of *intrinsic* properties, reproductive and genealogical views of the species category imply that the properties determining species membership for a given organism are not intrinsic

[1] Williams (2011) disagrees with Okasha's interpretation of Putnam. According to Williams, Putnam did not take essences to always be intrinsic. Instead, Williams argues that Putnam assigned relational essences to disease kinds such as tuberculosis. A different reading of Putnam's theory of natural kinds is proposed by Hacking (2007). According to Hacking, "hidden structures" for Putnam were not essences but properties we choose according to our interests. Hacking also notes that Putnam later rejects the idea of metaphysical necessity as going beyond physical necessity. As Putnam says in 1990, "I now think that the question, 'What is the necessary and sufficient condition for being water *in all possible worlds?*' makes no sense at all. And this means that I now reject 'metaphysical necessity' " (Putnam, 1990, p. 70).

> properties of that organism at all, but depend on the relations the organism bears to other organisms (Wilson, 1999, p. 192).

Because Okasha (2002) offers a more detailed defense of relational essentialism, I shall focus on Okasha's argument for relational essentialism in the remainder of this paper.[2]

2 Evaluating Okasha's argument

Before I turn to my criticisms of Okasha (2002), a few clarifications are in order. The word 'species' can have two meanings. The word 'species' may refer to species *taxa*, such as *Homo sapiens* and *Canis lupus*. Alternatively, 'species' may refer to the species *category* that contains all species taxa (Mayr, 1982, pp. 253–254). Defining a species taxon, such as *Homo sapiens*, consists in distinguishing *Homo sapiens* from other taxa. A definition of the species category, however, specifies what *Homo sapiens* and other species taxa have in common that distinguish them from taxa in other ranks, such as subspecies and genera.

Okasha's argument for species essentialism is based on the assumption that species concepts fix the extension of species 'taxa.' Species concepts are primarily definitions of the species 'category' (Mayden, 1997; Richards, 2010). That is, species concepts specify why a taxon belongs to the species rank—rather than the genus or the subspecies ranks. Species concepts are also used to fix the extension of species taxa (Sites and Marshall, 2003, 2004; Wiley and Lieberman, 2011).[3] However, it is worth noting that Okasha (2002) advances a specific account of how species concepts determine the extension of species taxa. In particular, Okasha's argument for species essentialism relies on two premises: (i) "all modern species concepts" make use of *relational*—rather than intrinsic—properties for determining the membership conditions of species taxa (ibid., p. 201); and (ii) species concepts fix the

[2] In addition to Okasha, other philosophers have recently criticized the received view (e.g., Devitt, 2008; Dumsday, 2012; LaPorte, 2004). See Ereshefsky (2010b) for a review of this recent essentialist trend in philosophy of biology.

[3] As Sterelny and Griffiths (1999) explain, "[s]pecies concepts have been seen as serving two functions. Seen one way, they specify the membership conditions for species: they tell us whether some arbitrarily chosen organism is (say) a member of *Canis familiaris*. . . . Seen another way, they tell us what all species have in common — what all the populations we think of as species share" (ibid., p. 211).

extension of species taxa by ascribing *essences* to species taxa. The thesis (i) alone does not imply (ii). For instance, Mayr and Ashlock contend that "the word 'species' in biology is a relational term" without endorsing species essentialism (Mayr and Ashlock, 1991, p. 27). I criticize these two premises in this section. My position is that Okasha's (2002) essentialism relies on an incorrect account of how the modern species concepts fix the membership conditions of species taxa. My first criticism is that Okasha wrongly assumes that the modern species concepts define species in terms of relational properties. My second criticism is that other species concepts that define species in terms of relational properties do not assume that these properties are species essences.

2.1 Criticism 1: not all modern species concepts define species in terms of *relational* properties

Okasha groups species concepts into four categories: phenetic, interbreeding, ecological, and phylogenetic concepts (Okasha, 2002, p. 199ff.). The phenetic concepts define species in terms of 'overall similarity.' Organisms would belong to the same species because they are more similar to each other than organisms belonging in a different species. Okasha rejects the phenetic species concept, however: "[g]iven the lack of principled grounds for choosing one similarity measure over another, phenetic concepts enjoy little popularity today" (ibid., p. 199). Different from the phenetic species concept, Okasha claims that the other three species concepts are well-accepted by current biology. Okasha describes the other three types of species concepts as follows (ibid., pp. 200–201). Interbreeding species concepts define species in terms of reproduction. Okasha's main example of an interbreeding species concept is Mayr's Biological Species Concept (BSC), which defines species as reproductively isolated populations.[4] Instead of defining species in terms of reproduction, the ecological concept defines species in terms of the ecological resources. For example, according to Van Valen's Ecological Species Concept (ESC), "two organisms are members of the same species

