The Selective Environment and Fitness Commensurability

The selective environment is the arena of natural selection: it is "where" natural selection takes place and must be held in common for two organisms to selectively compete. The selective environment, we argue, helps address the more general question of fitness commensurability: when can fitnesses of distinct entities be compared, such that their fitness differences constitute natural selection? In this paper we examine the main ways of analyzing the concept of the selective environment, but argue they do not ultimately account for fitness commensurability. Instead, what fundamentally matters is whether the two entities are engaged in what we call *phylogenetic competition*—competition for having one's offspring represented in future generations. On this view, the fitnesses of two entities are commensurable only if the entities are engaged in phylogenetic competition.

1. Introduction. The three conditions of *variation*, *fitness differences*, and *heritability* are often used to characterize the conditions for evolution by natural selection. However, it is often not acknowledged that these conditions are, strictly speaking, insufficient. Here is an exaggerated example: an orca and a krill individual may have heritable fitness differences,

yet this by itself does not allow one to say that the krill is being selected for over the orca, or vice versa. Their fitnesses can simply not be compared. This is what we call the *question of fitness commensurability*: what are the environmental and/or organismic properties that determine whether the fitnesses of two organisms or two populations can be meaningfully compared?

This is, of course, not controversial. In fact, to compare the fitnesses of entirely unrelated species would simply evince a fundamental misunderstanding of natural selection – something that science educators are concerned with (cf. Taber 2017). Yet this is not an artificial problem. In fact, the question of fitness commensurability is one faced by field biologists, where it is uncertain where the boundaries of populations, environments, or even species lie. Consider the following case: a field biologist discovers two nearby troops of Titi monkeys in the Amazon rainforest. Titi monkeys belong to a genus in which species categorization is notoriously difficult (Dalponte, Silva, and Silva Júnior 2014). And in fact, the field biologist is highly uncertain whether the two troops are conspecific or not, or even whether they may be considered to be part of the same (Darwinian) population (Stegenga 2016). If you ask of two of these monkeys, one from each troop, whether they are in selective competition with one another, what is such an answer fundamentally based on?

Typically the question of commensurability does not feature in discussions about the fundamental nature of natural selection. For instance, while the propensity definition of fitness acknowledges that fitness must be defined relative to an environment E (Brandon 1978), it does not give us criteria on how to decide whether two organisms inhabit the same environment $E.$ Similarly, the debate on the causal nature of natural selection, in enquiring

whether or not fitness differences are causal, typically assumes that fitnesses can be compared (Sober 1984; Matthen and Ariew 2002; Ramsey 2006; Millstein 2006). The distinction between selection and sorting anticipates this philosophical debate (Vrba and Gould 1986), but also there no conditions are given for when fitnesses are commensurable (and thus constitute selection, not sorting).

In his later work Brandon helpfully introduces the concept of *selective environment* (Brandon 1990). Here the idea is that organisms or populations can undergo natural selection only if they share a common selective environment. Thus, orca and krill do not share a common selective environment, but light and melanic forms of *Biston betularia*— the peppered moth—in a common patch of forest, do. On this view, the selective environment is the "arena" within which natural selection can occur. However, no precise conditions are given under which two organisms can be considered to "share" a selective environment.

In this paper we review some of the main approaches to analyzing the selective environment (Abrams 2014; Millstein 2014), and while these analyses have their own merits, we argue that they are not sufficient for addressing the commensurability question. Instead of fleshing out commensurability in terms of types of organism-environment interactions (Abrams 2014) or organism-organism interactions (Millstein 2014), we define commensurability in terms of effects, that is, in terms of the ensuing evolutionary dynamics. The basic idea is that selective competition is not fundamentally competition over resources or mating opportunities (even though these competitions may matter), but is competition over representation in future descendant populations. We call this *phylogenetic competition*.

The field biologist observing Titi monkeys will not be reasoning in terms of phylogenetic competition, but will look at ecological and populational indicators. What are the patterns of reproduction? What environmental factors could likely affect these patterns? The contribution of this paper lies in giving a deeper account *why* these indicators can be used to infer natural selection. We argue that the *meaning* of fitness commensurability lies in phylogenetic competition, and even though ecological and populational indicators are, in general, reliable indicators of phylogenetic competition. They are not always reliable however, and in those cases the proposed account offers a rationale to revise some intuitions about natural selection. Cases we discuss include extreme viability selection and differentially reproducing bacterial strains in environments with limitless resources: both are, we argue, not cases of natural selection.

The paper is structured as follows: after introducing the question of fitness commensurability in more detail (section 2), we will critically discuss the approaches to this question that draw on the selective environment (section 3). We then propose the account of phylogenetic competition (section 4), discuss how this could be operationalized (section 5), and finally discuss some cases where the account of phylogenetic competition implies unusual intuitions (section 6).

2. The Question of Fitness Commensurability. The concept of environment is central to how natural selection was originally contrasted with artificial selection by Darwin: whereas human agency is central to the latter, it is the environment—the "conditions of life"—that

assumes the selecting role in the former.[1] To flesh out the fitness commensurability question, it will be helpful to briefly review different ways the environment of an organism can be understood. We will label the broadest concept the 'external environment' (following Brandon 1990), which is constituted by all environmental variables that can potentially affect the fitness of organisms (or average fitness of populations). Such variables can be abiotic (temperature, humidity, acidity, precipitation, etc.) and biotic (density of competitors, predators, commensals, parasites, etc.).

