Environmental Grain, Organism Fitness, and Type Fitness

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Abstract

Natural selection is the result of organisms' interactions with their environment, but environments vary in space and time, sometimes in extreme ways. Such variation is generally thought to play an important role in evolution by natural selection, maintaining genetic variation within and between populations, increasing the chance of speciation, selecting for plasticity of responses to the environment, and selecting for behaviors such as habitat selection and niche construction. Are there different roles that environmental variation plays in natural selection? When biologists make choices about how to divide up an environment for the sake of modeling or empirical research, are there any constraints on these choices? Since diverse evolutionary models relativize fitnesses to component environments within a larger environment, it would be useful to understand when such practices capture real aspects of evolutionary processes, and when they count as mere modeling conveniences. In this paper, I try to provide a general framework for thinking about how fitness and natural selection depend on environmental variation. I'll give an account of how the roles of environmental conditions in natural selection differ depending the probability of being experienced repeatedly by organisms, and how environmental conditions combine probabilistically to help determine fitness. My view has implications for what fitness is, and suggests that some authors have misconceived its nature.

1 Introduction

1.1 Overview

Natural selection is the result of differences in fitness, and fitness depends on organisms' interactions with their environment. But environments vary in space and time, sometimes in extreme ways. Variation in what biologists call patches, habitats, environments, etc.—or what I'll call *subenvironments* of a *whole environment* over which a population ranges—is generally thought to play an important role in evolution by natural selection, maintaining genetic variation within and between populations, increasing the chance of speciation, selecting for plasticity of responses to the environment, and selecting for certain behaviors such as those involved in habitat selection and niche construction.[1] Variation in subenvironments can involve both spatial variation and temporal variation, and can partly result from migration and other kinds of dispersal (since these can expand the variety of environments to which a population is exposed), or from niche construction. Environmental variation goes beyond this, however. The interaction of any organism with its environment will nearly always differ from the interactions of other conspecifics with the same environment. Even if two organisms were genetically, physiologically, and cognitively identical, a consequence of the complexity of most environments is that the organisms' interactions with their surroundings will differ.

There is a wide variety of kinds and dimensions of environmental variation. Do all of these sorts of interaction and other kinds of environmental variation matter for natural selection? Do different kinds of environmental variation play different roles in natural selection? When biologists make choices about how divide up an environment into subenvironments for the sake of modeling or empirical research, are there any constraints on these choices, or is any way of dividing up the environment legitimate?

In this paper, I try to provide a general framework for thinking about how fitness and natural selection depend on environmental variation. It turns out, I'll argue, that some concepts of fitness popular among philosophers of biology cannot play the role they are thought to play. A concrete example at this point will help to suggest the range of environmental variation that I think must be discussed.

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[1]Odling-Smee et al. (2003) treat habitat selection—cases in which organisms "choose" their subenvironment—as a form of niche construction. I use the latter term in a narrower sense requiring modification of the environment by organisms (cf. Sterelny 2005).

1.2 An example

In order to illustrate kinds of environmental variation that might be thought to be relevant to interactions affecting fitness, I'll describe some characteristics of house sparrows. Some of the interactions that I want to highlight are not described in detail in the scientific literature; some variations are simply impractical to study systematically. However, my plausible stories are based on a large body of research about house sparrows, primarily that reported by Anderson (2006) where not otherwise noted. I'll use some research on other birds, too, following the common scientific practice of making reasonable hypotheses about a species' properties from what's known about closely related species.

A house sparrow that finds food in an area exposed to the sky may give a call to alert other house sparrows, waiting until others arrive—sometimes even forgoing food if they don't. This is not thought to be an altruistic behavior; it allows sparrows to feed more efficiently, as they share the task of visually scanning the sky for raptors. Whether an instance of such food-calling behavior makes survival and reproduction more or less likely than alternative behaviors plausibly depends on various factors: Are there any raptors or other predators who will notice the house sparrow feeding? Did the call bring the calling sparrow to the attention of a predator? How much food is there to share with other house sparrows? How many house sparrows are there nearby? How easy it to hear the call? Are other house sparrows upwind or downwind? Is there intervening foliage that will degrade the sound (Kirschel et al., 2009; Crozier, 2010)? Is there noise that will mask it (Hu and Cardoso, 2009)? Are nearby house sparrows already satiated? Are they busy with other tasks, such as nest building, courting, sitting on eggs? Would a male who is trying to attract mates to a desirable nest cavity have more offspring if he responds to the food call or remains to guard his nest cavity? Are there other areas with food which are safer, or do they have other dangers, such as nearby feral cats? Note that although a sparrow may be able to eat more if other sparrows share scanning duties, there is also competition for food within a feeding flock, and aggressive encounters use up some potential feeding time. Some sparrows are more aggressive than others, so the benefit of sharing the meal with other sparrows depends partly on which sparrows respond to the call.

