

# Phylogenetic Competition: Defining the Selective Environment

Hugh Desmond and Grant Ramsey

Institute of Philosophy

KU Leuven, Belgium

## ABSTRACT

Even though natural selection is often said to be simply a difference in fitness between individuals, this is strictly speaking inaccurate: the individuals must also share a selective environment. However, under what conditions do two individuals share a selective environment? Previous accounts, by analyzing the selective environment in terms of shared species, shared population, shared external environment, or a combination of those, have tended to trade one difficult concept for another. We propose instead to analyze the selective environment in terms of *phylogenetic competition*, where two individuals share a selective environment if and only if the branches of one individual's descendant lineage displace the branches of another's descendant lineage. We outline a quantitative measure and several empirical indicators for phylogenetic competition, and show how it can powerfully and flexibly deal with a range of cases.

**1. Introduction.** In 2011, researchers discovered large numbers of rodenticide-resistant mice in German populations of the Western European house mouse, *Mus musculus domesticus*. At first sight, one may suspect that this was nothing more than a textbook example of the spread of a beneficial mutation throughout a population. However, it turned out that the most probable explanation was “adaptive introgressive hybridization” (Song et al. 2011: 1296), where the rodenticide-resistant mice resulted from interspecific mating between *M. m. domesticus* and *M. spretus* (the Algerian mouse). The hybrid mice then went on to be in selective competition with *M. m. domesticus* individuals. Given that it is unclear whether the hybrids can even be considered to be members of *M. m. domesticus*, this raises a fundamental question: under what conditions may we say that two individuals are in selective competition? Do they, for instance, need to be in the

same region, or be exposed to the same environmental factors, or belong to the same population or species—or some combination of these conditions?

Central to the investigation of the fundamental question lies the identification the *selective environment* of the organisms (Brandon 1990). Only when the two populations (and by extension, two individuals) share a selective environment can they be said to be in selective competition. This can, for instance, help to determine whether a polymorphism in a population is the result of adaptive evolution, and whether the trait is likely to spread throughout the species (as in the example above). The selective environment also plays an important though often implicit role in many debates in philosophy of biology, including on how to distinguish drift from selection (Matthen and Ariew 2002; Walsh 2010), or to distinguish between different levels of selection (Bourrat 2014). A key role for the concept of the selective environment is that it allows *selection* to be distinguished from *sorting* (simple reproductive differentials)—a distinction central to many debates. Yet, despite its importance, there has been a surprising dearth of dedicated philosophical analysis of the concept of selective environment.

There is host of factors that may play a role in distinguishing sorting from selection: the similarity of the physical environments of the organisms in question (e.g., what causal processes is each exposed to?), behavioral similarity (e.g., how likely are they to migrate to new physical environments?), developmental similarity (e.g., how does the phenotypic development respond to changes in the physical environment?), and even the phylogenetic distance between the two organisms. The question at hand is which of these, if any, should be used to individuate selective environments.

The two main approaches to individuating selective environments emphasize one or more of these factors. The first is the population-based approach, where two individuals share a selective environment only if they are part of the same population (e.g., Millstein 2009, 2014). The second is the ecological approach, where two individuals share a selective environment when they share the same ecological conditions (e.g. Abrams 2014). Both accounts assume that the individuals are conspecifics. This assumption limits the reach of the accounts, since determining whether individuals are conspecifics is sometimes a difficult question and, as in the case of the house mouse, it is not clear that individuals need to be in the same species in order to share a selective environment.

What, then, are the conditions for two individuals to share a selective environment? What

information regarding phylogeny, ecology, behavior, development, and so on help to determine the boundaries of the selective environment? Are selective environment boundaries evolutionary facts independent of explanatory interests? (A key argument for the ‘statisticalist’ interpretation of natural selection is that selection, fitness, and drift are not causes of evolutionary change, but instead denote statistical summaries of this change—and because the summaries can be performed in a variety of different ways depending on one’s explanatory interests, selection, and the boundaries of selective environments, are partially constituted out of the interests of the biologists: see analysis in Desmond 2018; Ramsey 2013.)

In light of these considerations, in this paper we aim for a general account of the selective environment that is fully compatible with the states of affairs in taxonomy, where sorting populations into species can be a difficult task, one fraught with ambiguity (and sometimes even swayed by policy: see Frankham et al. 2012). Our goal is to give an account that does not rely on concepts that are themselves challenging to precisely define, like species, population, and niche—even though, as we will argue later, these concepts can be empirically relevant for determining whether two individuals share a selective environment. Finally, we initially develop the analysis with organisms in mind, but we aim for this account to be, in principle, applicable to other types of individual.

Our proposal is that two organisms share a selective environment if and only if they are in *phylogenetic competition*. Informally, phylogenetic competition occurs when two organisms compete to have their descendants represented in descendant populations. This occurs when branches from one descendant lineage displace branches from another descendant lineage. We hold that this is what it means for two individuals to share a common selective environment. While this account abstracts from the phylogenetic relatedness of the individuals, as well as the similarity of the factors in their respective physical environments, we will also argue how more traditional measures of populational or phylogenetic relatedness, or similarity in ecological conditions can be useful empirical indicators for phylogenetic competition.<sup>1</sup>

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<sup>1</sup> One assumption of the account in this paper is that it to be possible to distinguish between individuals of different generations, especially between parents and offspring. If one drops that assumption, the distinction between growth and reproduction becomes blurred (as is the case, for instance, for clonal plants or animals). However, because reproduction is central to the concept of natural selection, one could proffer that any limitations on individuation in phylogenetic competition are also limitations on the applicability of the concept of natural selection itself. Additionally, in many such cases where organismic individuality is blurred, or where some organisms are sterile workers, it is still possible to identify evolutionary individuals (Janzen 1977), and phylogenetic competition only

After introducing basic concepts of the environment (section 2) and giving a critical overview of the two main approaches to delimiting the selective environment (section 3), we outline in detail what phylogenetic competition is and how it can be formalized (section 4). In section 5, we discuss implications for phylogenetic competition.

**2. Environment Concepts.** Let's begin by situating the selective environment within a landscape of distinct environment concepts. The most basic environment concept is the *physical environment* of an organism. An organism is exposed to abiotic factors, such as temperature, humidity, acidity, or precipitation, and to biotic factors, such as conspecifics, predators, inquilines, or parasites. Such factors, assuming they can be quantified, can be represented as continuous or discrete variables. A physical environment can thus be represented as a hyperspace consisting of a finite but potentially very large number of independent variables. However, the physical environment is not very useful for the purpose of ecological and evolutionary explanations, since it does not isolate the causes that make a difference for population dynamics or the evolution of lineages.

For many ecological and evolutionary explanations, only some aspects of the physical environment matter. For instance, to explain why some species are more abundant than others, why some species have more varied habitats than others (niche breadth), or how multiple similar species coexist within the same physical space (niche partitioning), ecologists have tended to restrict the physical environment to only those variables representing resources. The *Hutchinsonian niche* is the classic formulation of this approach, representing the environment as an  $n$ -dimensional hyperspace, where each axis is a resource, ranging from food and nesting sites, to shelter and mating opportunities (Hutchinson 1957). However, other niche concepts are even more restricted. The *Eltonian niche* concept, for instance, focuses only on biotic variables that stand in food chain relationships to each other. In this way, the environment is represented as a food chain, and the organism as fulfilling a certain functional role within it (cf. Chase and Leibold 2003).