Consider again orca and krill: while both may inhabit (for at least a limited period of time) the same general region in the ocean, it is clear that different environmental variables impact their fitness. To begin with, their large difference in body size has various ecological implications (Bonner 2011): orcas are relatively insensitive to turbulent water flows and have ranges that are many orders of magnitudes larger, allowing them to take advantage of changes in resource density in ways unavailable to krill. Moreover, orca and krill consume different resources in the environment, mate with different individuals, have different predators, and interact with them differently (orca have no natural predators). Hence, to state the obvious, the external environments of orca and krill are vastly different, and this appears to be one reason why their fitnesses cannot be meaningfully compared. A krill individual may have a much larger number of offspring than an orca, but it is not meaningful to speak of that individual as being 'fitter' than the orca.

The commensurability question refers to the question of why precisely this is. In the particular case of orca and krill, the commensurability question may seem to have

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[1] See for instance: "natural selection is daily and hourly scrutinising, throughout the world, every variation […] silently and insensibly working […] at the improvement of each organic being in relation to its organic and inorganic conditions of life" (Darwin 1859, 84).

straightforward answers: you might argue that the fitnesses are incommensurable because what adaptativeness (or *fit* with the environment[2]) means for a krill is vastly different from what it means for an orca. Or you might point out that krill and orca each experience a very different external environment, and hence their respective fitnesses are impacted by very different environmental variables, leading to incommensurability. Or you may hold that because they represent different species, their fitness values are incommensurable.

This question is frequently backgrounded. In textbook cases of natural selection, it does not pose itself at all, since they take as a starting point locally-occurring conspecifics (e.g., Ridley 2004, 75). The setup is classically two different types of the same species inhabiting a common environment that is characterized by a single fixed state—in the case of the light and melanic forms of the peppered moth, this fixed state is either the presence or absence of soot-blackened birch trees. Here the fitnesses of the light and melanic types are obviously commensurable.

The commensurability problem becomes non-trivial once we start allowing for partial overlap between external environments. To this end, consider once more the example of the Titi monkeys: two troops with somewhat different phenotypes, consuming similar but slightly different resources, vulnerable to the same predators, and even able to interbreed. It may be objectively unclear whether the two troops represent two variants of the same species, or two subspecies, perhaps in the act of speciation. What factors should guide the field biologist's decision whether fitness differences across (and not just within) the troops constitute selection?

Inhabiting the same external environment is insufficient: if there is significant gene

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[2] The reason why expected offspring number is called 'fitness' is that it is a proxy for adaptiveness.

flow, then the two troops may be undergoing natural selection, despite inhabiting different environments. Neither is gene flow sufficient. Consider for instance ring species consisting of different interbreeding species (*pace* the biological definition of species; Mayr 1982), but without the capacity for interbreeding being transitive. Individuals from populations A and B, and B and C can breed, but not A and C. Which fitnesses are commensurable, and which are incommensurable? Gene flow in itself does not give the answer.

The commensurability problem does not arise in textbook cases of fitness differences. It only poses itself with any urgency when it is not clear whether the two individuals (or groups) are conspecifics, when gene flow is only partial, and when similar but nonidentical environments are inhabited. While such lack of clarity is routine for field biologists, it also emphasizes a fundamental question that is often ignored[3]: under what conditions do fitness differences constitute natural selection?

3. Is The Selective Environment a Solution? One of the most prominent existing answers to the commensurability problem is that fitnesses are only commensurable when a common selective environment is shared. However, taken at face value, this only shifts the problem: under what conditions do two entities share a common selective environment? It is thus a reduction of the commensurability problem to the 'commonality problem'—the problem of determining when organisms share a common selective environment. In this section we outline two *prima facie* plausible, but ultimately problematic, approaches to the commonality problem. In the first approach, commonality is determined by similarity of

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[3] Note that while Vrba and Gould (1986) argue that sorting should be distinguished from selection, their analysis does not go further than arguing that selection is a cause of sorting. They do not offer a detailed account of what actually distinguishes them, and thus do not tackle the commensurability problem.

interaction between individuals and their external environments. In the second, it is determined by the density of interactions between individuals undergoing selective competition. We will consider each in turn.

3.1. Selective environments as selective regimes. There are roles for selective environment concepts other than as a tools for solving the commensurability problem. Brandon (1990), for example, used a selective environment concept in order to delimit areas of selective homogeneity, areas we call 'selective regimes'. This is best understood for simple cases in which a species has two discrete variants, *A* and *B*. These variants are part of the same selective regime if the sign of the fitness differences between them remains the same, even if the actual magnitude of the fitness difference fluctuates over space. For instance, if in a plant species variant *A* has higher fitness than *B* in nutrient-poor soil, but lower fitness in rich soil, then these two types of soil denote regions where the direction of selection is opposite. Selective regimes thus partition space-time into different regions with 'positive' and 'negative' fitness differentials.

Identifying different selective regimes allows for predictions to be made, in this case that *A* variants will increase relative to *B* variants in one region, and vice versa in the other region. Over sufficiently long time-scales, a slight fitness advantage over a rival type can be sufficient to push that type to extinction. Hence the crossing of selective regime boundaries, while sometimes involving only a small change in fitness values in absolute terms, may lead to binary outcomes over longer time scales.