There are additional factors that affect the possible benefits of food-calling behavior. What kind of food is available in the exposed area? What nutrients is the calling house sparrow likely to need for energy for activity, for feather production, for maintenance of feather coatings, for fighting parasites, or for pigmentation? Male house sparrows may get substances from food that allow them to synthesize melanin used to create their black chest patches; these may influence attractiveness to females, or play a role in aggressive interactions between males. However, melanin and related substances may also be used

for processes which fight parasite infections (Catoni et al., 2009). Whether eating some substances or eating others is more or less beneficial for a given male house sparrow might depend on the season, the number and kinds of parasites that it has or will have, and the cognitive and physical properties of other nearby house sparrows.

The preceding discussion suggests ways in which very small-scale, detailed patterns of variation might affect the survival and reproduction of a house sparrow, though it ignores many aspects of house sparrow life, such as environmental interactions affecting development.[2] Notice, though, that many of the elements mentioned above are likely to exhibit large-scale spatial or temporal patterns. What foods are available and where they are located depend on plant growth patterns that vary across the landscape, and over time. Some plants grow best in some soils, at some heights, under certain weather conditions, etc. Kinds of predators vary, and depend on the presence of other prey, which in turn depend on what other plants and animals are present. Weather patterns affect house sparrow survival, but interact with other environmental conditions (Ringsby et al., 2002). Weather patterns of course vary from week to week, from season to season, from year to year, and across different parts of the world: House sparrows are found in Europe, northern Africa, southern Africa, the Middle East, central Asia, the Indian subcontinent, and the Americas. There are morphological and behavioral differences between these different subpopulations, and some of the differences plausibly have to do with differences in environmental conditions. House sparrows are known to live in urban, agricultural, and other rural areas, each of which might favor certain morphologies or behaviors over others (cf. Evans et al. 2009).

Environmental variations of different kinds at different spatial and temporal scales plausibly affect natural selection on house sparrows. Scientists doing research on house sparrow evolution may decide to study some such differences, but no one would try to study all such differences, and different scientists will make different choices about scales of variation to study. Nothing about the house sparrow example suggests that it is particularly unusual; similar points can be made about most species. I note that among humans, social interactions generate particularly complex large-scale and small-scale environmental variations. Although human behavioral plasticity and social institutions may make sustained gene-based evolution in humans less common, I suggest that the framework described below applies equally well to all species (see §5).

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[2]For example, the intensity with which a house sparrow nestling begs, influencing parents' feeding behavior and subsequent nestling survival, seems to be the result of an earlier gene-environment interaction (Dor and Lotem, 2009).

1.3   Goals of the paper

If we are interested in understanding what, in general, fitness and natural selection consist in, the following questions are important. Does *every* subset of conditions that might coexist within a whole environment count as determining fitness relative to it? If not, why not? Since diverse evolutionary models relativize fitnesses to subenvironments, it would be useful to understand when such modeling practices capture real aspects of evolutionary processes, and when structured environments count, instead, as mere modeling conveniences. This will help to clarify relationships between models, the systems they concern, and empirical evidence. Note that a working assumption here is that fitness differences and processes of natural selection are real aspects of the world that are investigated and approximated by empirical methods and modeling strategies. This assumption allows us to make a distinction between pragmatic fitness concepts which are useful for measurement and modeling, and theoretical fitness concepts which are assumed to represent underlying properties approximated by pragmatic concepts (Abrams, 2012a).

The following rough question is a reasonable starting point for this investigation:

> *What level of environmental grain (Levins, 1968) captures differences in fitness that can play a role in natural selection?*

Speaking of "environmental grain" may suggest that environmental variation always involves clear transitions from one state to another over space or time, but that seems unlikely. So rather than asking about a concept of "grain", we might simply ask about environmental variation itself:

> *What sorts of environmental variation make a difference to fitness that can play a role in natural selection?*

Note that these are *not* empirical questions about how environments affect organisms and populations. They are questions about what fitness is, and about what its relationship is to environmental variation, in general.