Ecological niche concepts must be sharply distinguished from environment concepts that

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applies to evolutionary individuals. It could, for example, be that entire ant colonies or groups of aphid clones are evolutionary individuals, not the individuals that compose these groups, and hence one would need to look for phylogenetic competition between colonies or groups, rather than between individual ants or aphids.

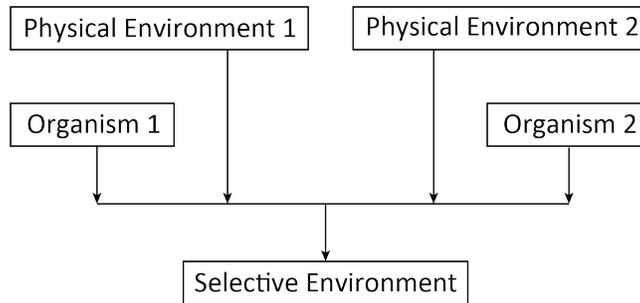
matter for evolution by natural selection. What we call the *fitness environment*<sup>2</sup> (of each individual) is the restriction of the physical environment to those environmental variables that make a difference to an individual's fitness. Each individual will have a unique fitness environment, though individuals that are similar and live near one another in similar conditions may have largely overlapping fitness environments. Further, if we were to ask not what affects an individual's fitness, but what affects fitness *differences* between two individuals, then the relevant concept is that of the *selective environment*, which maps those environmental variables that make a difference to the fitness difference obtaining between those two individuals.

Note that the variables that make a difference to fitness may not necessarily make a difference to fitness differences. To take an example from Brandon (1990), if soil molybdenum level has an equal impact on the fitness values of all the plants in a population, then while molybdenum is part of the fitness environment of the individuals, it is not part of their selective environment. But inversely, a variable that makes a difference to fitness differences necessarily makes a difference to fitness, so the selective environment is a proper restriction of the fitness environments.

To put the matter differently, the concept of the selective environment is the relevant environment concept if one wants to represent all the factors in the physical environment that matter for natural selection. What factors these turn out to be are not determined only by the properties of the physical environment, but also by the properties of the organisms that inhabit the physical environment. A helpful formal way of thinking of the selective environment is as a *mapping* that combines two distinct fitness environments into a single environment, but where organisms inhabiting the physical environment determine how precisely this mapping is done. In other words: to obtain a selective environment, one must map two physical environments and two organisms onto an abstract environment space, losing a lot of information in the process, but retaining those aspects of the physical environment and organism that matter for natural selection.

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<sup>2</sup> This term corresponds to Brandon's (1990) concept of the 'ecological environment', but we avoid that term here since it may invite confusion with ecological niche concepts.



**Figure 1:** The selective environment can be thought of as the outcome of an operation where two physical environments and two organisms are mapped onto an abstract environment space.

**3. Shared Populations and Environmental Conditions.** The redescription of the selective environment as delimited via a mapping operation allows for a reformulation of the central question: under what conditions can the mapping be carried out? Do the individuals in question need to be conspecifics? Need they reside in the same population? Must they experience very similar physical environments? In this section, we discuss two previously proposed answers to these questions before offering our own answer in the following section.

*3.1 The selective environment as delimited by a shared population.* Millstein (2014) argues that two organisms share a common selective environment if and only if they belong to the same population. Furthermore, two organisms are part of the same population if they (1) are part of the same species, and (2) are engaged in ‘survival and reproduction’ interactions over the course of a generation. In turn, survival and reproduction interactions refer to a broad range of activities, including unsuccessful and successful matings, offspring rearing, competition for limited resources, and cooperative activities. Such interactions can be more or less common; the boundaries of the population (and hence of the selective environment) are characterized by the groups of organisms where there is a markedly higher density of interaction between members than with other organisms.

Millstein’s account thus relies on two much-debated concepts: species and population. This creates unnecessary conceptual and epistemological burdens, since partitioning selective environments then requires first individuating species and populations. The field biologist studying house mice polymorphism may be interested in determining their selective environment without taking a stand on whether hybrid mice are a new species or not. Millstein’s approach is thus

problematic because it is explicating one difficult concept in terms of two difficult ones, and it seems that the selective environment can be studied without having to take stands on species and population concepts and their individuation criteria.

Let us first consider problems that ensue from the dependence of the selective environment on the species concept. Assume that two populations are undergoing sympatric speciation, in which a group within the larger population is gradually becoming reproductively isolated, even while inhabiting the same geographic region and interacting with the larger population. The process of speciation is gradual, and the group initially has strong survival and reproduction interactions with the larger population. Is a selective environment shared during the process of speciation? According to Millstein's criteria, the two groups form a single population during the process of speciation, but not after. Are they conspecifics? Millstein does not supply further details about which species concept(s) she operates with, so let us consider two separate cases. If they are conspecifics during but not after speciation, then the two populations share a selective environment. This conclusion is at odds with the widely-held judgment that the two populations are not in selective competition (e.g., one adaptation in the smaller population is unlikely to spread to the larger population since they are becoming separate species). By contrast, if they are no longer conspecifics from the beginning of the process of speciation, an implausible conclusion is avoided—but it implies that two populations can suddenly cease to be in selective competition at time  $t$  if, in retrospect at some later time  $t'$ , it can be determined that at  $t$  a process of speciation had begun. This implies an on/off view of the selective environment that is at odds with the gradual nature of speciation. Moreover, it depends on controversial positions within taxonomy: for instance, De Queiroz (2007) argues that species boundaries during speciation are objectively vague.

For difficulties in the population concept, consider how (conspecific) individuals in the same population may possess different selective environments. This happens in sexual populations where there is strong sexual dimorphism, such that males and females are exposed to very different physical environments and selection pressures during their life-histories. For instance, female scale insects (Coccoidea) are sessile, living their lives sucking sap while adhered to plant stems. Males, on the other hand, never feed as adults, generally have wings, are considerably smaller than females, and die within a couple of days of birth. These very different life histories also correspond to different selection pressures. The males but not the females are selected for their ability to fly,

for example. Hence it would not be accurate to attribute a single selective environment to the whole population.

Sexual dimorphism can simply result from niche partitioning, but the most extreme cases of sexual dimorphism occur through sexual selection. Sexual selection involves competition for mating opportunities, and typically involves a choosier and a less-choosy sex. The choosiest sex is generally the one that invests the most resources in their offspring. Since females are by definition the ones that produce the larger gamete, which usually requires more resources, in many species it is the female who invests more. However, in some cases offspring investment becomes decoupled from the resources involved in gamete production. In the Mormon cricket, *Anabrus simplex*, a male provides a mate with a very large nutrient-rich spermatophore as a nuptial gift, giving her the resources to lay the eggs. In this species, it is the females that swarm and compete for the choosy males (Gwynne 1981). The selective pressures on males can thus be very different than those on females (and this in turn can lead to sexual dimorphism).

These problems point to hurdles that a satisfactory account of the selective environment should be able to overcome. First, it should account for how a selective environment is a multilayered concept, by which we mean that while a population may have an average selective environment, each pair of individuals shares a unique selective environment, and the complex interwoven multiplicity of selective environments affects the evolutionary dynamics of the species. Second, the account should yield plausible conclusions for cases of speciation and cases where species boundaries are not clearly defined, and should ideally do so without relying on any particular definition of what a species is.