Understood as selective regimes, the selective environment has a clear important theoretical role to play, since selective regime features and boundaries can help to explain

and predict evolutionary dynamics. However, the commensurability problem cannot be resolved in terms of selective regimes, because the commensurability problem is one that needs to be answered *prior* to identifying selective regimes, since identifying these regimes presupposes that fitness differences can be compared in the first place. Two nearby *A* and *B* variants, each inhabiting different selective regimes, may have commensurable fitnesses if, for instance, the seed dispersal areas for the two plants overlap. Moreover, there is no sense in asking whether a given selective regime is favorable to krill or favorable to orca—there is simply no shared selective regime.

3.2. The Environment-Centered Approach. In this paper we are interested in the second way the selective environment concept can be used, namely as a concept that helps resolve the commensurability problem. (Brandon also intends the selective environment in this way; see e.g., Brandon 1990, 103.)[4] Here one could also define selective environment in terms of the variables that affect fitness differences (Brandon 1990). Hence, a selective environment is held in common whenever the same environmental variables affect the fitnesses of the two individuals (or individual types). We call this the 'environment-centered' approach to the commonality problem (and, by extension, to the fitness commensurability problem). This account allows one to readily make sense of, for instance, the incommensurability of orca and krill fitness—or for that matter, any two individuals that inhabit distinct external environments with different conditions. Even though they do not address the commensurability problem, we note that this emphasis on common

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[4] See also the requirement of a common environment in his principle of natural selection (Brandon 1978), or how the presence or absence of a common selective environment helps resolve the difference between species selection and sorting (Brandon 1988, 60–62).

environmental variables—or organism-environment interactions—is discernable in Abrams' and Glymour's analysis of the selective environment (Abrams 2014; Glymour 2014).

However, this approach to the commonality of selective environments has its limitations. Consider two populations with no gene flow, but facing identical environmental conditions—for instance, two populations of brown rats (*Rattus norvegicus*), one inhabiting a neighborhood in Oslo, the other a quarter in Brooklyn. Each inhabits an external environment defined by variables affecting the fitness of individual rats in ways that are effectively identical: the presence of rubbish and detritus, sewers, alleyways, predators such as cats and dogs, icy winters and warm summers. Thus, a rat well adapted to life in Oslo would also be well adapted to life in Brooklyn. They interact with similar environmental conditions, and the conditions in their respective sub-environments are characterized by similar probabilities.

Thus, it would seem, these rats are in the same selective environment, and thus fitness values across the Atlantic are commensurable. Yet few would say that there is selection on the ensemble of Oslo-Brooklyn rats. For instance, if the lineages spawned by the Oslo and Brooklyn rats diverge irreversibly, then any adaptive trait somehow generated among the Oslo rats would never spread to the group of rats in Brooklyn. When lineages diverge in this way, fitness differences cannot lead to the spread of the fitter trait and, in this sense, to adaptive evolution. This is why few would say that natural selection is involved, that there is fitness commensurability across these groups. Thus, while environmental similarity can play a role in commensurability, it is neither a necessary nor a sufficient condition.

3.3. The Population-Centered Approach. In the population-centered approach to the commonality problem—and, by extension, to the fitness commensurability problem—two organisms share a common selective environment if and only if they belong to the same population. There are many different population concepts (Stegenga 2016), but we will focus this subsection on Millstein's (2010, 2014) account since she has connected population and selective environment concepts. Then we will generalize.

In Millstein's account, 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 (Millstein 2014). In turn, survival and reproduction interactions refer to a broad range of activities, including unsuccessful and successful mating, offspring rearing, competition for limited resources, and cooperative activities (Millstein 2009). 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.

In this way, Millstein's approach is an example of defining the selective environment in terms of the (fitness-affecting) interactions between individuals. Such interactions can happen with greater and lesser frequency, and hence, on this approach, commonality is a gradient that is dependent on the density of interaction: the more fitness-affecting interactions there are between individuals, the more the individuals share a common selective environment. Thus, the field biologist needs to observe the behavior of

the Titi monkeys and, in particular, to document how frequently they interact with each other, in order to determine if a selective environment is shared.

This approach, besides explaining why spatially distinct populations should not be taken to share a common selective environment, has the general advantage of abstracting away from how, precisely individuals interact with their external environments. The similarity of interactions with external environments still matter, but only *insofar* as such interactions affect whether the two individuals are part of the same population.

As a general remark for population-centered approaches: in principle they allow for different individuals in a same population to inhabit very different external environments, and thus to be exposed to very different environmental challenges. As long as gene-flow (or some other criterion of population membership like survival and reproduction interactions) does not begin to cluster within parts of the population, but is maintained across the population as a whole, this means that different parts of the population will not be independently evolving. However, what purpose does a concept such as the 'selective environment' fulfill if it is, on closer analysis, not an environment concept? What point is there in speaking of a common selective environment, if the same selective environment can, in principle, refer to vastly different environmental conditions? The population-centered approach to the selective environment thus seems to suggest inherent limitations in thinking about the commensurability problem in terms of an environment concept.

How well does Millstein's population-centered approach resolve the commensurability problem? First, consider the conspecificity criterion: this means that populations are limited to conspecific organisms, implying that other biological units that are frequently held to be levels of selection (genes or groups or even whole species, for

example) cannot form populations, share a selective environment, and hence undergo natural selection. Of course, at which level natural selection "really" operates is a debate unto itself (Okasha 2006) and the claim that natural selection only operates at the level of individual organisms is a defensible one. However, it would be questionable to try to resolve this debate by mere *a priori* means, by defining the selective environment such that selection can occur only at level of individual organisms. This is one reason why it is desirable that an analysis of the commensurability of fitnesses would not be limited to conspecific organisms.