With a few exceptions, there has been little attention devoted to giving general characterizations of the relationship between environmental variation and natural selection. Such a characterization would help to clarify the view that the diversity of ways of modeling natural selection approximate a small set of evolutionary processes that can be given unitary characterizations. In (Abrams, 2009c), I proposed general ways of characterizing the extent of the *whole environment*—all those conditions determining probabilities relevant to natural selection and biological fitness for a population, providing answers to this question: What conditions constitute the overall, whole environment of a population? That is, what are all of the conditions that determine the fitnesses of types com-

peting across the population as a whole (independent of our models, empirical research, etc.)? Earlier, I'd argued that very detailed microenvironments or microhabitats, or *circumstances*, play only a very limited role in determining biological fitness (Abrams, 2007). Brandon (1990, Ch. 2) has discussed a kind of intermediate variation like that which is my focus, but I'll argue that his account is incomplete. Wimsatt, drawing on other work such as that due to Lewontin (1966) and Levins (1968) has also discussed differences in intermediate-level variation. My proposals can be viewed as an attempt to extend some of Wimsatt's, Lewontin's, Levins', and Brandon's ideas into more general principles.[3] More specifically, the argument of this essay proceeds along the following lines.

1.4   Outline of the paper

The role of environmental variation in determining fitness and natural selection depends on what entities are bearers of fitness: The range of environmental variation encountered by a single organism differs from the range of variation encountered by all instances of a heritable type. Much work in philosophy of biology has assumed that fitness is primarily a property of token organisms. I believe that this assumption has created unnecessary problems. In section 2, I'll argue that because natural selection requires heritable variation in fitness (Lewontin, 1970; Godfrey-Smith, 2009), only fitness treated as a property of heritable types is directly relevant to natural selection. Fitness as a property of token organisms may play a subsidiary role in natural selection, but if so, this role has usually been misconceived. A crucial step in my account will be to argue that, in part because of the subtlety of an individual's interactions with its surroundings, fitnesses of token organisms depend on extremely specific subenvironments, which I call "circumstances" (Abrams, 2007). Circumstances are unlikely to be experienced more than once, and I argue that as a result, any fitnesses which they help determine are not heritable. I will make a fundamental distinction between such circumstances, and broader subenvironments with a significant probability of recurring. (Throughout, I use "recurrence" and related terms to capture this idea.) Heritable biological types differ from token organisms in that the former can be repeatedly realized by different instances of the latter, and thus can enter into interactions with recurrent subenvironments. (I don't mean to suggest that the interaction between a subenvironment and an individual which realizes a type is the same for each individual, as will become clear below.)

The view that fitness must primarily be a property of types will provide a foundation

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[3]Smith and Varzi (e.g. (2002)) also discuss a concept of "environment", which they take as equivalent to "niche", but their discussion concerns issues which have little relevance here. More generally, niche concepts bring up issues other than those which are my focus (cf. Abrams 2009c).

for the discussion in the rest of the paper. Section 3 lays out a general way of thinking about how fitnesses relative to subenvironments combine to generate the overall fitness of a type in a whole environment. Section 4 then fills in the framework suggested by earlier sections. It begins with a summary of Brandon's (1990) distinction between three concepts of environment (§4.1): the external environment, which includes all physical characteristics in a population's surroundings; the ecological environment, which includes only properties that can affect fitnesses; and the selective environment, which includes only properties that affect differences in fitness. Brandon's discussion seems to suggest that only selective environments matter for natural selection, except in certain cases, as when when organisms choose which ecological environment to inhabit. I argue the latter point must be generalized, and that there are many cases in which fitness depends on probabilities of experiencing different ecological environments. I continue by elaborating a central point of section 2: Subenvironments that can play a central role in determining fitnesses will be the ones likely to occur with a systematicity to which natural selection can respond (§4.2). Senses of "fitness" that make it relative to more ephemeral subenvironments are not necessarily unimportant; fitness in this sense can function as a sort of "component" of fitness, but cannot by itself serve in the role that fitness differences play in natural selection (§4.3). Finally, in section 4.4, I present an objection to my view: It appears to make natural selection in response to continuous environmental gradients impossible. I'll argue, however, that there is a way of applying my framework that avoids this problem. Section 5 summarizes my conclusions and their implications for broader issues. Before continuing, I review assumptions that I'll use in the rest of the paper.

1.5   Assumptions

In the rest of the paper I'll make the following assumptions, except where noted:

- Natural selection occurs when the frequencies of heritable types (alleles, genotypes, phenotypes) in a population change over time *because* these types have different fitnesses, or when frequencies remain the same *because* the types' fitnesses are the same.[4]

- Conceptions of fitness must—at least—allow the possibility of natural selection over generational time. Natural selection must be capable of providing a causal explanation for the distribution of organisms and traits in the world, and for understanding

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[4]This assumption is uncontroversial for many philosophers and biologists, but "statisticalist" philosophers of biology have challenged it (e.g. Walsh 2010; Matthen and Ariew 2009). Their arguments are addressed in many other publications, including some of my own.

how populations change in systematic manners over time. This requires it to be able to act in a sustained manner over many generations, which usually means that fitnesses change slowly or in systematic ways.