*3.2 The selective environment as shared environmental conditions.* The second main approach to defining the selective environment is to attempt to base it on the interaction between organism and environment. Under this approach, if two organisms interact with the environment in similar ways, and if their fitnesses are affected by the same environmental variables, then they are in the same selective environment.

Interestingly, a place where this view of the selective environment has been (implicitly) discussed is with regards to species selection. A key argument against the coherency of the concept of species selection has been that different species do not share the same selective environment because, among other reasons, species are widely distributed in space (Damuth 1985). One

response to this is that spatially distant populations, and also spatially distant individuals, can share a selective environment, since what matters is that the fitnesses of the entities are affected by the same environmental factors (Sterelny 1996, see also Okasha 2006). For instance, all populations of a species, despite not being in physical proximity or causal contact, may yet be affected by a “species-typical parasite” (Sterelny 1996: 208). This can create an identical selection pressure for parasite resistance. Hence, so the argument goes, the populations share a common selective environment.

This touches on a more general question: to what extent are shared conditions in the physical environment important for determining whether a selective environment is shared? Consider the following example, where one brown rat (*Rattus norvegicus*) inhabits a neighborhood in Oslo, while the other inhabits a few blocks in Manhattan. Each inhabits distinct physical environments, yet the environmental conditions that affect the fitness of individual rats are very similar: the presence of rubbish and detritus, sewers, alleyways, and predators such as cats and dogs. Thus, a rat well adapted to life in Oslo would also be well adapted to life in Manhattan. They interact with the same environmental conditions, and the conditions in their respective sub-environments are characterized by the same probabilities. Do they share a selective environment?

We hold that this question cannot be answered by examining the shared environmental conditions alone. What if the lineage spawned by the Oslo rat and that spawned by the Manhattan rat would never causally interact even in the distant future? What if the lineages would diverge irreversibly? Then any adaptive trait somehow generated among the Oslo rats would never spread to the group of rats in Manhattan. Therefore, should the evolutionary trajectories of the Oslo and Manhattan lineages diverge, one cannot speak of natural selection occurring on the Oslo-Manhattan rat pair. Any fitness difference obtaining between the Oslo and Manhattan rats does not lead to adaptive evolution, and hence they cannot underlie a process of natural selection.

Brandon’s original analysis (1990) of the boundaries of the selective environment similarly decouples the physical environment from the selective environment. Two populations inhabiting the same physical environment may nonetheless not share a selective environment. The spatial boundaries of a (common) selective environment of two organisms is determined by the ordinal relation between their fitnesses. The spatial points where organism A becomes fitter than organism B (or vice versa) denote the boundary between two selective environments. This partitioning of

selective environment in effect subdivides regions in which the rank orderings of fitness values are constant, thus creating regions of ‘selective homogeneity’.

This approach has been followed by more recent discussions of the selective environment (Abrams 2014; Glymour 2011, 2014), where, in particular, Abrams argues that selective environments are distinguished from one another if they correspond to different ‘sub-environments’—the minimal units over space and time where the probabilities of recurring environmental conditions remain constant. We do not disagree with Brandon’s approach, since identifying regions in which fitness rank-orderings remain stable can help identify the spatio-temporal boundaries of selective environments. However, this does not address the core question of the paper, i.e., when do fitness differences between individuals constitute selection?

**4. The Selective Environment as the Arena of Phylogenetic Competition.** We would like to begin with a general observation about the conceptual link between competition and environment. Competition often plays out in a shared physical environment: think of how many sports competitions unfold in a shared space, whether a race course, football stadium, or ski slope. Likewise, a selective environment needs to be shared for two individuals to be in selective competition. In that sense, it is the “arena,” even though this arena is not necessarily, as we will see, a spatially contiguous area. The environment in which a competition unfolds is often connected to a *shared goal* that can only be realized by a *limited number* of competitors. That is to say, if everyone can equally be a winner, it is not a real competition, and if the individuals are attempting to reach different goals, it is not a real competition either. This dual aspect of competition is underlined by its etymology, *cum-petere*: together-seeking/striving. However, if the selective environment is the arena in which selective competition unfolds, what is the shared goal? This line of thought brings us to competition for future lineage representation, or for short, *phylogenetic competition*.

*4.1 Phylogenetic Competition.* We can first illustrate the idea of phylogenetic competition by discussing the difference between ecological and evolutionary competition. Two top predators (for instance, a lion and a cheetah) may compete for some of the same resources (e.g., Thompson’s gazelle), and they thereby compete with each other. Their ecological niche overlaps, whether defined as the Hutchinsonian or Eltonian niche: they share a common, finite resource, and they

also fulfil a near identical functional role in the food chain. Furthermore, increased fitness of one predator may lead to decreased fitness in the other, to the extent of extinction of the second predator in certain areas: this is known as competitive exclusion (Chase and Leibold 2003). Though it can prompt or modify selection pressures, competitive exclusion is widely held by ecologists not to be synonymous with natural selection. However, beyond stipulating that natural selection must act on conspecifics, why precisely is competitive exclusion not a form of natural selection?

The core idea here is that the two non-conspecific predators—the lion and cheetah—are not competing for the same positions in ‘descendant space’<sup>3</sup> since the lion and the cheetah cannot have common descendants (if they could, they would not be separate species according to the phylogenetic species concept: Mishler and Brandon 1987). Any two cheetahs, by contrast, could have common descendants, if not among the offspring generation, then among the grand-offspring (or subsequent) generation. For this reason two cheetahs can be said to share a common descendant space, where the size of this space is finite (constrained by availability of resources). If one cheetah reproduces at a higher rate, then this causes the descendants of the other cheetah to be edged out. This form of competition is what we are labeling phylogenetic competition. This is the essence of the proposal of this paper: natural selection involves fitness differences plus phylogenetic competition.

We will now construct a more precise definition of phylogenetic competition. Let the ‘descendant space at generation  $n$  of an individual’ be a finite space consisting of positions that can be occupied by the descendants of that individual. The size of the descendant space of an individual is the maximum number of possible descendants, limited only by the available resources needed for sustenance (e.g., nutrients, places to nest or to grow, and so on)—thus it represents a “best-case scenario” for that individual, in the absence of competition from other individuals. Finally, the descendant spaces of two individuals *intersect* when the possible lines of descendants (the possible descendant trees) of the two individuals could potentially intersect at some later time  $t'$ . In other words, the descendant spaces overlap when there are potential common offspring (or grandoffspring, etc.).

With the definitions of descendant space, size of descendant space, and intersection of descendant spaces in place, we can now define phylogenetic competition as follows:

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<sup>3</sup> We use the term ‘space’ to avoid the laden term of ‘population’. A space is not a biological population (see definitions later).

**Phylogenetic competition** between individuals  $X_1$  and  $X_2$  at time  $t$  occurs if and only if, their respective descendant spaces intersect (at some later time  $t'$ ), and a higher fitness of  $X_1$  causes a lower expected occupation of the intersection space at  $t'$  by descendants of  $X_2$ , and vice versa.

