Species, Historicity, and Path Dependency

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This paper clarifies the historical nature of species by showing that species are path-dependent entities. A species' identity is not determined by its intrinsic properties or its origin, but by its unique evolutionary path. Seeing that species are path-dependent entities has three implications: it shows that origin essentialism is mistaken, it rebuts two challenges to the species-are-historical-entities thesis, and it demonstrates that the identity of a species during speciation depends on future events.

1. Introduction. The idea that species are historical entities is arguably the received view in the philosophy of biology. According to Sterelny and Griffiths (1999, 8), "Contemporary views on species are close to a consensus in thinking that species are identified by their histories." A partial list of philosophers that hold this view includes Hull (1978), Sober (1984), Ereshefsky (1991), Matthen (1998), Griffiths (1999), Okasha (2002), and LaPorte (2004).

The species-are-historical-entities thesis has two main tenets. First, historical relations rather than intrinsic similarities determine species identity. As Sober (1994, 165) writes, "Organisms are conspecific in virtue of their actual historical relationships to each other, not in virtue of their degree of genotypic or phenotypic similarity." Burt the beaver is a member of *Castor canadensis* not because he is similar to other beavers but because he stands in the right relations to other beavers and their common ancestor. According to the second tenet, a species is a spatiotemporally continuous entity. A species cannot be historically gappy, nor can it consist of spatiotempo-

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rally isolated lineages. Burt and his conspecifics form a spatiotemporally continuous lineage of beavers tracing back to the founding population of *C. canadensis*.

Both tenets of the species-are-historical-entities thesis have come under fire. Devitt (2008) and Elder (2008) maintain that mere history is insufficient for determining species membership. Intrinsic differences, they argue, are also required. Devitt and Elder take this stand in an attempt to revive intrinsic essentialism for species. A second challenge to the species-are-historical-entities thesis asserts that species can be historically gappy, that species need not be spatiotemporally continuous entities. A number of philosophers pose this challenge, including Kitcher (1984), Ruse (1987), Boyd (1999, 2010), Devitt (2008), and Elder (2008).

This paper defends the species-are-historical-entities thesis from these challenges. It also tries to do something more fundamental, namely, clarify the historical nature of species. Species, as we shall see, are path-dependent entities. A species' identity is not determined by its origin or its intrinsic properties but by its unique evolutionary path. Seeing that species are path-dependent entities implies that origin essentialism is mistaken. It also shows that the identity of a species during speciation depends on future events.

2. Challenge 1: Mere History Is Insufficient for Determining Species Membership. Let's review the first challenge to the species-are-historical-entities thesis. Devitt (2008) and Elder (2008) argue that membership in a species cannot solely depend on historical relations among the organisms of a species. They contend that some intrinsic difference is necessary for distinguishing membership in different species. Their argument focuses on speciation. It can be described using figure 1.

Suppose that A is a species and B is a species that branches off A. The little rectangle at the branching point between A and B is the ancestral, or founder, population of B. According to the historical approach, B is a different species than A because it has a distinct ancestor, its founder population. All and only the members of B have that ancestor. Devitt and Elder ask, what makes that ancestor, the organisms in that little box, different from the organisms in lineage A such that we should think that there is the start of a new species? In the case imagined, the organisms in the ancestral population of B are not phenotypically or genotypically different from the organisms in A. That is, they are in the same range of variation. Devitt and Elder conclude that if B is a new species starting at the founder population, then the organisms in that population must be intrinsically different from the organisms in A. Devitt's and Elder's challenge raises a good question for the species-are-historical-entities thesis: How is the existence of a new genealogical branch, having a distinct insertion in history, sufficient to individuate a species?

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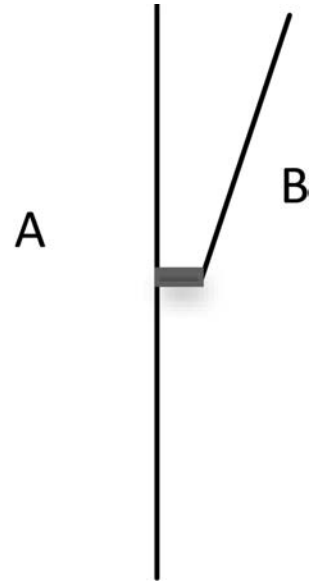


Figure 1.