[4] Another example of a interbreeding species concept Okasha considers is Paterson's (1992), which defines species in terms of mate-recognition systems. See Okasha (2002, p. 200).

if they share the same ecological niche" (Okasha, 2002, p. 200). Finally, the Phylogenetic Species Concepts (PSC) defines species as "particular chunks of the genealogical nexus, bounded by speciation events and extinction events" (ibid., p. 200).

Okasha contends that the three well-accepted species concepts define species in terms of relational essences. In more detail, Okasha claims that these species concepts define species in terms of the following relational properties: "being able to interbreed successfully with one group of organisms and not another" (BSC); "occupying a particular ecological niche" (ESC); and "being a member of a particular segment of the genealogical nexus" (PSC) (ibid., p. 201). Because species concepts are species definitions, Okasha claims that these relational properties are species essences: all and only members of a species *must* satisfy one of these properties. Briefly, the gist of Okasha's argument is that species taxa contain relational essences because that is how species are defined in current biology.

According to Okasha, the phenetic species concept uses intrinsic features to define species (overall similarity), but biologists have abandoned this species concept because it relies on the ill-defined notion of 'overall similarity.' Nevertheless, as I shall show below, the phenetic species concept is not the only concept that defines species in terms of intrinsic properties. Instead of using the notion of 'overall' similarity, some of the modern species concepts define species in terms of a 'special' type of similarity, such as homologous characters and genotypic similarity. Thus there are two problems with Okasha's characterization of the modern species concepts. First, species concepts can make use of intrinsic properties without embracing the pheneticist notion of 'overall similarity.' Secondly, the modern species concepts do not favor relational over and against intrinsic properties when defining species. These points show that Okasha is wrong to think that the modern species concepts justify relational essentialism. The goal of this section is to establish these points by introducing how different species concepts define species in terms of intrinsic properties.

Okasha claims that the Phylogenetic Species Concept (PSC) defines species in terms of genealogical relations. That is not correct (see e.g., Wheeler and Meier, 2000). More specifically, there are two types of PSC: character-based and history-based PSC (Baum and Donoghue, 1995). According to the *character-based* PSC, species are defined in terms of a type of characters called 'homologies.'[5] For the *history-based* PSC, species are defined by historical relations (i.e., ancestor-descendant relations). Character-based PSCs define species in terms of intrinsic properties (homologous characters); history-based PSCs define species in terms of relational properties (ancestor-descendant relations). History-based PSCs agree with Okasha's argument, but not character-based PSCs.

Before I consider some versions of character-based PSCs, I must introduce the distinction between 'patterns' and 'processes' (Beatty, 1982). Character-based PSCs define species in terms of the results of evolution, the *patterns* of shared homologies. This feature of character-based PSCs sets them apart from other species concepts that define species in terms of the *processes* responsible for the evolution of species, such as the Biological Species Concept (BSC) and the Ecological Species Concept (ESC). According to BSC, reproductive isolation is necessary to explain the stable coexistence of species. Without reproductive barriers, a promoter of BSC would say, the species would fuse together. According to ESC, it is not reproductive isolation but the environmental processes in different niches that cause the stable coexistence of species. Processes are typically relational properties: interbreeding relations (BSC) and relations between organisms and their environment (ESC). Okasha is right about species concepts that define species in terms of processes, but not about species concepts that define species in terms of patterns. Having introduced the distinction between process and pattern, I now turn to Cracraft's character-based PSC.

Cracraft (1992) claims that species should be defined in terms of patterns rather than processes:

> Biologists have now come to believe that these processes [that produce species] are highly variable and often depend upon the group being studied. To have a number of species concepts, each possibly applying to a different group, obscures

[5] And for the character-based PSCs homologies are not defined in terms of historical relations. See Baum and Donoghue (1995) for further details.

> the potential discovery of common phylogenetic and evolutionary patterns from one taxon to another. The results of evolution appear to be more or less the same in all groups. ... Thus, by defining species in terms of the resulting *pattern*, it allows us to investigate these processes, unbiased by a species concept that is derived from our preconceptions of those processes (Cracraft, 1992, pp. 102–103).