A second reason why the conspecificity criterion should be dropped is that it presupposes that taxonomic debates about how species boundaries should be drawn can be clearly resolved (De Queiroz 2007). Given our example of Titi monkeys, it would seem desirable to be able to provide an account of whether two populations share a selective environment even if it may be objectively unclear whether or not they are conspecifics. In fact, shifts in fitness commensurability may help to explain speciation events—thus having to first determine species boundaries is an undesirable prerequisite to commensurability determinations.

Next, turning to the condition placed on biotic interactions (i.e., they must affect survival and reproduction), this seems much less restrictive than the conspecificity condition. Nonetheless, when one considers cases of natural selection on groups of bacteria, it becomes unclear to what extent survival and reproduction interactions are necessary. To begin with, bacteria are asexual and thus do not engage in reproduction interactions. Any account that restricts natural selection to sexual organisms should be discarded. Second, in the hypothetical case of infinite resources, different bacteria types

can reproduce at different rates without engaging in survival interactions. Similarly, for a group of immobile organisms—like trees spread out over different latitudes—that consume resources and reproduce at different rates: why should they be considered, per definition, not to undergo natural selection? Darwin (1859) considered "the struggle for existence" to sometimes occur without direct interaction, as with "a plant on the edge of the desert" fighting to survive with little moisture (62), or flowering plants competing "to tempt birds to devour and thus disseminate its seeds rather than those of other plants" (63). It seems wrong to rule out such cases as genuine competition, even though there may be little or no direct interaction among the individuals. We will revisit these cases later (see section 6), and show how the concept of survival interactions is more ambiguous than it may seem, and only indirectly relevant for whether fitnesses are commensurable.

Many of these considerations can be applied to population-centered approaches in general, not merely that championed by Millstein. It can be argued that no membership criterion for populations is beyond reproach (Stegenga 2016). This does not give a secure foundation by which to analyze questions about the selective environment, much less about the commensurability problem. Moreover, the questions of population membership and fitness commensurability are distinct enterprises: it does not seem that the former should be resolved before engaging in the latter. Indeed, for any membership criterion—such as conspecificity and/or survival and reproduction interactions—there seem to be examples of groups of individuals that do not fulfill that membership criterion and yet of which we would like to ask whether they are undergoing natural selection. This motivates a more bottom-up approach to the commensurability problem.

To sum up, an account of the commensurability problem should be (1) flexible

enough to be applicable to all cases that potentially involve natural selection, regardless of the causal connection between the entities or their "level," and (2) minimalist enough to avoid basing the commensurability problem on equally complicated or controversial concepts (like species or population). To this could be added that a solution to the commensurability problem should also give insight into why some fitness differences count as selection, and why others do not. This is why we propose the concept of phylogenetic competition, which we will now describe.

4. Phylogenetic Competition. When Darwin introduced the concepts of natural selection and the "struggle for existence," he did not make a strict distinction between intra- and interspecific competition (nor between individual-individual interactions or individual-environment interactions for that matter):

> Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. (Darwin 1859, 63)

The distinction he had in mind thus seems to be one of degree rather than of kind: Darwin notes multiple times how competition is more severe when the two entities are more alike in "structure, constitution, and habits" (Darwin 1859, 110). In this way, taxonomic considerations seemed to be relevant for the struggle for existence only if they influenced competitive interactions following from Malthusian limits.

This competitive aspect of natural selection is downplayed by approaches to natural selection informed by population genetics (see argument in Lewens 2010). Given the latter's reliance on common garden experiments—experiments, that is, involving conspecifics (of different phenotypes) in identical environments—to investigate patterns of selection, this is not surprising. In common garden experiments, one need not enquire what precisely distinguishes natural selection among conspecifics from either competitive interactions between heterospecifics, or from competitive interactions across heterogenous environments.

In returning to the original Darwinian insight, one can raise the question of what, precisely, is being competed over in the struggle for existence. The answer to this question will turn out to be a solution to the commensurability problem. In this section we first sketch phylogenetic competition (4.1), and then show how it helps resolve the commensurability problem (4.2). In section 5, we discuss implications for how phylogenetic competition relates to common-environment and common-population approaches to the commensurability problem.

4.1. Phylogenetic and Ecological Competition. Here is a first illustration of the idea of phylogenetic competition: Orca and krill are not competing for having their descendants represented in offspring populations; by contrast, two Titi monkeys in nearby troops may potentially be competing for such representation (whether they are actually competing depends on the details of the situation).

In order to define phylogenetic competition, we must make precise *what* is being competed over. The original Darwinian insight is that nothing less that 'existence' is being

competed over. For this, we avoid talk of "slots" because the term seems to presuppose a clear concept of organismic individuality. To allow for more graded distinctions we introduce the notion of a *descendant space*:

> The **descendant space at time _t_ of individual _X_** is a finite space consisting of positions that can be occupied by the descendants of _X_.