To answer this question, we need to look more carefully at what makes species *historical* entities. I suggest that species are historical entities because they are path-dependent entities. This will answer Devitt's and Elder's challenge by showing that a new species at its start, at its branching event, need not be intrinsically different from its parent species. What is important is that the founding population of a species is on an evolutionary path that results in speciation.

3. Path Dependency. Desjardins (2011) highlights two forms of historicity: dependence on initial conditions, and path dependency. We can think of both of these notions as describing how events in the past affect a future event. According to the first notion of historicity, the probability of an outcome is largely a function of initial conditions. For example, the probability that Joe will die as a result of radiation exposure is largely a function of how much radiation he was exposed to at the Chernobyl nuclear power plant disaster. According to the second notion of historicity, path dependency, not only do initial conditions affect the probability of an outcome but so do events along the path, as well as the order of those events.

Consider Blount, Borland, and Lenski's (2008) "long-term experimental evolution" project. The experiment started with the production of 12 identically cloned populations from a single bacterium of *E. coli*. Blount

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et al. placed those populations in identical but separate environments. After 10,000 generations, one population acquired the adaptive phenotype of metabolizing citrate. The pressing question is, why did those populations end up having different traits, given that they started with the same genes and phenotypes and were kept in identical environments? The general answer is that something along the populations' paths, between initial conditions and outcomes, affected the outcomes. The specific answer is that the different populations had different sets of mutations. Moreover, the order of those mutations varied among the populations, and mutation order is a significant factor in the evolution of a new trait (Blount et al. 2008). Prior mutations and their occurrence in a particular order created the genetic background needed for a later mutation that caused an adaptive trait. This should not be surprising, given the well-known biological fact that traits are often the result of a number of genetic factors, and those factors must be in place before a final mutation can cause an adaptive trait. What I want to highlight is that the order of mutations is important. The same mutations might occur in another population. But vary the order, and the resultant adaptive trait may not occur (Beatty 2006).

Stepping back, we have a nice example of path dependency. Initial conditions were insufficient to produce an outcome: all 12 populations had the same initial conditions (same genotypes, phenotypes, and environmental factors); nevertheless, a citrate metabolizing phenotype evolved in one and only one population. That population's path—the occurrence of certain mutations in a particular order—was fundamental in causing the evolution of a citrate metabolizing phenotype.

4. Species Are Path-Dependent Entities. With the idea of path dependency in hand, let's see why species are path-dependent entities. In brief, the argument is this:

Premise 1. Species are independent lineages.

Premise 2. The question of whether something is an independent lineage (a species) is settled not by an initial branching event but by events that happen later in the path of that branch.

Conclusion. Species are path-dependent entities.

I won't argue for the truth of premise 1 now, but I will do so in section 7. Let's turn to the evidence for premise 2. As we shall see, prominent theories of speciation imply that speciation is a path-dependent process. They imply that whether a branch (on the Tree of Life) is a species is determined by events in the path of that branch, not merely at its initial branching event.

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The allopatric model of speciation is the most prominent account of speciation for sexual organisms. It states that speciation begins when a population becomes geographically separated from its parental species. Speciation is complete when such a population is reproductively isolated from its parental species. The members of a new species, in other words, must acquire reproductive isolating mechanisms that prevent them from interbreeding and producing fertile offspring with the members of its parental species. Reproductive isolating mechanisms come in two forms. Prezygotic mechanisms, such as incompatible sexual physiologies, prevent members of different species from mating. Postzygotic mechanisms stymie the development of viable offspring after mating. How do such isolating mechanisms come into existence? According to Mayr (1970), isolating mechanisms are by-products of new adaptations. For example, Podos (2001) observes that some of Darwin's finches are reproductively isolated because they have different mating calls. Furthermore, this difference in mating calls is a by-product of evolution for beaks that provide different ways to forage for food. (Some beaks are good for probing in wood, whereas others are good for pecking off the ground.) Different beak physiologies cause birds to have different mating calls. The next question to ask is, what is the source of new adaptations, such as beak shape? On the basis of their long-term evolution experiments, Blount et al. (2008) suggest mutation and mutation order. In other words, mutation order may be an important factor in speciation: reproductive isolating mechanisms are by-products of adaptations, and adaptations are due in no small part to mutation order.