As opposed to Mayr and Van Valen, Cracraft does not believe that there is a single type of process that is responsible for the evolution of every single species. Cracraft's point is that we can overcome this problem if we define species in terms of evolutionary patterns—since there is a *single* evolutionary pattern. More specifically, Cracraft defines species "as the smallest diagnosable clusters of individual organisms within which there is a parental pattern of ancestry and descent" (ibid., p. 103). For Cracraft these "diagnosable clusters" are delimited via unique combination of (homologous) characters (ibid., p. 103).

A more recent version of a character-based PSC has been proposed by Wheeler and Platnick (2000). Like Cracraft (1992), they believe that species should be defined in terms of patterns rather than the evolutionary processes that shaped such patterns. According to them, "[a]s phylogeneticists divorced the discovery of historical patterns of cladistic relationships from unnecessary assumptions about evolutionary processes (Platnick, 1979), it became apparent that modes of speciation need not be confounded with criteria used to distinguish among species" (Wheeler and Platnick, 2000, p. 55). Moreover, Wheeler and Platnick maintain that whereas "evolutionary patterns are the cumulative result of countless kinds of processes acting singly and in combination" (ibid., p. 62), there is a single resulting pattern from the confluence of these many processes. Their character-based definition of species is then compatible with different speciation theories. Wheeler and Platnick's species definition is similar to Cracraft's. Species for them are "the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states" (ibid., p. 58). Thus, for the promoters of the character-based PSC such as Cracraft, Wheeler and Platnick, defining species in terms of evolutionary 'patterns' (intrinsic properties of organisms) is preferable to defining species in terms of evolutionary 'processes' (relations).[6]

Another example of a character-based species concept is Mallet's (1995) genotypic cluster species concept, which defines species in terms of genotypic similarity. Like promoters of the character-based PSC, Mallet claims that a species concept should not contain assumptions of how new species evolve. Instead, Mallet contends that species should be defined in terms of how they are recognized. In opposition to Mayr's BSC, Mallet says: "it has never been clear why we need to improve on a good taxonomist's or naturalist's definition. Viewing species as anything other than definable groups of individual organisms risks weaving hidden evolutionary constraints into the definition, just as the creationist concept of species made it hard to imagine evolution" (Mallet, 1995, p. 296). That is, by defining species in terms of how we recognize them, we can study how species evolve without privileging a particular evolutionary process beforehand, such as reproductive isolation. To that end, Mallet proposes we define species as genotypic clusters:

> [W]e see two species rather than one if there are two identifiable genotypic clusters. These clusters are recognized by a deficit of intermediates, both at single loci (heterozygote deficits) and at multiple loci (strong correlations or disequilibria between loci that are divergent between clusters) (ibid., p. 296).

Hence, like the character-based PSC, Mallet's species concept define species in terms of intrinsic properties. The difference is that Mallet uses genotypic similarity instead of homologous characters.

Summarizing, even if we follow Okasha in discrediting the phenetic species concept, intrinsic properties are widely used by modern species concepts. That is because of the dispute concerning whether species should be defined in terms of characters (intrinsic properties) or processes (typically relational properties). Some like Mayr and Van Valen think that a species concept should specify the process responsible for species evolution, such as

[6] For other examples of character-based PSC, see Eldredge and Cracraft (1980), Nelson and Platnick (1981) and Nixon and Wheeler (1990).

reproductive isolation. Others such as Mallet, Cracraft, Wheeler, and Platnick disagree. According to them, defining species in terms of evolutionary processes adds an unwelcome bias to the species concept. My point here is not to defend character-based species concepts, but to show that Okasha's depiction of the modern species concepts is incorrect. Moreover, as Lewens (2012) points out, the use of character-based species definitions are not exceptional in current biology. Character-based species definitions are used in different fields of biology such as microbiology (Ereshefsky, 2010a), botany (Stuessy, 2009) and protistology (Finlay, 2004; Harper et al., 2009). Thus, my criticism of Okasha (2002) is that his argument relies on a false premise; viz., that the modern species concepts define species taxa in terms of relational properties. Not only are some prominent species concepts character-based, but also character-based species definitions are widely used in current biology. Accordingly, an argument for relational essentialism cannot be neutral concerning the species problem: Okasha's argument for relational essences can only take off if complemented with an argument against every non-relational species concept, such as Mallet's (1995). Nevertheless, even if complemented with such an argument, I think there is a further difficulty with Okasha's argument.