In some cases, such as sessile organisms, the "positions" can be concrete, such as locations for a barnacle or tree to establish itself. In other cases, the positions may be abstract and uncountable, and the boundaries of individuality vague—the lines of descent may blur strict distinctions between growth, persistence, and replication may not be clearly delineated (Dupré and O'Malley 2009; Stencel 2016). The only assumption that the definition above makes is that the size of the space is finite. This is biologically defensible, since limited resources needed for sustenance (e.g., nutrients, places to nest or to grow) puts an upper bound on the "best-case scenario" in terms of number of descendants for the individual.

Second, in order to express the idea of competition, we need to define *reproduction* and *fitness* in a more abstract way. To this end, the notion of descendant space allows us to define a *descendant line* of an individual _X_, which is a sequence of individuals X_i across descendant spaces, where each is a descendant of the previous. Finally, when we speak of _X_'s *descendant tree*, we refer to all possible descendant lines of _X_. This terminology allows us to introduce the notion of *intersecting descendant spaces*:

> The descendant spaces of two individuals at time _t_ **intersect at some later time _t′_** when their descendant trees intersect at _t′_.

When descendant lines *actually* intersect, then the two individuals have common offspring

(or their descendants have common offspring); however, as we will now see, various causal processes may prevent the descendant lines from actually intersecting.

With these definitions in place, we can now define phylogenetic competition as follows:

> **Phylogenetic competition** between individuals X_1 and X_2 at time t occurs if and only if their respective descendant trees intersect at some later time t', and that the occupation of this intersection by descendants of X_1 at t' causes fewer descendants of X_2 to occur at t', and vice versa.

More informally, this definition sketches the following image: phylogenetic competition describes the dynamic situation where there is a zero-sum game being played for the occupation of intersecting spaces in descendant trees. If one tree gains more occupants, this means that the trees of other individuals will tend to gain fewer. The competitive element is thus defined by causal relations occurring through the occupation of descendant trees.

Let us now unpack this definition further, and show what function each element of the definition has. The condition of having intersecting descendant spaces distinguishes phylogenetic competition from *ecological competition*. In ecological competition, there are no intersecting lines of descent, and hence adaptations in the descendant space of one cannot spread to the other. An adaptation in the descendant space of a krill individual cannot spread to the descendant space of the orca. We define ecological competition as follows:

> **Ecological competition** between individuals X_1 and X_2 at time t occurs if and only if the occupation of the descendant space of X_1 at t' causes fewer descendants of X_2 to occur at t', and vice versa.

To see clearly the relationship between phylogenetic and ecological competition, consider a lion and a cheetah in an African savanna. The lion and cheetah are competing for the same population of gazelles, but are not competing for descendants in an intersecting descendant space. They do, however, have a competitive relationship, such that if the lion has more offspring, the cheetah will tend to have fewer, and vise-versa.

By contrast, two lions can compete for descendants in offspring populations. While the lion and cheetah are competing for ecological real estate, the two lions are competing for phylogenetic real estate over and above ecological real estate. They are in the same phylogenetic tree, a novel adaptation by one lion can spread through the descendant space of other lions[5]. But a cheetah cannot compete for phylogenetic real estate with a lion, and cheetah adaptations have no chance of spreading through the descendant space of lions.

While it is necessary for phylogenetic competition that the descendant trees overlap, it is not necessary that the overlap occurs in the next generation. Instead, the overlap could occur two or more generations later. Consider the three generations represented in figure 1. Each circle represents a possible organism and the arrow represent possible lines of descent (with their thickness representing the probability of placing a descendant in the indicated spot). Thus, A has three possible descendants, while B has five. A and B are in competition because they are vying for the same spots in the next generation (the stippled circles). B and C, by contrast, are not vying for spots in the next generation. They are, however, vying for spots in the third generation (the striped circles).

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[5] This property maps on to the concept of exchangeability as outlined by Templeton and Matthewson: see Matthewson (2015).
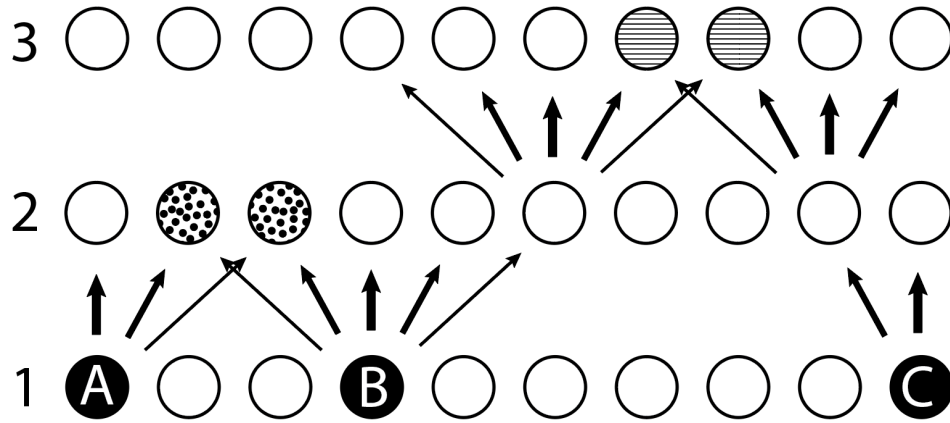
Figure 1: A schematic illustration of phylogenetic competition. Competition occurs between A and B, and between B and C, but whereas descendant trees of A and B intersect at $t = 2$, descendant trees of B and C intersect only at $t = 3$.