Thus far we have seen one reason why speciation is a path-dependent process, namely, the importance of mutation order in causing adaptations that result in reproductive isolation. There are other processes that contribute to speciation, and those processes may be path dependent as well. Mayr (1963) and Coyne and Orr (2004) argue that given the relatively small size of geographically isolated populations, genetic drift can have a greater effect on the evolution of isolated populations than on entire species. Consequently, genetic drift can contribute to speciation by causing an isolated population to be genetically different from its parental species. The relevance to path dependency is that genetic drift is due to the sampling of genes in a population generation after generation. The *order* of those sampling events can affect the evolutionary trajectory of a population undergoing speciation.

Let's turn to a model of speciation that is particularly relevant to the topic of path dependency: Schluter's (2009) mutation order model of speciation. Schluter writes, "I define mutation-order speciation as the evolution of reproductive isolation by the chance occurrence and fixation of different alleles between populations" (737). For Schluter, mutation differences are important in speciation, and so is mutation order: "Evidence for mutation-order speciation comes from instances in which reproduction isolation ap-

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parently evolved as a by-product to conflict resolution between genetic elements within individuals," such as meiotic drive. "Distorter and restorer mutations are unlikely to be the same in different populations regardless of environment: thus the process leads to divergence" (740). Schluter is citing examples of speciation in which first there are mutations for distorter genes and then there are mutations for restorer genes. A by-product of these mutations and the order in which they occur is reproductive isolation.

I bring up Schluter's work not to argue that all speciation occurs this way but merely to provide evidence for the idea that speciation is a path-dependent process. Earlier I hypothesized that the evolution of reproductive isolating mechanisms is due in part to mutation and mutation order, and hence allopatric speciation is a path-dependent process. Schluter provides evidence of actual cases where this happens.

Now one might be wondering, surely there are instances of speciation that are complete at the branching event of a new species. In particular, there is speciation by polyploidy. Though philosophers of biology often talk of polyploidy as a form of instantaneous speciation, it is far from instantaneous. Polyploidy occurs when offspring have a greater number of chromosomes than their parents. Polyploidy can occur for several reasons (Coyne and Orr 2004, 324ff.). For instance, meiosis may accidently produce diploid gametes from diploid cells. Those gametes then self-fertilize and produce tetraploid zygotes. The resultant offspring have chromosomes that come in sets of four rather than diploid chromosomes that come in sets of two. Organisms from the parental stock and the resultant polyploids have different numbers of chromosomes. Thus, when the polyploids and the parental stock interbreed, their offspring are inviable.

It might seem that polyploidy is a case of speciation that is not path dependent but a type of speciation that occurs at a branching event. That is not correct. As Coyne and Orr (2004, 330–31) observe, most polyploids fail because even though they have postzygotic isolating mechanisms, they lack needed prezygotic mechanisms. Polyploids frequently backcross with their parental species, and their offspring are inviable. Consequently, polyploids are usually "mated to death" (330–31). Successful polyploids need to evolve prezygotic isolating mechanisms or become asexual. That takes time and does not occur at the initial increase in chromosome number. Briggs and Walters (1997) make a similar observation concerning polyploids' ability to compete ecologically. They argue that polyploids tend to be less adapted to their environments than their parental stock. Polyploidy does release "a great range of variation" (Briggs and Walters 1997, 242). Over time, new traits can occur that allow polyploids to outcompete their parents or exploit a new niche—but only over time.

The upshot is that the origin of a branch through polyploidy (the increase in chromosome numbers) is insufficient to make a new species. Whether

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there is a new species at a polyploidy branching event is determined by later events along the path of that branch, namely, whether polyploids develop prezygotic isolating mechanisms or become asexual, or whether they acquire traits to outcompete organisms in their parental stock. Polyploids have a leg up in the process of speciation, but speciation is not a done deal at the time chromosome numbers are multiplied.

Stepping back from these various speciation models, we see that a branching event, a unique origin, does not make for a new species. Whether there is a new species at that branching event depends on what happens later. It depends on the historical path of that branch. Species are historical entities in no small part because they are path-dependent entities. Sober (1984) nicely illustrates this historical component of species with a humorous analogy. In a comedy skit on the old TV show *The Show of Shows*, Syd Caesar opens a newspaper at the start of World War I. Its headline reads "WORLD WAR I BREAKS OUT." This headline is funny because World War I was not known as such at the time; what made that war World War I was that later there was World War II. By analogy, a branching event, a unique origin, is not sufficient for the existence of a new species. Whether that branch is a new species at the branching event depends on what happens later. It depends on the historical path of that branch.