2.2 Criticism 2: BSC does not ascribe relational essences to species

In this section I argue that Okasha's essentialism is incompatible with the Biological Species Concept (BSC). According to Okasha, the interbreeding concepts such as Mayr's BSC "are probably the most widely favoured" (ibid., p. 200). Furthermore, prominent phylogenetic species concepts depend on BSC, such as Meier and Willman (2000) and Mishler and Brandon (1987). Hence, if Okasha's essentialism is incompatible with BSC, that shows that Okasha is wrong to say that his essentialism is justified by the interbreeding and the phylogenetic species concepts. In what follows, I first discuss why the notion of 'population' is central for BSC, and then show why BSC is incompatible with relational essentialism.

Earlier attempts of defining species in terms of interbreeding did not use the notion of 'population' (Mayr, 1982, pp. 270–271). At the beginning of the Modern Synthesis, Dobzhansky (1935) formulates reproductive isolation as a property of individual organisms: "a species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of hybrids, or both)" (Dobzhansky, 1935, p. 353). However, his definition has the drawback of implying that interspecific organisms do not exchange genes (Coyne and Orr, 2004, p. 28). Although Dobzhansky acknowledges that reproductive isolation is not all-or-nothing, the possibility of species hybridization is not built into his species definition. The same is not true about Mayr's definition. According to him, "[s]pecies status is the property of populations, not of individuals. A population does not lose its species status when occasionally an individual belonging to it makes a mistake and hybridizes with another species" (Mayr, 2004, p. 178). So, reproductive isolation is a population-level phenomenon: two populations can be said to be reproductively isolated while individual organisms belonging to those different populations hybridize with each other.[7] Furthermore, current formulations of BSC follow Mayr's lead in understanding reproductive isolation as a relation between populations (see e.g., Coyne and Orr, 2004; Ghiselin, 1997; Johnson, 2006; Sober, 2000).

While Mayr and others describe reproductive isolation as a property of 'populations', Okasha construes essences as relations between individual 'organisms.' Okasha's relational essentialism is aimed at accounting for why an individual organism, say, a pet dog, belongs to *Canis lupus* rather than another species. According to him, a pet dog belongs to the species *C. lupus* because of how this dog relates "to other organisms and/or to the environment" (Okasha, 2002, p. 199). Okasha claims that membership in a BSC-species is fixed by the relation 'being able to interbreeding with' (ibid., p. 201). I disagree with Okasha that this relation is an *essential* property of conspecific organisms. Given what we know about species evolution, complete reproductive isolation should not be the rule. Incomplete

[7] Like BSC, ESC is also concerned with populations. For Van Valen (1976) species are *lineages* that occupy a certain adaptive zone, and a lineage is "a clone or an ancestral-descendant sequence of populations" (ibid., p. 233). And similar to Mayr, Van Valen understands populations as groups in which individuals inside the population exchange genes "more frequently than with individuals outside the population" (ibid., p. 234).

reproductive isolation occurs not only during speciation—since speciation is often a gradual process, but also with well-established BSC-species, such as Darwin's finches (Grant, 1993) and *Drosophila* species (Powell, 1983). That is why Mayr and others describe reproductive isolation as a population-level relation; for two populations can be reproductively isolated while some individual members of these populations interbreed with each other. Accordingly, the relation 'interbreed with' is not essential but an *accidental* property of conspecific organisms. Okasha and others are wrong to think that 'interbreed with' is an essential property of conspecific organisms.

According to the above objection, interbreeding is a *population*-level relation whereas essences are *organism*-level relations. But what if we suppose that the relation 'interbreed with' is an essential property of populations instead? Would that save relational essentialism? This sort of essentialism would be different from what Okasha and other relational essentialists aim for; yet, that could show that relational essentialism could be grounded on BSC. My contention, however, is that 'interbreed with' cannot be an essential feature of conspecific populations either. Let me explain why by way of an example.