Note, however, that the slot visualization is a heuristic representation of phylogenetic competition: the latter can hold between any two phylogenies, and thus does not require discrete generations. Also, descendants can represent clonal growth instead of sexual reproduction. In this sense, phylogenetic competition is to be distinguished from the condition of reproductive competition used to demarcate populations (Godfrey-Smith 2009; Stencel 2016; Matthewson 2015).

4.2. Phylogenetic Cooperation. The condition of a negative causal relationship is necessary for phylogenetic competition because X_1 and X_2 can have an intersecting descendant space without there being detrimental effects of the occupation of the intersection. This is particularly clear in cases of infinite resources. In such cases, even

though if X_1 has a descendant that occupies intersecting space S, there will always be an alternative space S' for any descendant of X_2. Thus, X_2's offspring pool is not negatively impacted by that of X_1.

The causal relationship is also specified as negative since an occupation of an intersection by one descendant tends to decrease the descendant number of the competing individual. The mirror of this relationship—in which there is a positive causal relationship such that the occupation of the intersection by one individual tends to *increase* the other individual's descendant number—is *phylogenetic cooperation*:

> **Phylogenetic cooperation** between individuals X_1 and X_2 at time t occurs if and only if their respective descendant trees intersect at some later time t', and that the occupation of this intersection by descendants of X_1 at t' would tend to cause more descendants of X_2 to occur at t', and vice versa.

Perhaps the paradigmatic example of phylogenetic cooperation is monogamous mating. In such cases the descendant lines of the mating pair are fused. With perfect lifetime monogamy, the descendant space for the pair would be identical. Serial monogamy would result in less overlap, and random mating in even less. In such cases, only part of the descendant trees of the mating individuals may fuse (representing the common descendants), whereas other parts of the descendant tree (representing the descendants with other mates) may result in competition. A pair of individuals can thus at once be cooperating and competing. Potential mating (or the potential mating of descendants) is in fact a *condition* for phylogenetic competition between sexual organisms; only certain mating behaviors minimize phylogenetic competition and maximize phylogenetic

cooperation.

Phylogenetic cooperation can come about not just through the fusion of descendant trees via mating, but also through other ways of tying the fitness of individuals together. One example of phylogenetic cooperation is cooperation to access previously inaccessible resources. For instance, conifer bark beetles require the death of the host tree for their success. Some beetles have developed the ability to cooperate by using aggregation pheromones to attract others in order to attack *en masse* to kill live host trees (Berryman et al. 1989; Birch 1984). This group behavior increases the amount of nutritional resources available for each individual, thus increasing the size of the descendant space for all cooperating beetles. Hence, the increased occupation of an intersection point by one beetle may be (positively) causally related to the branching of a cooperating beetle.

4.3. Phylogenetic Competition and the Commensurability Problem. The implications of phylogenetic competition for the commensurability problem was already implicit in our unpacking of the definition of phylogenetic competition. Nonetheless, the implications should also be spelled out explicitly.

According to the account of phylogenetic competition, fitness differences between two individuals or entities are commensurable (and thus constitute natural selection) only when the two individuals/entities involved are phylogenetically competing with each other. Otherwise fitness differences may represent ecological competition, or they may be unrelated and merely represent independent evolution, as with the orca and krill.

The *rationale* for this account is that phylogenetic competition is necessary for adaptations spreading throughout a population or species. This is why, we believe,

approaching fitness differences through the lens of phylogenetic competition can deliver genuine insight as to what is at stake in natural selection. One of the core explanatory functions of natural selection—i.e., one of the reasons why the concept was introduced in the first place—is to explain adaptive evolution by conceptualizing it as the differential spread of adaptive traits (over less-adaptive traits) by differential reproduction.

Phylogenetic competition is simply a way to further analyze what conditions must be placed on differential reproduction (fitness differences of individuals) in order to allow for the spread of adaptations. The proposal is that there is a negative causal relationship between descendants in a finite space, and this is what allows the less-adaptive traits to be 'pushed out of existence' by the more adaptive traits. Thus, the concept of phylogenetic competition is not a mere artificial construct, but rather something inherent in the very concept of natural selection itself, and to the explanatory function it is designed to fulfill.

The phylogenetic competition account has two further advantages: minimalism and flexibility. First, regarding minimalism, no assumption is made about whether an environment or population is shared, or even whether the entities belong to the same species. This has the advantage of conceptual simplicity, though a potential downside of this approach is that it is less obvious how to operationalize phylogenetic competition. We will discuss this in the next section.

5. Operationalizing Phylogenetic Competition. Using phylogenetic competition to solve the fitness commensurability problem is not at odds with the environment- and population-centered approaches discussed earlier. Shared factors in the external environment still matter, as does a shared population, however defined. In this section we will argue that,

while phylogenetic competition is conceptually prior to these approaches, such approaches can be used in the operationalization of phylogenetic competition

This operationalization is of genuine philosophical significance because of the way phylogenetic competition is defined: whether two individuals compete *now* depends on whether their descendant trees intersect *in the future.* This means that, strictly speaking, one can only determine whether two individuals competed phylogenetically in retrospect. The counterfactual nature of phylogenetic competition adds another layer of epistemological opacity, since one can only establish phylogenetic competition by evaluating counterfactual scenarios. Only in this way can we evaluate the degree to which the occupation of one descendant tree inhibits the occupation of another. For field biologists who cannot run repeated experiments, this is a problem. How can they know whether two populations or individuals are in phylogenetic competition?