- Fitness can be defined partly in terms of probabilities causally relevant to the number of descendants that instances of a biological type have. Call these *reproductive probabilities* (cf. e.g. Brandon 1990; Abrams 2009b).

- In studying evolution, biologists make some choices, at least in a rough sense, about what aspects of the world to investigate (Abrams, 2009b,c, 2012a). In particular, they choose how to delineate populations and what properties of populations to study. This last choice includes a choice about an interval of time over which the population might evolve, and with it, what environmental factors might be relevant to that evolution. (It would be theoretically convenient to restrict populations to sets of organisms experiencing a common environment, and to sets of organisms unlikely to experience gene flow to or from other populations. However, neither restriction is observed in actual biological practice. What is required is that the possibility that subpopulations experience different conditions and that the population is not reproductively isolated be taken into account, either by incorporating these possibilities into models and measurements, or by having reasons to think that their effects can be ignored.[5])

- Nevertheless, for a specified population in a specified environment in a particular period of time, natural selection takes place independent of our decisions, modeling, empirical studies, etc. (Abrams, 2009b,c, 2012a).

- An environment of a population can be viewed as corresponding to a range of variation in conditions that might be experienced by members of the population over a specified interval of time, along with probabilities of such conditions being experienced (Abrams, 2009c).

- All probabilities mentioned below can be understood as objective probabilities, perhaps even with causal implications.

There is some ambiguity in how "organism" is used in practice. In what follows, I'll use "organism" exclusively to refer to individual, particular members of a population, rather than to a species.

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[5]The constrained arbitrariness of population definitions is illustrated by contemporary research using the Human Genome Diversity Panel (Li et al., 2008). For example, Thompson et al. (2004) divides this whole-genome data (from roughly 1000 individuals) into 52 populations, while Moreno-Estrada et al. (2009) cluster the same data into 39 populations for some analyses, and seven populations for others.

2 Token fitness and fine-grained variation

In this part of the paper, I'll distinguish different concepts of fitness in order clarify what aspects of these concepts will be included in my focus (§2.1). Among other things, I'll make a distinction between token fitness concepts and type fitness concepts. This will then allow me to argue that certain token fitness concepts are problematic because of the way that they make fitness depend on environmental circumstances (§2.2). Most of the rest of the paper will then focus on type fitness: Section 3 lays out a framework for thinking about how type fitness depends on environmental variation, and section 4 clarifies various points about the relationship between type fitness, token fitness, and environmental variation.

2.1 Dimensions of fitness

This section will delineate several classes of fitness concepts in order to clarify which ones are and are not the focus of this essay.

In evolutionary biology, "fitness", related terms such as "adaptive value", "growth rate", and "selection coefficient", as well as related parameters and variables in models, are all defined and used in diverse ways. I'll use "fitness" as a blanket term for all such related concepts. Ambiguity in these terms generally causes no problem: Context, area-specific traditions, and researchers' explicit definitions make intended senses clear enough for practical use. To avoid unnecessary complications or confusion, I'll begin by setting aside certain dimensions of variation in fitness concepts that I'll ignore in this essay.

It will be useful to distinguish between several classes of fitness concepts. Some fitness concepts are essentially tied to methods of empirical measurement; others might be thought to characterize underlying processes of evolution. My focus here will be on the latter. I distinguish elsewhere (Abrams, 2012a), first, between measurable and tendential token fitnesses.[6] A *measurable token fitness* concept is one, such as actual number of offspring, which allows one to measure some property of an individual, where that property is relevant to evolutionary success.[7] A *tendential token fitness* concept, on the other hand, attempts to capture the idea that a particular individual in its particular circumstances has one or more tendencies to realize properties relevant to evolutionary success. Some

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[6]I use "token fitness" rather than "individual fitness" because some biologists use the latter for a property of heritable types. For example, Michod (1999, p. 9). writes that "…fitness is often defined as the expected reproductive success of a type …. I refer to this notion of fitness as individual fitness". I avoid "organism fitness" for related reasons, although it made sense to include it in the title of the paper.