Hybrid zones are regions where two BSC-species meet and hybridize (Barton, 2001; Barton and Hewitt, 1985; Secondi, Faivre, and Bensch, 2006). An example of a hybrid zone occurs with the two bat species, *Myotis blythii* and *M. myotis*, that meet and hybridize in Southern and Central Europe (Berthier, Excoffier, and Ruedi, 2006). An important feature of hybrid zones is that they can be responsible for interspecies *introgression*, where genes of one species are permanently incorporated into another species (Currat et al., 2008). For instance, hybridization events caused the mitochondrial genome of the bat species *M. blythii* to be replaced by that of *M. myotis* (Berthier, Excoffier, and Ruedi, 2006). In short, hybrid zones not only illustrate hybridization between species, but also that hybrid zones can foster interspecies introgression.

When formulated in terms of populations, relational essentialism implies that two populations must belong to the same species if they can successfully interbreed with each other.

Cases of interspecies introgression show that this is false; populations of *M. blythii* and *M. myotis* can successfully interbreed at the hybrid zone while belonging to different species. But if interbreeding alone does not distinguish *M. blythii* and *M. myotis* from each other, what accounts for them being different species? What matters for species status is not gene flow alone, but how gene flow *affects* the gene pools of the two populations. Let me elaborate this point by returning to the two bat species, *M. blythii* and *M. myotis.* Although there is interspecies introgression of mitochondrial DNA between these two bat species, both species are well differentiated with respect to their nuclear DNA. The nuclear and the mitochondrial genomes have different evolutionary dynamics (Berthier, Excoffier, and Ruedi, 2006). This gene flow pattern is what accounts for why *M. blythii* and *M. myotis* are different species: they constitute different species because their nuclear DNA continue to diverge despite mitochondrial gene flow.[8] Interbreeding does not fuse the *M. blythii* and *M. myotis* into a single species because interbreeding only affects part of their genome, the mitochondrial DNA.

BSC is in the business of tracking genetic divergence between population lineages. As explained above, this allows BSC to be successfully applied to the study of hybrid zones with interspecific introgression. In contrast, relational essentialism wrongly depicts BSC as being concerned with whether interbreeding happens, without taking into account the *effects* of such interbreeding events. But if the relation 'interbreed with' were thought of as an essential feature of populations, BSC would fail to account for why *M. blythii* and *M. myotis* are different species—because populations of these two species can successfully interbreed with each other. Okasha's relational essentialism is supposed to be justified by systematists' practice; my point is that the application of BSC in the study of hybrid zones shows that relational essentialism conflicts with systematists' practice.

In short, the relation 'interbreed with' is not an essential feature of BSC-species, no matter

[8] According to Petit and Excoffier (2009), mitochondrial and nuclear DNA are subject to different levels of gene flow because the dispersive sex in these two bat species is male. In species with female-biased dispersal like the warbler species *Hippolais icterina* and *H. polyglotta*, Petit and Excoffier predict the opposite pattern: nuclear DNA should introgress more readily than maternally inherited mitochondrial DNA.

if interbreeding is thought of as a relation between individual organisms or whole populations. Viewing 'interbreed with' as an essential feature of conspecific *organisms* fails because well-established BSC-species such a Darwin's finches are known to hybridize with each other. Treating 'interbreed with' as an essential feature of conspecific *populations* fails because conspecific populations can also interbreed with each other, as illustrated by the hybrid zone between the species *M. blythii* and *M. myotis*. This is an important limitation of relational essentialism given the popularity of BSC, and considering that other prominent species concepts rely on BSC, such as Mishler and Brandon (1987). While relational essentialism depicts interbreeding as the sole criterion for individuating BSC-species, BSC takes into account both interbreeding and the effects of interbreeding events. This is not a new point. Hull had also made this point:

> Contrary to popular opinion, the production of an occasional fertile hybrid is not enough for biologists to consider two species one. What matters is how extensive the introgression is (Hull, 1978, p. 349).

Hence, supposing that 'interbreed with' is a species essence goes both against how BSC has been applied in nature and the theoretical motivations behind BSC. Relational essentialism is thus incompatible with BSC.

3 Conclusion

An appealing feature of Okasha's essentialism is its purported neutrality with respect to the species problem debate. That is, no matter which of the current species concepts one chooses, relational essentialism is supposed to hold. Okasha attempts to accomplish that by defending a general thesis of how the modern species concepts fix the extension of species taxa. For him, species concepts fix the members of species taxa by ascribing relational essences to them. The goal of this paper is to show that this view is incorrect. There is a substantial gulf between species concepts and species essentialism. Rather than being justified by the modern species concepts, Okasha's relational essentialism is incompatible with character-based species concepts (e.g., Mallet, 1995), Mayr's BSC, and history-based PSCs that depend on BSC (e.g., Mishler and Brandon, 1987). Character-based species concepts show that species concepts do not favor relational properties to intrinsic properties when defining species. Recent applications of BSC to hybrid zones show that BSC does not treat the relation 'interbreed with' as an essential feature of species. Instead, species status for BSC is contingent upon the effects of interbreeding events, such as the region of the genome affected by interbreeding. Therefore, different from Okasha and others have suggested, the modern species concepts do not warrant relational essentialism.