Thus phylogenetic competition has two elements: the common goal of occupying a shared descendant space, and a negative causal relationship between lines of descent.<sup>4</sup>

Why are these two elements necessary? If the former is dropped, we get what we call ecological competition: the fitness of individuals of one species may cause individuals of the other to have fewer descendants, but since they have no potential common descendants (necessarily so, if we assume they are and will remain distinct species) adaptations in the descendant space of one cannot spread to the other. An adaptation in the descendant space of the lion cannot spread to the descendant space of the cheetah. This occasions the following definition:

**Ecological competition** between individuals  $X_1$  and  $X_2$  at time  $t$  occurs just in case a higher fitness of  $X_1$  causes a lower expected occupation of  $X_2$ 's descendant space at some later time  $t'$ , and vice versa.

By contrast, the selective competition between two cheetahs may entail that the fitness-enhancing traits of the fitter cheetah may eventually be adopted by the descendants of the less fit cheetah. In sum: without intersecting descendant space, adaptations cannot spread. Given that explaining the spread of adaptations is a core explanatory function of the concept of natural selection, an account of the selective environment should allow for this explanatory function to be realized.

In the definition above, the causal element of phylogenetic competition is stated very abstractly—as a relation holding between two facts—and may involve a diversity of phenomena. It could involve competition for nutritional resources, where a higher fitness of  $X_1$  would mean that its descendants consume more of the environmental resources, leaving less for the offspring of  $X_2$ , and decreasing  $X_2$ 's number of grand-offspring. Or, it could involve the timing of reproduction, so if an increase in  $X_1$ 's fitness would be achieved by reproducing earlier on in its life cycle timing, and subsequently leading to  $X_2$ 's descendants being in disadvantaged position

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<sup>4</sup> Thus while we will discuss implications for phylogenetic competition between organisms, in principle the account is extendable to other evolutionary individuals. For instance, two alleles may inhabit the same selective environment when they compete for representation in a common locus; similarly, two species of the same clade may inhabit the same selective environment when they compete for representation in a common descendant space.

with regard to exposure to predators, nutritional resources, mating opportunities, and so on.

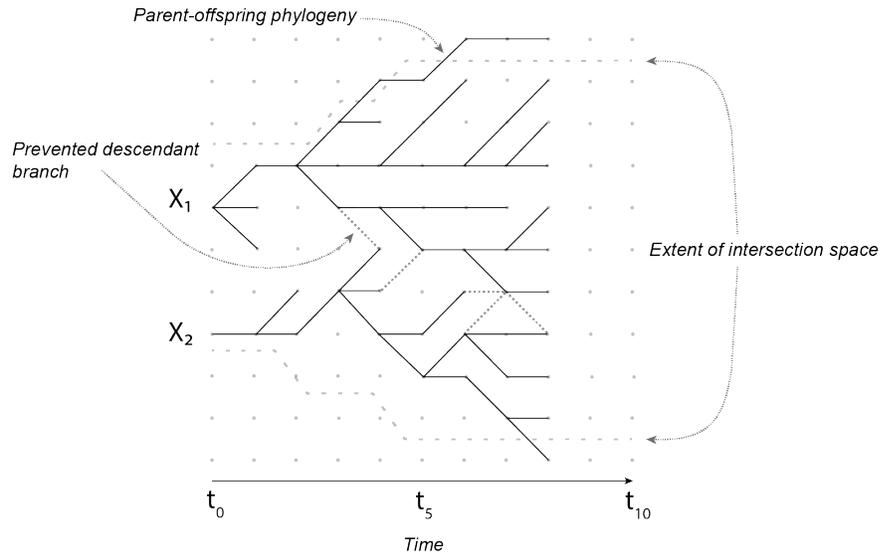
From these definitions, it might be assumed that any given  $X_1$  and  $X_2$  will tend to be in either ecological or phylogenetic competition, since they will generally have a negative impact on one another. But this is not the case. One can distinguish between several scenarios where increasing the fitness of  $X_1$  does not have an impact (negative or otherwise) on the descendant tree of  $X_2$ . First, increasing the fitness of  $X_1$  could also increase the fitness of  $X_2$ , leaving the fitness differential intact. Second, if the fitness of  $X_1$  and  $X_2$  depend on different traits, altering the fitness of one will not necessarily affect the descendant tree of the other. For instance, if  $X_1$  is fast but weak, and  $X_2$  is slow but strong, increasing  $X_1$ 's fitness by increasing its speed will not necessarily affect how many descendants  $X_2$  will have: the descendent trees of  $X_1$  and  $X_2$  may simply merge given sufficient time. Finally,  $X_1$ 's fitness and  $X_2$ 's number of descendants at some time  $t$  may be causally affected by some chance environmental factor held in common. This would lead to a counterfactual relationship, but not phylogenetic competition.

Figure 2 gives an illustration of various facets of phylogenetic competition.<sup>5</sup> For instance, at  $t_3$ , a descendant of  $X_2$  reproduces and thereby prevents a descendant of  $X_1$  from reproducing twice (instead it reproduces just once). By contrast, at  $t_4$ , an  $X_1$ -descendant of  $X_1$  reproduces twice, thereby preventing an  $X_2$ -descendant from reproducing at all. After eight generations,  $X_1$  has seven descendants, versus  $X_2$ 's four. Given the few counterfactual relationships indicated in Figure 2, it is clear that if  $X_1$ 's fitness were lower, such that it had not reproduced three times at  $t_2$  (eliminating

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<sup>5</sup> Note that while the definition of phylogenetic competition concerned how changes in fitness value would impact expected descendant trees, Figures 2, 3, and 4, illustrate in more specific ways how, if one descendant were not produced by individual A, then individual B would have had more descendants. So by themselves, Figures 2-4 would not be sufficient to establish phylogenetic competition: one would need much more complicated diagrams, mapping out all possible ways in which changes in the fitness of one individual could affect the descendant tree of the other individual

the lower branch starting at  $t_3$ ), then  $X_2$  would have had more descendants at  $t_5$ .



**Figure 2:** an example of phylogenetic competition between two asexual individuals.

The importance of a *negative* causal relationship is to distinguish phylogenetic competition from phylogenetic cooperation. *Phylogenetic cooperation* refers to situations where an increased fitness of  $X_1$  causes  $X_2$  to have more descendants (and vice versa). Certain mating behaviors, such as monogamy, promote phylogenetic cooperation between individuals in a mating pair (fusing their descendant lineages), whereas random mating minimizes phylogenetic cooperation within a mating pair (for further discussion, see section 6.1).

To complete the conceptual introduction of phylogenetic competition, we contend that the *meaning* of selective environment should be fleshed out in terms of phylogenetic competition. Phylogenetic competition should not be seen as a controversial concept, since (as we will argue) it is contained in the very concept of natural selection. Consider following deductive argument:

- (P1) Evolution by natural selection can only occur when two individuals  $X_1$  and  $X_2$  differ in fitness, and where the fitness difference is due to a difference in heritable traits.
- (P2) Evolution by natural selection causally explains the spread of adaptations (heritable traits of the fitter individuals increase proportional representation in descendant populations).
- (P3) There is a limit in the number of descendants that a physical environment can support.
- (S1) From P2, P3: after a finite number of generations, the descendant spaces of  $X_1$  and  $X_2$

must intersect, and the intersection space is finite.

**(S2)** From P1: it is expected that  $X_1$  has more descendants than  $X_2$ , that the descendants of  $X_1$  will have more descendants than the descendants of  $X_2$ , and so on (or vice versa).