[7]I intend "evolutionary success" to be vague, capturing the idea of increase in frequency in future generations, or at least maintenance of a type in the population; this vague notion will be sufficient for my purposes here. See (Abrams, 2009b) for relevant discussion.

versions of the propensity interpretation of fitness describe tendential token fitness concepts (e.g. Beatty and Finsen 1989; Brandon 1990, chapter 1; Ramsey 2006). Bouchard and Rosenberg's (2004) characterization of fitness in terms of solving design problems can also be viewed as a tendential concept. I also distinguish (Abrams, 2012a) between statistical type fitness concepts and parametric type fitness concepts: A *statistical type fitness* concept is one that defines fitness as a property of a heritable type, in such a way that fitness is a mathematical function of measurable token fitnesses. For example, if we measure the fitness of a trait as the average of the number of offspring that (actual) individuals with that trait have in a certain generation, we are treating the trait's fitness as a statistical type fitness.[8] A *parametric type fitness* concept, by contrast, is one which treats the fitness of a type as an underlying property of the type which might be estimated by one or more statistical type fitnesses; this is a concept of fitness as something potentially entering into processes in the world.[9] Finally, a *purely mathematical fitness* concept is a mathematical concept, defined for use in certain mathematical models, which might usefully be interpreted as one of the other kinds of fitnesses in particular research contexts. For example, de Jong (1994) seems to treat fitnesses in Price's equation as type fitnesses, whereas Price (1970) himself seemed to treat the fitnesses in his model as token fitnesses. In the rest of the paper, my focus will be on tendential token fitnesses and parametric type fitnesses, which I will usually refer to as simply token and type fitnesses.

Warren Ewens, a well-known population geneticist, writes:

> First, while it is universally agreed that fitness is a property of the entire genome of an individual, it is also apparently agreed, with Wright (1931), that to a first approximation, for a short time, a constant net selection value of any allele may usefully be defined. (Ewens, 2004, p. 277)

This remark occurs in a book which surveys a broad range of population genetics models, typically representing fitness as a property of alleles or simple genotypes, rather than of whole genomes. While I doubt Ewens' claim about universal agreement, he is no doubt correct that fitness is sometimes viewed (1) as a property of a whole genome. Researchers also sometimes view fitness (2) as a property of the organism as a whole—not just its genome—or (3) as a property of an organism and its *particular*, detailed environmental circumstances. Note that all three of these kinds of concepts take fitness to depend on the environment in some sense. What's different about the third set of concepts is that they

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[8]Stearns (1976) and de Jong (1994) survey a variety of statistical type fitness concepts.

[9]The "statistical"/"parametric" terminology is derived from the use of "statistic" and "parameter" in statistics, and is not directly related to the distinction between "statisticalist" and "causalist" views about evolutionary "forces".

make it explicit that very specific, particular environmental circumstances can make a difference to fitness. Such fitness concepts would allow even genetically and developmentally identical organisms to have different fitnesses as soon as they are placed in different circumstances within an environment. (The first and second concepts, by contrast, might instead refer to a complex type which might be realized in different, particular environmental circumstances.)

The third conception of fitness seems to be popular among philosophers of biology (e.g. Brandon 1990, ch. 1; Mills and Beatty 1979; Bouchard and Rosenberg 2004; Ramsey 2006), and it has been used as a basis for some attacks on causal conceptions of natural selection (e.g. Ariew and Ernst 2009; Walsh 2007). It's not clear to me how widespread this conception of fitness is among biologists; I believe that biologists' focus is usually on conceptions of fitness with obvious practical utility: measurable token fitnesses, statistical type fitnesses, and purely mathematical fitnesses. As noted above, statistical type fitnesses are defined in terms of measurable token fitnesses, and similar constructions have sometimes been given in terms of tendential token fitnesses: Mills and Beatty (1979) and Sober (1984) defined the fitness of a type in a population as an average of tendential token fitnesses for actual individuals with that type in that population. (See section 4.3 for criticism of this strategy.)

2.2 Inadequacy of token fitness and environmental circumstances

I'll argue now that (tendential) token fitnesses do not play a direct role in natural selection because they are not heritable.[10] I'll argue that type fitnesses, by contrast, can play the role required by natural selection, because they depend on recurrent environmental conditions. In later sections of the paper, I'll explain in more detail how fitness depends on organisms' interactions with varying environmental conditions (§3, §4). This discussion will include a description of a possible role for token fitness in natural selection (§4.3).

Consider the role of fitness in natural selection, taking as our starting point Lewontin's formulation of the conditions required for natural selection by Darwin:

As seen by present-day evolutionists, Darwin's scheme embodies three principles…:

1. Different individuals in a population have different morphologies, physiologies, and behaviors (phenotypic variation).

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[10]My argument is related to some given by Sober (1984) and Hodge (1987), who argue that overall individual fitness is not causal, but my argument is different. My argument is also related to arguments in Ariew and Ernst (2009) but is more general, and makes it clear that it is not the propensity interpretation of fitness per se that is the problem.

2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness).