5. Answer to Challenge 1. Let's return to Devitt's (2008) and Elder's (2008) challenge to the species-are-historical-entities thesis. They argue that mere history is insufficient for determining species membership. Their argument was rehearsed in section 2. Recall figure 1, which contains two species: species A and its daughter species B. According to the historical approach, B is a different species from A because it has a distinct ancestor (its founder population), represented by the rectangle in figure 1. Devitt and Elder ask, what makes that ancestor, the organisms in the rectangle, different from the organisms in A such that we should think that there is a new species? This is a good question because typically the organisms within a founder population and its parental species are in the same genotypic and phenotypic range. Devitt and Elder conclude that if B is a new species starting at the ancestral population, then the organisms in that population must be intrinsically different from the organisms in A. This shows, they contend, that historical relations are insufficient for determining species membership.

We now have an answer to their challenge. Devitt and Elder are right that there may be no significant intrinsic difference between a parental species and the founding population of its offspring species. But that does not mean that we do not have the start of a new species. Whether speciation is occurring at a branching point depends on what happens later. Speciation is a path-dependent process affected by events after the initial branching event. If later stages in the path of a branch include events that give rise to a new

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species, then speciation has started at that initial branching event. If there are no such later events, then that branching event was not the start of a new species but an unsuccessful twig on the Tree of Life. Devitt and Elder are wrong to require an intrinsic property difference between a parental species and the founding population of a new species at an initial branching event. Whether that branching event is the start of a new species depends on how the history of that branch unfolds.

Suppose Devitt and Elder were to respond that, yes, there is no intrinsic difference at the branching event, but there is one later, so there is an intrinsic property difference between A and B. The problem with this response is that Devitt and Elder cannot say that there is a new species at the branching event, because there is no intrinsic difference there. Furthermore, if they claim that new species do not begin at branching points, they contradict the well-received view in biology that new species do begin at branching events (De Queiroz 2007). Alternatively, Devitt and Elder might argue that speciation is a vague process and that it is indeterminate whether a branching event is a speciation event. The problem with this reply is that if no speciation-causing events happen after the branching event, then that branching event, by virtue of what happens (or does not happen) later, never was an indeterminate speciation event. It was merely the branching off of a population of an existing species. On the other hand, if speciation-causing events do occur after that branching event, then that branching event was indeed the start of a new species.

6. Challenge 2: Species Can Be Historically Gappy. Recall the second main tenet of the species-are-historical-entities thesis: species are spatiotemporally continuous lineages. A species cannot consist of separate disconnected lineages. A number of philosophers have challenged this tenet, including Kitcher (1984), Ruse (1987), Boyd (1999, 2010), Devitt (2008), and Elder (2008). They argue that a species can consist of spatiotemporally disconnected lineages. To bolster their case, they offer hypothetical examples of species that are historically gappy. Let's look at the example given by Kitcher (1984) and discussed by Boyd (1999, 2010).

Kitcher begins his example by citing the case of the lizard species *Cnemidophorus tesselatus*, which is the result of hybridization between *C. tigris* and *C. septemvittatus*. Kitcher observes that the hybrid species probably does not consist of spatiotemporally disconnected lineages, but he suggests that "it might all too easily have been" (1984, 322). He asks us to imagine that the first instance of the hybrid species is wiped out, yet the same speciation event between the same parental species occurs again later. Kitcher asks us to suppose that the lineages that result from these two speciation events fall within the "same range of genetic (morphological, behavioral, ecological) variation" (322). He concludes that we should consider them

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parts of the same species. If we consider them parts of the same species, then we have an example of a historically gappy species.

7. Answer to Challenge 2. As we have seen, there are various reasons for thinking that speciation is a path-dependent process. The evolution of reproductive isolating mechanisms, according to Mayr and others, is a by-product of selection for other traits. Such traits, given Blount et al.'s (2008) experiments, are likely the result of mutations in a particular order. Similar considerations apply to speciation involving adaptations that allow a new species to compete with its parental species (as in the case of speciation by polyploidy). Again, the acquisition of such traits may often depend on mutation order. Further evidence for speciation being a path-dependent process comes from Schluter's (2009) mutation order model of speciation. Then there is the observation that the order of gene sampling in genetic drift can affect a founder population's trajectory.