**(S3)** From S2 and S1: after a finite number of generations, the higher fitness of  $X_1$  causes less of the intersection space to be occupied by descendants of  $X_2$  (or vice versa).

∴ **(C)** From S3, S1: Natural selection entails phylogenetic competition

*4.2 Degree of Phylogenetic competition.* The definition of phylogenetic competition implicitly includes a dependence on two degrees of freedom that we would now like to make explicit. The first is the *time until intersection*, which is measured by the number of generations until a potential common descendant. A male and female individual's line of descent can intersect in the next generation; two females' or two males' line of descent can cross at soonest in two generations; the lines of descent of two individuals from spatially distant populations may cross only after many generations.

The second degree of freedom, derived from the causal relation between the lines of descent, is the *intensity of competition*. This is reflected by the strength of the causal connection between the two descendant lineages. If the intensity of exclusion is positive, then the actualization of one line of descent indicates the other will not be realized. By contrast, if negative, then the actualization of one line of descent promotes the realization of the other line of descent (e.g., for a male and female mating with each other). This is *phylogenetic cooperation*, as described above. Only phylogenetic competition can be considered to be a necessary condition for natural selection. Phylogenetic cooperation between two individuals is a measure of how the descendant tree of individual promotes the realization of the other. Two individuals that form a mating pair will exhibit phylogenetic cooperation, since the realization of one individual's descendant lineage will mean that the other's is realized as well, and lifetime monogamous pairing would maximize the degree of phylogenetic cooperation.<sup>6</sup>

Can these various properties of phylogenetic competition be reflected in a single scalar variable? We propose one way (not necessarily the only way) in which this can be done, and in

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<sup>6</sup> Note that the condition of intersecting descendant spaces in the definition of phylogenetic competition means that some possible branches of the individuals' lineages must possibly overlap, but that this does not necessarily imply phylogenetic cooperation. The latter implies a causal connection underlying the intersection of lines of descendants.

the process aim at further clarifying the precise causal nature of phylogenetic competition. Let the overall phylogenetic competition between  $X_1$  and  $X_2$  be the sum of the competition for each position  $s_j(t_i)$  at a particular time  $t_i$ :

$$C(X_1, X_2) = \sum_{i,j} C(X_1, X_2, s_j(t_i))$$

When lineages only potentially intersect at time  $t_n$ , then the terms  $C(X_1, X_2, s_j(t_i))$  are zero for  $t_i < t_n$ . In other words, two organisms  $X_1$  and  $X_2$  may be in phylogenetic competition at time  $t_0$  even though their respective descendants may only begin to displace each other from the common descendant space after a large number of generations.

We will now construct a measure for the individual additive terms, in such a way that the measure reflects important (intuitive) properties of phylogenetic competition. Let  $P(X \rightarrow s_i(t))$  be the probability distribution of the descendants of  $X$  at time  $t$  across positions  $s_i(t)$ . The sum of the probabilities  $P(X \rightarrow s_i(t))$  is 1, and the positions  $s_i(t)$  are ordered as monotonically decreasing:  $s_1(t)$  has the largest probability,  $s_2(t)$  has an equal or lower probability of being occupied, and so on until  $s_n(t)$  with the lowest probability. This means that  $X$ 's maximum number of offspring at time  $t$  is  $n$ . (This probability distribution can be also used to obtain expected number of descendants at time  $t$ .)

Phylogenetic competition between organisms  $X_1$  and  $X_2$  concerns how  $P(X_1 \rightarrow s_i(t))$  differs from  $P(X_1 \rightarrow s_i(t)|X_2)$ , in other words, how the unconditional probability distribution of descendants  $X_1$  across positions  $s_i(t)$  changes when (the descendants of)  $X_2$  are taken into consideration<sup>7</sup>. Therefore, a measure of phylogenetic competition would need to be large when the difference between conditional and unconditional probability distribution is large (and small when it is small). A second property the measure would need to have is symmetry: the phylogenetic competition between  $X_1$  and  $X_2$  is the same as that between  $X_2$  and  $X_1$ .

One well-established way to measure the difference between probability distributions is to use mutual information:

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<sup>7</sup> Note that in this way, we are interpreting the causal relationship between descendant lineages as a probability-raising or probability-lowering one.

$$C(X_1, X_2, s(t)) = I(X_1 \rightarrow s_i(t); X_2 \rightarrow s_j(t))$$

Mutual information does not strictly measure the difference between  $P(X_1 \rightarrow s_i(t))$  and  $P(X_1 \rightarrow s_i(t)|X_2)$ . Rather, it concerns the joint distribution  $P(X_1 \rightarrow s_i(t), X_2 \rightarrow s_j(t))$ —which assigns a probability value to descendants of  $X_1$  occupying  $s_i(t)$  and the descendants of  $X_2$  occupying  $s_j(t)$ <sup>8</sup>—and the product of the unconditional distributions  $P(X_1 \rightarrow s_i(t)) P(X_2 \rightarrow s_j(t))$ :

$$I(X_1 \rightarrow s_i(t); X_2 \rightarrow s_j(t)) = D_{KL}[P(X_1 \rightarrow s_i(t), X_2 \rightarrow s_j(t)) || P(X_1 \rightarrow s_i(t)) P(X_2 \rightarrow s_j(t))]$$

$D_{KL}$  is the Kullback-Leibler divergence: a standard measure of divergence between two probability distributions (Cover and Thomas 2006).

In this way, phylogenetic competition can be quantified by how much the distribution of branches of the lineages of  $X_1$  and  $X_2$  differs from how the lineages would be expected to branch out if the other were not there. Changing the fitness of  $X_1$  changes the expected descendant tree of  $X_1$ , and if  $C(X_1, X_2)$  is nonzero, this means that the expected descendant tree of  $X_2$  also changes (and vice versa). This clarifies how the causal aspect of phylogenetic competition is to be thought of as a counterfactual relation between two probability distributions, each capturing the probabilities of different possible descendant trees.

**5. Empirical indicators of Phylogenetic Competition.** It may seem puzzling to propose an analysis of an environment concept in terms of phylogenetic competition, since the latter refers to lineages and seems to have nothing to do with the physical environment. However, we are offering phylogenetic competition as a way of delimiting the selective environment, according to following steps: first, begin with a pair of organisms,  $X_1$  and  $X_2$ . The framework tells us what is needed for  $X_1$  and  $X_2$  to be in competition, and how this competition comes in degrees. Second, we can then ask which environmental variables count as difference makers for this competition. Finally, the selective environment is simply a sum of these variables. This is how properties of two organisms and their respective physical environments are mapped onto the selective environment (see Figure 1).

Phylogenetic competition thus provides a way of conceptually delimiting the selective

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<sup>8</sup> For the case  $i=j$ , that the probability that the descendants of  $X_1$  and of  $X_2$  occupying the same position in descendant space need not be zero: this probability value is a measure of the probability that that position will be occupied by a common descendant.

environment, but this is of course distinct from the epistemological question of how one can know whether a given situation involves phylogenetic competition (or how one can estimate the degree of competition). The epistemological question should also be taken seriously; otherwise, phylogenetic competition may seem like an unoperationalizable, and even artificial concept.

Ideally, establishing the presence of phylogenetic competition would require several (mini) replays of the evolutionary tape: at least one that establishes that the lineages can potentially cross, at least two replays to observe how each lineage evolves without the other, and then at least one where each lineage evolves simultaneously, to observe the strength of the competition (in contrast to the previous two replays). Because such replays are not possible, one must rely on empirical indicators to estimate the possibility of lineage crossing and strength of causal exclusion.