5.1 Niches and Selective Environments. There is a strong relationship between environment and competition: think of how many sports competitions unfold in a shared space, whether a race course, football stadium, or ski slope. In arguing that phylogenetic competition is foundational, we have argued that natural selection should be defined by the competitive dynamics rather than by the space in which it unfolds. However, this does not mean that the space does not matter. One can examine a race course, football stadium, or ski slope for evidence of what type of competition is taking place.

In this way, the criteria that help establish whether a niche is held in common can also indicate whether two individuals are competing phylogenetically. Criteria like habitat and population distribution, life-history traits, resource consumption, and biotic interaction

(Chase and Leibold 2003) indicate the size of the descendant space (maximum number of descendants) as well as the strength of the negative causal relationship associated with occupying this space. The more likely individuals are to interact ecologically (competition or cooperation for resources), the more likely they are to compete phylogenetically, either in the directly ensuing generation, or some number of generations hence.

It is important to emphasize that while these criteria do provide evidence for phylogenetic competition, they are neither necessary nor sufficient. Two people can attend a chess tournament without competing, or they could compete over the internet from different parts of the globe. Similarly, two individuals could share a niche and yet be independently evolving (and hence not be in phylogenetic competition), or they could inhabit very different ecological niches and yet be in phylogenetic competition. What is foundational in all these cases is the competition, what the goal is, and which individuals are in competition for the goal. Nevertheless, the environment carries some information about the existence and nature of the competition.

5.2 Populations and Species. Recall how Darwin claimed that an intraspecific struggle for existence is more intense than an interspecific one:

> But the struggle almost invariably will be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers. (Darwin 1859, 75)

Conspecificity is not a condition for struggle for existence, but is instead a factor determining its intensity. In a similar way, we understand conspecificity as a factor that can indicate both the probability of phylogenetic competition occurring, as well as its

intensity. Closely related lineages will have a much higher chance of possessing intersecting descendant lineages than distantly related lineages. Moreover, the more that descendant trees intersect, the more intense the phylogenetic competition will be. This means that because natural selection is conceptually orthogonal on conspecificity (*pace e.g.* Lewontin 1983): two non-conspecifics could have commensurable fitnesses, whereas two conspecifics could have incommensurable fitnesses.

In this way, the criteria for specificity can be coopted for phylogenetic competition. Species are typically defined as independently evolving metapopulations (cf. De Queiroz 2007), and as such there is a large number of criteria for determining whether two individuals (or populations) are part of the same species. These criteria include phenotypic distinctness, ecological distinctness, reproductive compatibility, reproductive isolation, and being part of a monophyletic group. In this way, the criteria for conspecificity refer to the constituents of the selective environment: the structure of organism-organism interactions (reproductive isolation, reproductive compatibility, phenotypic distinctness) or to interactions between organisms and their respective external environments (ecological distinctness, phenotypic distinctness). Since these criteria can be used to estimate whether two populations are independently evolving, they can also be used to estimate how probable the descendant lineages of two individuals are to cross in the future. Thus, criteria for conspecificity matter for the commensurability problem insofar as they bind the phylogenetic destinies of two individuals. The criteria can thus serve to operationalize phylogenetic competition.

As for population criteria, some causal connectivity between individuals—whether via survival or reproduction interactions—is likewise evidentially relevant for whether

fitnesses are commensurable. However, also here, survival and reproduction interactions are neither necessary nor sufficient for fitness commensurability, and hence, natural selection. In sum, while both the environment-centered and population-centered approaches to common selective environments ultimately fail to offer necessary and sufficient criteria for fitness commensurability, they do offer useful operationalizations.

Additionally, a focus on biological species or populations of organisms is overly restrictive. While we defined phylogenetic competition relative to two individuals, we do not necessarily mean two individual organisms. Two alleles, two populations, and even two species can potentially be in phylogenetic competition. Alleles compete for representation in a common locus; two species of the same clade may compete for representation in a common descendant space. Of course, species selection would require crossing descendant lines, and thus some form of introgression (for sexual species) or gene flow (in general).[6]

6. Implications. We argued for phylogenetic competition as a minimal and flexible way of approaching the fitness commensurability problem. Moreover, because such competition allows for adaptations to spread, it seems to capture a crucial dimension of natural selection. Nonetheless, the account has some unusual implications when applied to concrete cases. Three cases in particular appear to be problems for our account, and we will discuss them in this section: (1) the case of no biotic interactions and infinite resources,

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[6] This implication opens up further questions, such as: in what way does phylogenetic competition at the level of individual organism, given that this involves intersecting descendant lines, require phylogenetic competition at the level of alleles? We will not further pursue such connections with level-of-selection issues here.

(2) the case of extreme viability selection, and (3) the case of future selection.

6.1. The case of no biotic interactions and infinite resources. Consider an asexual species which is suddenly provided with infinite resources—all food, nesting sites, etc. are in unlimited supply. Here one variant, *A,* could systematically outperform another variant, *B*, and in this sense one could judge fitness differences to be present. Yet, because of infinite resources, the success of one variant does not decrease the probable success of the other: there is no phylogenetic competition. Even if *A* would outcompete *B* over a given quantity of resource, then *B*-organisms would still be able to find other resources to consume. The descendant spaces of both *A* and *B* are filled to the maximum, implying that a negative counterfactual relation between the descendant trees of an *A*-organism and a *B*-organism is impossible. Yet, are the different fitnesses not commensurable, and is this not a case of natural selection? (This is the case that Matthewson 2015 deemed problematic for the concept of Darwinian population.)