3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable). (Lewontin, 1970)

Lewontin's formulation spells out fundamental conditions for natural selection in a perspicuous manner, and similar formulations have been given by others (cf. Godfrey-Smith 2009).[11] Now, if fitness is attributed to an entire genome, as Ewens (2004) suggested, the heritability of fitness across more than a few generations will often be very low in those species that undergo significant recombination. Thus if natural selection were to be understood as the result of differences in whole-genome fitness, it would be hard to understand how it could act in a sustained way over many generations, except in special cases (as required in section 1.5). A similar point could be made about the view that fitness attaches to the whole organism. Thus a concept of fitness which is to fill a role like that specified by Lewontin's conditions must be a concept of type fitness—a fitness either of an allele, a genotype, or a phenotype.

(Though this conclusion concerns heritable type fitnesses in general, the argument for it is analogous to a well-known argument by Williams (1966), later championed by Dawkins (1976), usually described as an argument that only alleles are units of selection.[12] However, in the Williams/Dawkins account, alleles usually just function as types which are realized by individual organisms. This can be seen from the fact that Williams and Dawkins measure the effects of natural selection by counting token organisms which bear particular alleles, rather than, for example, counting all of the tokens of a given allele which might be found in an organism's cells (cf. Sterelny and Kitcher 1988). Thus what Williams and Dawkins argued for was that natural selection only acts on the distribution of organism types defined by alleles. The mistake that Williams and Dawkins made was to assume that only types which can be replicated nearly perfectly are subject to natural selection. My argument generalizes Williams' by assuming that merely heritable properties associated with fitness are all that natural selection requires.[13])

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[11]Lewontin suggests that these three conditions are necessary and sufficient for evolutionary change by natural selection. In fact they are neither necessary nor sufficient for natural selection (Godfrey-Smith, 2009). However, they capture the core of the notion of natural selection sufficiently well for my purposes here.

[12]Actually, the notion of "allele" that Williams and Dawkins used was unusual, but this subtlety needn't concern us.

[13]Wimsatt (1980b; 1981) argued that when there are nonlinear interactions between alleles, it's inappropriate to treat alleles as units of selection. Analogously, one might argue that when there are nonlinear interactions between heritable types of any sort, its inappropriate to assign fitness values to each type as such. However, given a probability distribution over possible combinations of types, fitness values for any

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There is a related, deeper problem with token fitness if it's defined so as to depend not just on an individual's genome, but also on the way in which the genes interact with *particular* environmental circumstances, either during development or during mature life stages. (I pointed out above that some philosophers of biology seem to view fitness in this way (e.g. Ramsey 2006).) Then variations that can affect the reproductive success of an individual are not limited to the kinds of patterns explicitly referenced in models and empirical studies of environmental variation, and labeled with terms such as "patch", "habitat", "niche", and "environment"—"micro-habitats" or circumstances might matter as well. As suggested by the house sparrow example in section 1.2, survival and reproduction of an individual can be affected by variation in wind direction in the presence of a predator, variation in numbers and kinds of viruses in nearby conspecifics, or variations in activities of potential mates and potential prey (Abrams, 2007). There is no obvious limit to the sorts of minute variations that might affect such individualized fitnesses. For example, the fitness of a prey might be affected by fact that a leaf is blown in such a way as to allow the prey to be noticed by a predator because the predator's gaze followed an unusual movement perceived as that of a potential mate. It's plausible that there are real situations in which any variation in such conditions could make the difference between survival, injury, or death. Even two clones beginning life in (merely) measurably identical circumstances might have very different token fitnesses due to the different circumstances they experience during development and later life.[14] I have argued elsewhere (Abrams, 2007) that interactions of individual organisms with their circumstances are effectively deterministic, and that this means that circumstance-relative token fitnesses are equivalent to actual reproductive successes. However, even if we allow that for any token organism in particular circumstances, there is some sort of objective probability distribution over possible outcomes, situations like those described above appear to be ones in which small differences in circumstances would make large differences in fitnesses.

The problem with making fitness depend on circumstances is that survival and reproductive success in response to environmental variation of such a fine-grained kind is not heritable: The sum of those particular circumstances affecting an individual's fitness is unlikely to recur among its descendants, so any effects of circumstances on organisms' types are, likewise, unlikely to recur. Survival or reproductive success in this sense is therefore

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one type can in principle be computed (Abrams, 2009b). This is in effect to treat those alternative types, which might be combined with a particular type whose fitness is to be calculated, as the alternative environmental states discussed in section 3 (cf. Dawkins 1976; Sterelny and Kitcher 1988).