We discuss this question by pointing to two classes of empirical indicators that help determine whether a selective environment is shared (i.e., its operationalization). This will also clarify the relation between phylogenetic competition and population-based and ecological accounts of the selective environment.

*5.1 Indicators for Lineage Separation.* While Millstein (2014) or Abrams (2014) stipulate that only conspecifics can share a selective environment, we have denied that this is an essential condition for a shared selective environment (i.e., it is not entailed by what the selective environment means). However, we do hold that the various indicators for conspecificity are relevant for determining whether two individuals are in selective competition: two conspecifics have a much higher probability of having intersecting offspring lineages than two individuals from distantly related species.

There are a large number of criteria for determining whether two individuals (or populations) are part of the same species: phenotypic distinctness, ecological distinctness, reproductive compatibility, reproductive isolation, being part of a monophyletic group, and so on. Under one influential interpretation (De Queiroz 2007), all these indicators matter for establishing whether the two individuals are part of independently evolving metapopulation lineages. By extension, these indicators can also be used to estimate whether the descendant lineages of two individuals can possibly cross in the future. In this way, indicators for lineage separation are indicators for phylogenetic competition.

Finally, to connect back to the initial example concerning *M. m. domesticus* and *M. spretus*,

the presence of hybrids or hybrid zones between two species thus is always an indication of an intersecting descendant space. However, for the two parent species to be in selective competition with each other, or with the hybrid species, it is necessary that there is a negative causal relationship between the respective descendant lineages. This is why sterile hybrids cannot be in selective competition with parent species, since their descendant space is empty. This brings us to the second class of indicators.

*5.2 Indicators for a shared ecological niche.* Ecological niches (however defined, as Hutchinsonian, Eltonian, etc.) define the common resources over which competition occurs. Strictly, two individuals could inhabit very different ecological niches and yet be in selective competition. Nonetheless, since these resources are what define the size of the descendant space, indicators for a shared ecological niche also indicate the strength of the negative causal relationship involved in phylogenetic competition. Establishing the niche of a population is far from straightforward (even if we bracket the controversies surrounding the niche concept), and ecologists routinely distinguish between potential and realized niches (Soberón and Nakamura 2009) or niche breadth and niche partitioning (Chase and Leibold 2003). Measurable factors that help establish various types of niche include habitat and population distribution, life-history traits, resource consumption, biotic interaction, and so on (Chase and Leibold 2003).

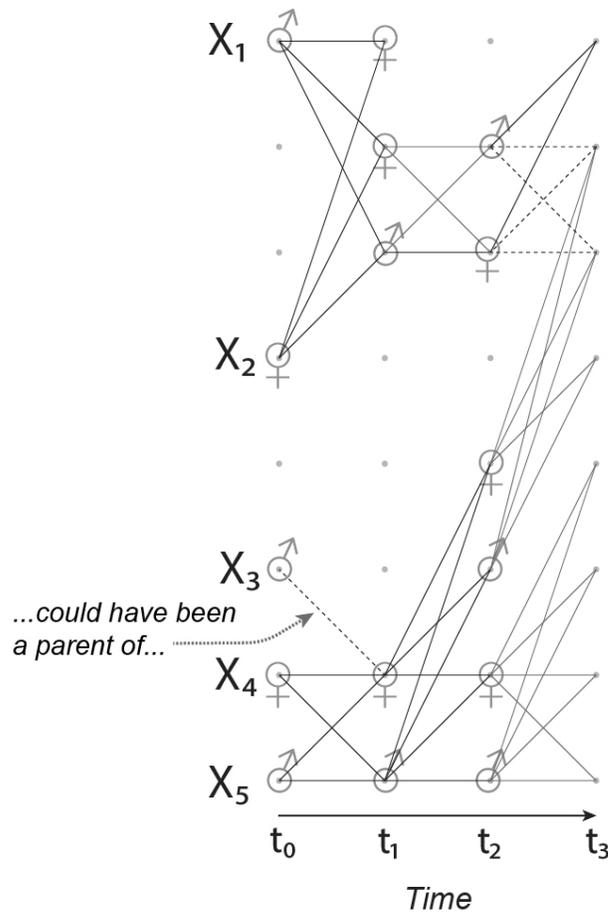
Not all niche concepts focus on the resources in the environment and competitive interactions over them. Grinnellian niches identify basic abiotic variables in the environment, and are used to explain coarse-grained properties of species (Soberón 2007). Thus, for instance, water is part of the selective environments of fish, whales, seals, and penguins, and has driven similar adaptations in an aquatic environment (Brandon 1990: 69). However, not all of these aquatic organisms share a selective environment, because there is zero (or extremely little) probability of lineage intersection. In this way, while overlapping features of the physical environment is not sufficient to allow a shared selective environment (there needs to be an intersection in descendant space), it can, by shaping the ecological niche, affect the intensity of the negative causal relationship between descendant lineages. This also helps connect phylogenetic competition to the analysis of the selective environment in terms of recurrent factors in the physical and fitness environments (section 3.2): while we disagree that such factors *define* the selective environment,

they can be used as (imperfect) indicators to estimate the strength of phylogenetic competition, and thus help predict the rate and direction of evolution by natural selection.

In this regard, the phylogenetic competition account of the selective environment does not adopt an ‘engineering’ perspective of natural selection, where the environment poses problems, and natural selection engineers a solution. Natural selection entails competition, and so only when an environmental ‘problem’ engenders a competition for future lineage representation, does natural selection take place.

**6. Implications of the phylogenetic competition framework.** We have seen that phylogenetic competition can help us to conceptually understand what a selective environment is, and to indicate which empirical measures can probe selective environment boundaries. Let’s now consider some broader implications of the phylogenetic competition framework.

*6.1 The Case of Sexual Populations.* Do males and females in the same environment possess the same or different selective environments? In sexual populations with sexual dimorphism, one would intuitively expect males and females to be subject to different selection pressures. Sometimes sexual dimorphism is caused by sexual selection and results in secondary sexual characteristics, like the peacock’s extravagant tail feathers. In other cases the difference represents resource partitioning, with one sex being smaller and having a correspondingly different diet, for example. However, in general, the diverging phenotypes are both the result and cause of different interactions with the external environment. Yet at the same time, males and females in a population have an intersection space—i.e., they potentially have common descendants, either directly by mating or indirectly through their descendants mating. The fitness of a male can causally affect the descendant tree of a female, and vice versa, suggesting there can be phylogenetic competition (and cooperation) between males and females.



**Figure 3:** Phylogenetic competition and cooperation between sexual organisms

In random mating, the choice of mating partner happens randomly, and the expected number of offspring of an individual is distributed over a random number of mating partners. Male-female phylogenetic competition occurs here, even between mates, since the descendants of a very reproductively successful male may edge out the descendants of the less successful female (or vice versa), despite the male and female having mated, and having a line of descendants in common. Thus for instance, in figure 3, there is competition between  $X_2$  and  $X_3$ , because even though they have one common descendent,  $X_2$  also mated with  $X_1$ , and the  $X_1$ - $X_2$  male descendant at  $t_1$  prevented the  $X_3$ - $X_2$  male descendant at  $t_1$  from having three further offspring. In random mating, there is no difference at all between selective environments of males and females<sup>9</sup>: the degree of intrasexual phylogenetic competition is basically equal to intersexual phylogenetic competition,

<sup>9</sup> This assumes that males and females have equal probability reaching sexual maturity – i.e., no viability selection. We discuss viability selection separately in section 6.4.