References

Barton, N. (2001). "The role of hybridization in evolution." *Molecular Ecology* 10, pp. 551–568.

Barton, N. and G. Hewitt (1985). "Analysis of hybrid zones." *Annual Review of Ecology and Systematics* 16, pp. 113–148.

Baum, D. and M. Donoghue (1995). "Choosing Among Alternative 'Phylogenetic' Species Concepts." *Systematic Biology* 20, pp. 560–73.

Beatty, J. (1982). "Classes and Cladistics." *Systematic Zoology* 31, pp. 25–34.

Berthier, P., L. Excoffier, and M. Ruedi (2006). "Recurrent replacement of mtDNA and cryptic hybridization between two sibling bat species *Myotis myotis* and *Myotis blythii*." *Proceedings of Royal Society B* 273, pp. 3101–3109.

Coyne, J. and H. Orr (2004). *Speciation*. Sunderland: Sinauer Associates, Inc.

Cracraft, J. (1992). "Species Concepts and Speciation Analysis." In: *The Units of Evolution: Essays on the Nature of Species*. Ed. by M. Ereshefsky. Cambridge: MIT Press, pp. 93–120.

Currat, M. et al. (2008). "The hidden side of invasions: massive introgression by local genes." *Evolution* 62, pp. 1908–1920.

Devitt, M. (2008). “Resurrecting biological essentialism.” *Philosophy of Science* 75, pp. 344–382.

Dobzhansky, T. (1935). “A Critique of the Species Concept in Biology.” *Philosophy of Science* 2, pp. 344–355.

Dumsday, T. (2012). “A new argument for intrinsic biological essentialism.” *The Philosophical Quarterly* 62, pp. 486–504.

Eldredge, N. and J. Cracraft (1980). *Phylogenetic Patterns and the Evolutionary Process*. New York: Columbia University Press.

Ereshefsky, M., ed. (1992). *The Units of Evolution: Essays on the Nature of Species*. Cambridge: MIT Press.

— (2010a). “Microbiology and the species problem.” *Biology and Philosophy* 25, pp. 553–568.

— (2010b). “What’s Wrong with the New Biological Essentialism.” *Philosophy of Science* 77, pp. 674–685.

Finlay, B. (2004). “Protist taxonomy: an ecological perspective.” *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 359, p. 599.

Ghiselin, M. (1997). *Metaphysics and the Origin of Species*. State University of New York Press.

Grant, P. (1993). “Hybridization of Darwin’s finches on Isla Daphne Major, Galapagos.” *Philosophical Transactions: Biological Sciences* 340, pp. 127–139.

Hacking, I. (2007). “Putnam’s theory of natural kinds and their names is not the same as Kripke’s.” *Principia* 11, pp. 1–24.

Harper, J., G. Gile, E. James, K. Carpenter, P. Keeling, and R. Redfield (2009). “The Inadequacy of Morphology for Species and Genus Delineation in Microbial Eukaryotes.” *PLoS One* 4.

Hull, D. (1965). “The Effect of Essentialism on Taxonomy – Two Thousand Years of Stasis (I).” *The British Journal for the Philosophy of Science* 15, pp. 314–326.

Hull, D. (1978). “A Matter of Individuality.” *Philosophy of Science* 45, pp. 335–360.

Johnson, N. (2006). “The evolution of reproductive isolating barriers.” In: *Evolutionary genetics*. Ed. by C. Fox and J. Wolf. Oxford University Press, pp. 374–386.

LaPorte, J. (2004). *Natural kinds and conceptual change*. Cambridge: Cambridge University Press.

Lewens, T. (2012). “Pheneticism reconsidered.” *Biology and Philosophy* 27, pp. 159–177.

Mallet, J. (1995). “A species definition for the Modern Synthesis.” *Trends in Ecology and Evolution* 10, pp. 294–299.