Note first that the variants that reproduce at a higher rate are not "more adaptive" than the less fit strains: each has no difficulty in surviving and reproducing in an environment with limitless resources. Such environments are so benign that all types (or at least, a very wide range of viable types) can be considered "adaptive." Yet, the reason why fitness differences matter in the first place was to explain the spread of adaptations in evolution. By contrast, in an environment with unlimited resources, traits that allow for a higher reproductive rate do not spread throughout a population. Types with higher and lower reproductive rate exist in parallel.

Thus, on a conceptual level, it makes sense to judge that the fitness

commensurability problem does not arise in environments with unlimited resources, and insofar as natural selection involves commensurable fitnesses (though see next subsection), in such environments where individuals do not interact, fitness differences do *not* constitute natural selection.

6.2. The case of zero-fitness individuals. A second interesting case occurs when type *A* has a nonzero fitness value, whereas *B* has a fitness value of zero, meaning that reproduction is not merely improbable, it is impossible. According to the account of phylogenetic competition, the fitness differences are not commensurable. This is because *B* individuals have no descendant trees, and intersecting descendant trees are a necessary condition for phylogenetic competition. Yet one may object that such fitness differences represent extreme selection against *B*, not a lack of selection.

The core of the response is that the commensurability problem simply does not arise in such situations. In this case the fitness of one individual (token or type) is zero, and this is sufficient to judge that it is being culled, regardless of the fitness of the other individual. If a krill individual has zero fitness, it does not matter what fitnesses other krill individuals have, let alone orca individuals. In this sense, the commensurability problem does not arise in cases of zero-fitness individuals, and hence the latter does not represent a case that the account of phylogenetic competition needs to cover.

However, one could still wonder to what extent such culling represents a process of natural selection, and hence whether not all natural selection processes necessarily involve commensurable fitnesses. [7] Let us give some more empirical detail here. The onset

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[7] Our thanks to <Blinded> and <Blinded> for pressing us on this point.

of a novel infectious disease represents perhaps the most common alteration of the environment with dramatic fitness consequences, and such onsets are typically judged important for selective dynamics, leading populations to adaptive states. Such selection "decreases the frequency of mutations that prove to be disadvantageous to carriers in a given environment, the magnitude of this decrease depending on the degree to which the mutation is deleterious" (Vasseur and Quintana-Murci 2013, p. 597).

It is clear from such empirical studies that the relevant adaptation (resistance to disease) arising from this culling process is to be situated at the population level. At the group level one may speak of (commensurable) fitness differences between more and less disease-resistant populations. However, at the individual level, the culled trait(s) confer zero fitness and are thus not heritable: they have no chance of spreading through the population or beyond. The individuals possessing the traits are evolutionary zombies, phylogenetic living dead. In this way, at the individual-level, fitness differences can be judged not to constitute natural selection on grounds of zero heritability, even regardless of the commensurability problem.

6.3. The case of intersecting lines in the distant future. Consider a case where the descendant branches of two organisms (or organism types) displace each other only in the distant future. The concept of phylogenetic competition holds then that the two individuals or types are in phylogenetic competition *now* despite the displacement occurring in the future. Formulated in this way, the worry can be raised that the concept of phylogenetic competition involves an implicit endorsement of retrocausation.

To make the case more concrete, let us revisit the example of the Oslo and Brooklyn

rats. Suppose rats in these cities occasionally sneak onto ships and make the voyage across the sea in their holds. Thus, rats in Oslo have a low probability of having a descendant eventually make its way to Brooklyn, and vice versa. Because of this, the descendant trees of any Brooklyn and Oslo rat pair may intersect. And if they do intersect, they will be in phylogenetic competition. Phylogenetic competition in such a case refers to a distant future possibility, but is not causally dependent on it.

In a sexual population, over a sufficiently long time-scale, the descendant lines of reproducing individuals will criss-cross and eventually merge. If the descendant tree of Brooklyn rat X_1 intersects with that of Oslo rat X_2 at some future time $t' \gg t$, then the individuals are in phylogenetic competition. This does not mean that this competition is important, especially in the short term. In such a case, it is likely that because there is little travel of rats across the Atlantic, in explaining the short-term evolutionary trajectory of Oslo and Brooklyn rats, the fact that the fitness values across the Atlantic are commensurable is readily ignored. However, if we ask long-term questions about the fates of the rat metapopulations, phylogenetic competition across the Atlantic may become important. Will the metapopulations diverge into separate species? Their transatlantic phylogenetic competition argues against this. If a highly adaptive novel trait emerges among the Oslo rats, will this make its way to—and eventually sweep through—the Brooklyn rats? Their phylogenetic competition implies yes.

The retrocausation worry can thus be dispelled: the long-term effects of phylogenetic competition are relevant to higher levels or units of evolution, which have a larger temporal extension than individual organisms. Taking a long-term perspective shifts the focus away from token individuals to questions such as how rat traits will change over

time, or whether adaptations from one population will eventually make it to the species as a whole. This also suggests why, when we consider trajectories over longer time-scales, it is often populations or metapopulations—or even whole species—that we are concerned with.

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 important? In this paper we attempted a deeper understanding of when and why fitness differences are commensurable and can constitute natural selection. We proposed the account of phylogenetic competition, where fitness differences are only commensurable if organisms compete to have their descendants represented in an intersecting 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.

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