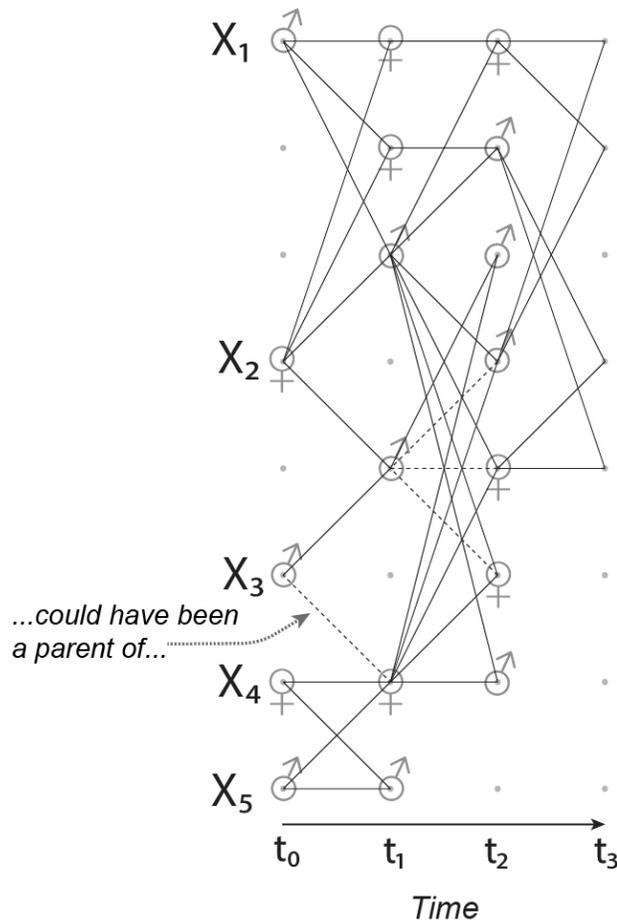
over all time scales.

However, depending on the mode of partner choice, Figure 3 can also be read as involving assortative (non-random) mating. Thus  $X_4$  could have mated with  $X_5$  instead of  $X_3$  because  $X_5$  exhibits signals of high fitness, either through secondary sexual characteristics, or through amassing resources, etc. Thus assortative mating can give rise to intrasexual phylogenetic competition on the short term (i.e., the competition determines representation in the next generation). However, over the longer term, the differences between intra- and intersexual phylogenetic competition even out: a male and female can have a large degree of phylogenetic competition over a longer period, and two males or two females can have significant phylogenetic cooperation over a longer period (for instance,  $X_1$  and  $X_3$  cooperate phylogenetically through common descendants at  $t_2$ ).

Monogamous mating is a particular kind of assortative mating where phylogenetic competition ceases between the male and female of the mating couple. There can be competition for the formation of mating couples: for instance, in Figure 4,  $X_3$  competes with  $X_5$  to form a mating couple, but loses the competition and does not reproduce. There could also be competition to form a couple with a high-fitness male or female (not illustrated in Figure 4), with losers forming mating couples with lower-fitness individuals. However, once mating couples are formed, competition only occurs between the phylogenies of mating couples. Figure 4 illustrates how the  $X_4$ - $X_5$  descendant tree grows faster than the  $X_1$ - $X_2$  descendant tree<sup>10</sup>, and as a consequence  $X_1$ - $X_2$  have fewer descendants occupying the intersection space at  $t_3$ . In sum: in the case of monogamous mating, there can be intense intrasexual phylogenetic competition for couple formation, but after that there is maximal phylogenetic cooperation between a male and female in the mating couple.

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<sup>10</sup> Notice that there is no interbreeding in Figure 3, but this is merely for ease of representation. Otherwise, a larger population would be needed to illustrate phylogenetic competition between mating couples.



**Figure 4:** Phylogenetic competition and cooperation between sexual organisms (monogamous mating)

In sum, the framework allows distinctions to be made between selective environments of males and females, but it depends strongly on mating patterns, and must be relative to a time-scale. In randomly mating populations, differences between the selection pressures faced by males and females are minimized; once assortative mating is introduced (and the vast majority of species mate assortatively to some degree: de Cara et al. 2008), the sex of the individuals becomes relevant for determining the intensity of phylogenetic competition between them. However, even here the sex becomes increasingly less relevant for the intensity of phylogenetic competition between two given individuals over longer time-scales: precisely what one would expect, since males and females share an intersection space, and can have both female and male descendants.

*6.2 The case of spatially distant populations.* Let the two individuals be part of spatially distant populations: for instance, the rats in Oslo and in Manhattan mentioned above. An individual

in the same species as another may be geographically separated and experiencing different environments. A Norway rat in Oslo and one in Manhattan are not part of the same selective environment, or so it seems. Instead, they are competing with their local rats, and it is this competition that drives their evolution.

According to phylogenetic competition-account, the rat in Oslo and the rat in Manhattan could conceivably be in phylogenetic competition if their lineages would potentially cross some time in the future, and if the differential success between the lineages would mean that branches from one lineage would displace branches from another lineage. If the probability of this distant lineage overlap is very small, then it is highly likely that the branching evolution of one lineage is unaffected by the branching evolution of the other lineage. They may have a minimally overlapping selective environment.

The shared environmental variables may influence the probability of the two lines of descent converging at some time in the future. The converse is easier to argue for: if the environmental conditions were radically different, and very different types were reproductively successful in Oslo and Manhattan, then this would be a good reason for assigning a higher probability that they are undergoing (what will eventually turn out to be) speciation. Hence, if the environmental conditions were identical, this will not guarantee phylogenetic competition, but does allow for a higher probability than would otherwise be the case. Individuals inhabiting non-contiguous physical environments may nonetheless share a common selective environment, even though establishing a shared selective environment will depend on many indicators and will even then only be able to be established with a certain probability (since whether or not the selective environment is shared depends on future events).

*6.3 The noninteracting case.* Consider first a population of heat-resistant and heat-vulnerable bacteria in a hot physical environment with infinite resources of one particular type. Because resources are infinite, there is no competition for resources, and hence the reproductive success of one will not affect the other. There is no ecological competition and there is no phylogenetic competition. In other words, the indefinite growing of bacteria populations in the idealized case of infinite resources is not natural selection; it is sorting. Natural selection requires the Malthusian premise: resources are finite. If the resources are finite, even if they may be abundant, then after some time the carrying capacity would be reached, and slowly but surely it

can be expected that the lineage of lower fitness (heat-vulnerable) bacteria would be pushed into extinction. This then would be a case of natural selection.