[14]In Brandon's (1990, chapter 2) terms, I am arguing that his assumption that there are broad regions of the space of environmental conditions which are objectively homogeneous or which vary only gradually with respect to probabilities relevant to fitness is incorrect, when we consider environmental variation in sufficient detail.

not a kind of fitness in the sense required by concept of natural selection. The point holds even for organisms that undergo little or no genetic recombination, as in many asexual species. In the general case then, differences in token fitnesses are not the kind of fitness differences that are essential to the concept of natural selection: No heritability, no natural selection.

Note that Ramsey's (2006) concept of a *fitness environment* is defined in terms of probable conditions that descendants of an individual will encounter. However, Ramsey's fitness environment is defined relative to a particular individual. Different individuals in the same population can have different fitness environments, even if they are genotypically and phenotypically identical. This means, though, that fitnesses relative to such environments need not be heritable.[15]

Now in most species, there will have been selection for robustness of patterns of survival, reproduction, etc., in the face of environmental variation (Wagner 2005; cf. Wimsatt 2007). Complete robustness to environmental circumstances would mean that a given type of organism would have the same number of descendants for any circumstance included in the range of circumstances possible in the population's environment. This seems unlikely in general, and if the members of a population did achieve this sort of robustness, it's likely that fitter variants would eventually arise which allowed the exploitation of new, varying resources despite greater risk of failure. Moreover, even if there were a population which was robust to all variation in circumstances within its environment, a general understanding of fitness could not depend on such cases, since most populations do not have this characteristic.

Thus fitnesses capable of playing the sort of role outlined by Lewontin must attach not to individuals, but to heritable types. In section 4.3, I argue that there may be a sense in which type fitnesses are derived from token fitnesses, but in a way that token fitness advocates have not discussed

3   How do subenvironment-relative fitnesses combine?

We saw a problem with token fitness concepts in the preceding section. This section will lay out a general framework for thinking about how type fitnesses that are relative to subenvironments combine to determine overall fitness.[16] This framework will provide a foundation for section 4, in which I relate Brandon's views about fitness and subenvi-

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[15]There are some similarities between aspects of Ramsey's (2006) concept of a fitness environment and some of my own ideas (Abrams, 2009a,b,c), but the latter focus on type fitnesses.

[16]Glymour (2006; 2011) seems to focus on different questions about environments than I do, but his approach and conclusions are broadly complentary to and compatible with mine.

ronments to the framework described in this section (§4.1), discuss how the distinction between circumstances and other subenvironments might be drawn (§4.2), explain what role circumstances and token fitnesses might have in natural selection (§4.3), and discuss a problem that environmental gradients pose for my view (§4.4).

For a given partitioning of the whole environment into subenvironments E_j, the over-all fitness of a type a is a function of subenvironment-relative fitnesses $\mathsf{F}\,(a|E_j)$ (Abrams, 2009a) and probabilities that instances of a will experience each subenvironment (Levins, 1968; Wimsatt, 1980a) over an interval of time. If each organism experiences only a single subenvironment for its entire life, this function is an average over m subenvironments:

$$\mathsf{F}\,(a); \;=\; \mathsf{E}\,(\mathsf{F}\,(a|E_\bullet)) \;=\; \sum_j^m \mathsf{F}\,(a|E_j)\,\mathsf{P}(E_j)$$

$$=\; \mathsf{F}\,(a|E_1) \times \mathsf{P}(E_1) \;+\; \mathsf{F}\,(a|E_2) \times \mathsf{P}(E_2) \;+\; \cdots \;+\; \mathsf{F}\,(a|E_m) \times \mathsf{P}(E_m)\,.$$

cf. e.g. (Gillespie, 2004; Roughgarden, 1979).[17] This is represented schematically in Figure 1. Where the fitnesses are viabilities, and subenvironments are experienced for short periods of time with independent probabilities, fitnesses combine multiplicatively (Levins, 1968; Wimsatt, 1980a; Nagylaki, 1992):

$$\mathsf{F}\,(a) \;=\; \prod_j \mathsf{F}\,(a|E_j)^{\mathsf{P}(E_j)}$$

$$=\; \mathsf{F}\,(a|E_1)^{\mathsf{P}(E_1)} \;\times\; \mathsf{F}\,(a|E_2)^{\mathsf{P}(E_2)} \;\times\; \cdots \;\times\; \mathsf{F}\,(a|E_m)^{\mathsf{P}(E_m)}\,.$$

However, in general overall fitness is a more complex function of subenvironment-relative fitnesses (Levins 1968; cf. Abrams 2009a,b).

This framework applies recursively all the way down to the level of circumstances: Subenvironment-relative fitnesses of types are a function of fitnesses in, and probabilities of, narrower subenvironments, which in turn are a function of fitnesses relative to even narrower subenvironments, and so on, all the way down to the level of circumstances (cf. §4.3). This conception allows partitioning the environment into subenvironments in different ways for different purposes. For example, one study of a given population of organisms might focus on the effects of variation in amount of rainfall over time, another might focus on variation in rainfall between different regions, while a third might focus the differences between forests and fields.