Mayden, R. (1997). “A hierarchy of species concepts: the denouement in the saga of the species problem.” In: *Species: the Units of Biodiversity*. Ed. by M. Claridge, A. Dawah, and M. Wilson. London: Chapman & Hall, pp. 381–424.

Mayr, E. (1982). *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge: Harvard University Press.

— (1991). *One long argument: Charles Darwin and the genesis of modern evolutionary thought*. Cambridge: Harvard University Press.

— (2004). *What Makes Biology Unique?* Cambridge: Cambridge University Press.

Mayr, E. and P. Ashlock (1991). *Principles of systematic zoology*. McGraw-Hill.

Meier, R. and R. Willman (2000). “The Hennigian species concept.” In: *Species concepts and phylogenetic theory*. Ed. by Q. Wheeler and R. Meier. New York: Columbia University Press, pp. 30–43.

Mishler, B. and R. Brandon (1987). “Individuality, pluralism and the phylogenetic species concept.” *Biology and Philosophy* 2, pp. 397–414.

Nelson, G. and N. Platnick (1981). *Systematics and Biogeography: Cladistics and Vicariance*. New York: Columbia University Press.

Nixon, K. and Q. Wheeler (1990). “An amplification of the phylogenetic species concept.” *Cladistics* 6, pp. 211–223.

Okasha, S. (2002). “Darwinian metaphysics: species and the question of essentialism.” *Synthese* 131, pp. 191–213.

Paterson, H. (1992). “The Recognition Concept of Species.” In: *The Units of Evolution*. Ed. by M. Ereshefsky. Cambridge: MIT Press, pp. 139–58.

Petit, R. and L. Excoffier (2009). “Gene flow and species delimitation.” *Trends in Ecology & Evolution* 24.

Platnick, N. (1979). “Philosophy and the transformation of cladistics.” *Systematic Zoology* 28, pp. 537–46.

Powell, J. (1983). “Interspecific cytoplasmic gene flow in the absence of nuclear gene flow: evidence from *Drosophila*.” *Proceedings of the National Academy of Sciences* 80, pp. 492–495.

Putnam, H. (1990). “Is water necessarily H_2O?” In: *Realism with a human face*. Ed. by J. Conant. Cambridge: Harvard University Press, pp. 54–79.

Richards, R. (2010). *The species problem: a philosophical analysis*. Cambridge: Cambridge University Press.

Secondi, J., B. Faivre, and S. Bensch (2006). “Spreading introgression in the wake of a moving contact zone.” *Molecular Ecology* 15, pp. 2463–2475.

Sites, J. and J. Marshall (2003). “Delimiting species: a Renaissance issue in systematic biology.” *Trends in Ecology and Evolution* 18, pp. 462–70.

— (2004). “Operational Criteria for Delimiting Species.” *Annual Review of Ecology and Systematics* 35, pp. 199–227.

Sober, E. (1980). “Evolution, population thinking, and essentialism.” *Philosophy of Science* 47, pp. 350–383.

— (2000). *Philosophy of Biology*. 2nd. Westview Press.

Sterelny, K. and P. Griffiths (1999). *Sex and death: An introduction to philosophy of biology*. University of Chicago Press.

Stuessy, T. (2009). *Plant Taxonomy: the systematic evaluation of comparative data*. 2nd ed. New York: Columbia University Press.

Van Valen, L. (1976). "Ecological Species, Multi-Species and Oaks." *Taxon* 25, pp. 233–39.

Wheeler, Q. and R. Meier, eds. (2000). *Species Concepts and Phylogenetic Theory*. New York: Columbia University Press.

Wheeler, Q. and N. Platnick (2000). "The phylogenetic species concept (*sensu* Wheeler and Platnick)." In: *Species concepts and phylogenetic theory*. Ed. by Q. Wheeler and R. Meier. New York: Columbia University Press, pp. 55–69.

Wiley, E. and B. Lieberman (2011). *Phylogenetics: theory and practice of phylogenetic systematics*. 2nd ed. Wiley-Blackwell.

Williams, N. (2011). "Putnam's traditional neo-essentialism." *The Philosophical Quarterly* 61, pp. 151–170.

Wilson, R. (1999). "Realism, Essence, and Kind: Resuscitating Species Essentialism?" In: *Species: New Interdisciplinary Essays*. Ed. by R. Wilson. Cambridge: MIT Press, pp. 187–208.