It may seem strange to claim that two bacteria strains occupy the same environment yet do not share the same selective environment. The response to this is that the case implicitly assumes that there is no horizontal gene transfer (otherwise there could be no two distinct types). When this idealization is relaxed, the conclusion implied by the concept of phylogenetic competition makes much more sense. First, consider how horizontal gene transfer is nearly ubiquitous in the bacterial world: it is caused by basic types of interaction such as cell-to-cell contact, or predation (Polz et al. 2013), and some have even denied that bacterial lineages form species or monophyletic groups (Doolittle 2012).<sup>11</sup> The ubiquity of horizontal gene transfer is simply due to the ease with which genetic material can be incorporated due to various types ecological interaction (Polz et al. 2013). If there is no horizontal gene transfer between two bacterial lineages, there is most likely no ecological interaction, nor even a common habitat. Thus, once this further empirical detail is taken into account, it seems much more intuitive to judge that if there is no phylogenetic competition between two lineages of bacteria, then there is no shared selective environment.

*6.4 Viability Selection.* Consider a case of extreme fitness difference between two individuals, to such an extent that one individual is simply not viable in the environment. In this case, the offspring space of one individual is simply empty, regardless of whether the rival individual is present or not. There is no competitive relationship between the individual's future lineages: there is no phylogenetic competition. Does this imply the rather revisionary conclusion that viability selection does not involve a common selective environment, and thus cannot be considered natural selection?

Yes, but only when one of the types has zero fitness, and in this case the conclusion is not revisionary. Consider the analogous case of a mutation causing infertility: this mutation will not spread, but this is not due to natural selection, since there is no phylogenetic competition. After all, mutations causing infertility are, per definition, a non-heritable trait, and therefore cannot lead to evolution by natural selection, which can only act on heritable trait differences. Likewise, if a mutation would cause an individual to be non-viable, such a mutation is non-heritable and

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<sup>11</sup> For this reason, population-based and ecological accounts of selective environment would not be able to deal with bacterial selective environments.

therefore cannot evolve by natural selection. Instead, the death of the nonviable individuals and the absence of offspring from infertile individuals should be understood as developmental processes, not evolutionary ones.

**7. Conclusion.** It is a common judgement that two organisms can undergo natural selection only when they are members of the same species. It is also a common judgment that their respective external environments must be sufficiently similar. However, why should conspecificity or environmental similarity be so important? In this paper we attempted a deeper explanation, one in terms of phylogenetic competition, understood as the degree to which organisms compete to have their descendants represented in a finite descendant space. Phylogenetic competition allows natural selection to be precisely distinguished from sorting (mere fitness differences), and also offers a fundamental explanation of how natural selection is closely related yet distinct from speciation, mating, and ecological interaction between non-conspecifics.

## References

- Abrams, M. (2014). Environmental Grain, Organism Fitness, and Type Fitness. In G. Barker, E. Desjardins, & T. Pearce (Eds.), *Entangled Life* (Vol. 4). Dordrecht: Springer Netherlands. doi:10.1007/978-94-007-7067-6
- Bourrat, P. (2014). From survivors to replicators: evolution by natural selection revisited. *Biology & Philosophy*, 29(4), 517–538. doi:10.1007/s10539-013-9383-1
- Brandon, R. N. (1990). *Adaptation and Environment*. Princeton University Press.
- Chase, J. M., & Leibold, M. A. (2003). *Ecological niches: linking classical and contemporary approaches*. Chicago: University of Chicago Press.
- Cover, T. M., & Thomas, J. A. (2006). *Elements of Information Theory*. New York, USA: John Wiley & Sons, Inc. doi:10.1002/0471200611
- Damuth, J. (1985). Selection Among “Species”: A Formulation in Terms of Natural Functional Units. *Evolution*, 39(5), 1132–1146. doi:10.1111/j.1558-5646.1985.tb00453.x
- de Cara, M. A. R., Barton, N. H., & Kirkpatrick, M. (2008). A Model for the Evolution of Assortative Mating. *The American Naturalist*, 171(5), 580–596. doi:10.1086/587062
- De Queiroz, K. (2007). Species Concepts and Species Delimitation. *Systematic Biology*, 56(6), 879–886. doi:10.1080/10635150701701083
- Desmond, H. (2018). Selection in a Complex World: Deriving Causality from Stable Equilibrium. *Erkenntnis*, 83(2), 265–286. doi:10.1007/s10670-017-9889-z
- Doolittle, W. F. (2012). Population genomics: how bacterial species form and why they don’t exist. *Current biology: CB*, 22(11), R451-453. doi:10.1016/j.cub.2012.04.034
- Frankham, R., Ballou, J. D., Dudash, M. R., Eldridge, M. D. B., Fenster, C. B., Lacy, R. C., et al. (2012). Implications of different species concepts for conserving biodiversity. *Biological Conservation*, 153, 25–31. doi:10.1016/j.biocon.2012.04.034

- Glymour, B. (2011). Modeling Environments: Interactive Causation and Adaptations to Environmental Conditions. *Philosophy of Science*, 78(3), 448–471. doi:10.1086/660303
- Glymour, B. (2014). Adaptation, Adaptation to, and Interactive Causes. In G. Barker, E. Desjardins, & T. Pearce (Eds.), *Entangled Life* (Vol. 4). Dordrecht: Springer Netherlands. doi:10.1007/978-94-007-7067-6
- Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427. doi:10.1101/SQB.1957.022.01.039
- Janzen, D. H. (1977). What Are Dandelions and Aphids? *The American Naturalist*, 111(979), 586–589. doi:10.1086/283186
- Matthen, M., & Ariew, A. (2002). Two Ways of Thinking About Fitness and Natural Selection: *Journal of Philosophy*, 99(2), 55–83. doi:10.2307/3655552
- Millstein, R. L. (2009). Populations as individuals. *Biological Theory*, 4(3), 267–273.
- Millstein, R. L. (2014). How the concept of population resolves concepts of environment. *Philosophy of Science*, 81(5), 741–755.
- Mishler, B. D., & Brandon, R. N. (1987). Individuality, pluralism, and the phylogenetic species concept. *Biology and Philosophy*, 2(4), 397–414. doi:10.1007/BF00127698
- Okasha, S. (2006). *Evolution and the levels of selection*. Oxford : Oxford ; New York: Clarendon Press ; Oxford University Press.
- Polz, M. F., Alm, E. J., & Hanage, W. P. (2013). Horizontal Gene Transfer and the Evolution of Bacterial and Archaeal Population Structure. *Trends in genetics : TIG*, 29(3), 170–175. doi:10.1016/j.tig.2012.12.006
- Ramsey, G. (2013). Organisms, Traits, and Population Subdivisions: Two Arguments against the Causal Conception of Fitness? *The British Journal for the Philosophy of Science*, 64(3), 589–608. doi:10.1093/bjps/axs010
- Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10(12), 1115–1123. doi:10.1111/j.1461-0248.2007.01107.x
- Soberón, J., & Nakamura, M. (2009). Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences*, 106(Supplement 2), 19644–19650. doi:10.1073/pnas.0901637106
- Song, Y., Endepols, S., Klemann, N., Richter, D., Matuschka, F.-R., Shih, C.-H., et al. (2011). Adaptive Introgression of Anticoagulant Rodent Poison Resistance by Hybridization between Old World Mice. *Current Biology*, 21(15), 1296–1301. doi:10.1016/j.cub.2011.06.043
- Sterelny, K. (1996). Explanatory pluralism in evolutionary biology. *Biology and Philosophy*, 11(2), 193–214. doi:10.1007/BF00128919
- Walsh, D. (2010). Not a Sure Thing: Fitness, Probability, and Causation. *Philosophy of Science*, 77(2), 147–171. doi:10.1086/651320