Putting these observations together, we have good reason to believe that two disconnected founder populations will not evolve the same species 'defining characters'.[1] Even if two populations start with genotypically and phenotypically identical organisms, they need to take the same evolutionary path to acquire the same set of characters. But given that different populations have different mutations, different mutation orders, different instances of genetic drift, and perhaps different selection regimes, it is unlikely that two populations will evolve the same species 'defining characters'. In other words, whether a new species results from a branching event depends on a series of later events, and it is unlikely that two distinct populations will undergo the same path of events. It is possible, but it is very unlikely given current biological knowledge.

Returning to Kitcher's hypothetical example of a species with disconnected lineages, the various theoretical considerations cited in this paper imply that such examples are unlikely in the real world. The path-dependent nature of speciation implies that the evolution of separate lineages with the same species 'defining characters' is not biologically plausible.

However, some biologists maintain that there are polyploid species consisting of spatiotemporally disconnected lineages. Soltis et al. (2009) report that the *Tragopogon* (Goatsbeard) genus consists of two such polyploid species. *T. miscellus*, they suggest, may have as many as 21 separate origins. *T. mirus* may have 11 origins. To support their claim that *T. miscellus* and *T. mirus* each consist of multiple lineages, Soltis et al. cite morphological,

1. By "defining characters" I mean those intrinsic traits that Kitcher and others believe are sufficient for membership in a particular species. Advocates of the species-are-historical-entities thesis would deny that species have such characters.

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cytological, and microsatellite marker evidence. How should a supporter of the species-are-historical-entities thesis respond to such cases?

Three responses are available. One is to deny that these polyploid species consist of lineages with independent origins. *T. mirus* is the result of hybridization between *T. porrifolius* and *T. dubius* (Soltis et al. 2009). Hull (1978) and Wiley (1981) suggest that hybrid species have one ancestor, namely, the two parental species of that hybrid. Thus, for Hull and Wiley the ancestor of *T. mirus* is *T. porrifolius* × *T. dubius*. Their motivation for counting *T. porrifolius* × *T. dubius* as a single ancestor is to preserve the cladistic assumption that every taxon has a single origin. If one is unsympathetic to this cladistic motivation, there is another reason to think that the different lineages of *T. mirus* have one origin. The various lineages of *T. mirus* are the result of hybridization from the same parental lineages. Consequently, each lineage of *T. mirus* is drawn from the same gene pool. If coming from the same gene pool is sufficient for having the same origin, then *T. mirus* has a single origin in the biologically relevant sense.

A second response to the suggestion that a species can consist of disconnected lineages is to put down one's foot and deny that such 'species' are species. Following Hull (1978), one could argue that such alleged species are not species because species are foremost units of evolution, and to be a unit of evolution a species must be a spatiotemporally continuous lineage. In brief, here is Hull's argument: 'Species' is a theoretical term from evolutionary theory and should be defined by that theory. In evolutionary theory, species are units of evolution, meaning that species are groups of organisms that evolve as a unit. Natural selection is the primary force that causes species to evolve. For evolution by natural selection to occur, a trait must pass through the generations of a species. That requires that reproductive relations connect the organisms of a species: parent-offspring relations and sexual relations between parents in sexual species. Such relations require that organisms, or their parts (gametes and DNA), come into contact. Therefore, evolution by selection requires that the generations of a species be spatiotemporally connected.

Returning to Soltis et al.'s (2009) case, the supporter of the species-are-historical-entities thesis can use Hull's argument as follows. Despite what Soltis et al. (2009) suggest, *T. mirus* is not an example of a historically gappy species because if it is historically gappy, it is not a species. Asserting otherwise conflicts with the fundamental role of species in evolutionary theory, to be units of evolution.

There is a third way a supporter of the species-are-historical-entities thesis can defend that thesis. She can allow that Soltis et al.'s cases are examples of historically gappy species but point out that such spatiotemporally disconnected species are the exception. Such species rarely occur because speciation is a path-dependent process. As we saw, it is unlikely that

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two populations will undergo the same path of events and evolve the same species 'defining characters'. This response is more modest than the previous one. That response asserts that it is impossible, given current biological theory, for species to be historically gappy. The path-dependent response asserts that gappy species are extremely unlikely. It predicts that the vast majority of species are historical entities.

In summary, there are three responses to the claim that Soltis et al.'s cases of polyploidy are examples of historically gappy species. First, one can deny that such species have multiple origins because in each instance a species' lineages are derived from the same gene pool. Second, one can follow Hull's evolutionary unit argument and deny that any group of disconnected lineages forms a species. Third, one can allow that these may be examples of spatiotemporally disconnected species but point out that they are the exception given that speciation is usually a path-dependent process. While the last response does not show that species must be spatiotemporally continuous entities, it provides a new reason to think that species are such entities.

8. Clarifying the Historical Nature of Species. Seeing that species are path-dependent entities helps answer prominent challenges to the species-are-historical-entities thesis. It also clarifies the idea that species are historical entities. Many philosophers point out that species have unique origins. They argue that a requirement of being a member of a particular species is having a certain origin or ancestor (Hull 1978; Griffiths 1999; Okasha 2002; LaPorte 2004; Matthen 2009). That is right, but what I want to highlight is that a species' origin, its branching event, is an important but insufficient component of a species' identity. A species' identity rests on both its origin and its historical path after that origin. If one looks at the branching event at the time it occurs, a species' identity is not determined (ontologically) because the existence of that species is not yet established. Further along the historical path of the branch, we can retrospectively say that the new species began at the branching event. To say that there is a unique species at a branching event requires the occurrence of events after the branching event. As we have seen, this is true even in the case of speciation by polyploidy. The point is that the historical nature of species includes not only their unique origins, as many philosophers emphasize, but also the evolutionary paths they take. Seeing that species are path-dependent entities adds an important component to the idea that species are historical entities.

Finally, I would like to turn to another idea associated with the species-are-historical-entities thesis. Sober (1980) suggests that species may have origin essences akin to the origin essences of individual organisms. Sober borrows the idea of origin essentialism from Kripke. Here is Sober's (1980 [1992], 254–55) description of how that idea applies to species: "Kripke

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(1972) has suggested that each individual human being has the essential property of being born of precisely the sperm and the egg of which he or she was born. If such individuals as organisms have essential properties, then it will presumably also be possible for individuals like *Drosophila melanogaster* to have essential properties as well." Sober does not say what a species' origin would be. He is merely suggesting the possibility of origin essentialism in species. Nevertheless, he is using Kripke's notion of origin essentialism, and for Kripke the essence of an organism is its particular sperm and egg. By analogy, the origin essence of a species would be its original population: the first population that branched off from its parental species.

How does origin essentialism for species fare given that speciation is a path-dependent process? At a branching point, when a population becomes separated from the main body of a species, it is not yet determined (ontologically) whether that group of organisms is a new species. As we have seen, it depends on future events. Therefore, a species' origin—when a population branches off from the main body of its parental stock—cannot be that species' essence. That origination event is insufficient for determining whether the isolated population is the beginning of a new species. If we want to talk about a species' essence in a historical sense, then that essence must be a species' origin plus its unique path. But in that case, the notion of origin is redundant: the idea of a unique path assumes a starting point. If species are path-dependent entities, then origin essentialism is false. At best, the historical essentialist can say that the essence of a species is its unique historical path.

How much of that path must be included in a species' historical essence (assuming that one wants to talk in terms of historical essences)? I have argued that the sequence of events a species undergoes during speciation is part of its historical path. Undergoing that sequence of events is obviously important for a species to be a different taxon from its parental species. Some biologists maintain that a species' identity also depends on the entire life of a species—its entire historical path (Wiley 1981; O'Hara 1993). They suggest that a lineage now thought to be a unique species may in fact not be a unique species but part of another species owing to future events. For example, future massive introgression may cause a lineage now thought to be its own species to be part of another species. According to these biologists, not until a species goes extinct is it determined whether a lineage thought to be a species is truly a unique species. I will not take up this suggestion here. (See O'Hara 1993 for discussion.) What we have seen in this paper is that speciation is a path-dependent process. That implies that species are path-dependent entities. Seeing that species are path-dependent entities clarifies the historical nature of species. It also rebuts two major challenges to the species-are-historical-entities thesis.

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