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[17]For example, suppose fitness is expected number of offspring O_a for type a, i.e. $\mathsf{F}\,(a) \;=\; \mathsf{E}\,(O_a) \;=\; \sum_k k\,\mathsf{P}(O_a = k)$. The probability of having k offspring is the average across subenvironments E_j, weighted by probability of E_j: $\mathsf{P}(O_a = k) = \sum_j \mathsf{P}(O_a = k|E_j)\mathsf{P}(E_j)$. Together these equations imply that $\mathsf{F}\,(a) = \mathsf{E}\,(\mathsf{F}\,(a|E_\bullet))$, as in the text.
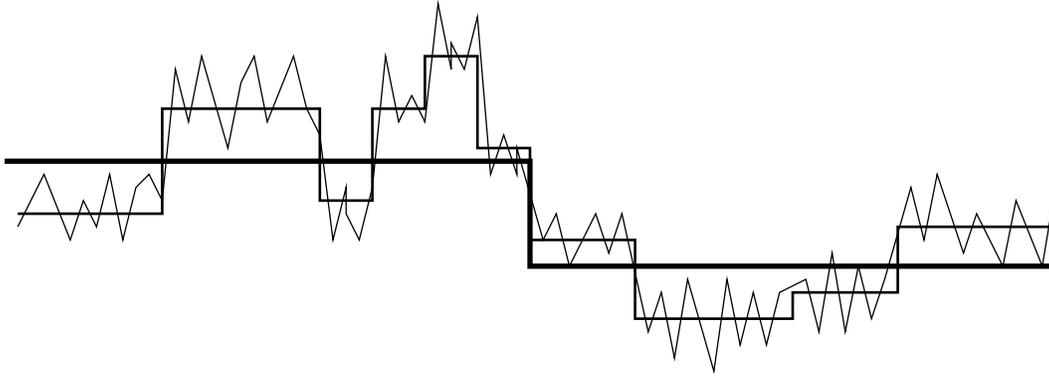
Figure 1: Schematic representation of variation in fitness in subenvironments at different levels of grain. The horizontal axis represents positions in a space, time, or one or more other continuously varying properties. Heights of lines represent fitnesses of a single heritable type. The line with the most variation in height represents changes in fitness resulting from environmental differences between small regions. Lines with less variation in height represent fitnesses relative to larger regions, treating these fitnesses roughly as averages over fitnesses in smaller regions.

4   Type fitness and coarse-grained environmental variation

The preceding section provided a framework for thinking about how fitness depends on environmental variation. In this section, I'll discuss in more detail my claim that parts of the environment with a significant probability of recurring—of being experienced repeatedly by members of a population, over generational time—give rise to fitness in a sense different than do circumstances that are idiosyncratic to a particular time, place, configuration of organisms, etc. I begin by relating Brandon's previous discussion of environmental variation to my view (§4.1). I then discuss the how one might draw a formal distinction between circumstances and other subenvironments, thus placing a lower limit on what kinds of subenvironments are worth modeling or studying empirically (§4.2). I explain how token fitnesses and environmental circumstances might contribute to type fitnesses relative to larger subenvironments (§4.3), and respond to a challenge that environmental gradients pose for my view (§4.4).

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4.1 Brandon's three concepts of environment

Brandon (1978; 1990) sometimes seems to treats fitness as token fitness, but chapter 2 of Brandon (1990) is relevant to type fitness.[18] There Brandon defined three concepts of environment. The *external environment* of a set of organisms consists of any properties of the world external to the organisms. The subset of properties in the external environment whose variations can affect these organisms' future contribution to the population count as components of the *ecological environment*. Not all variation in the ecological environment differentiates between distinct heritable types, however. For example, if two genotypically different strains of the roundworm *Caenorhabditis briggsae* in a population respond to differences in climate in ways that affect fecundity (cf. Prasad et al. 2011), but the *relative* fitness between them is constant, then variation in climate counts as variation in ecological environment but not variation in *selective environment*. The selective environment varies only when relative fitnesses of competing types vary. Brandon also defined a concept of selective environment "neighborhoods": roughly, regions of similar relative fitness between competing types. Also note that Brandon often spoke of environmental variation as spatial, using plants as illustrations, but it's natural to extend his notions to complex combinations of variation in many properties over space and time.

Although Brandon initially proposed that it is selective environments that matter to natural selection, his discussion showed that factors *other than* fitness differences relative to selective environments also matter for natural selection. Suppose that the relative fitness relations between two heritable types a and b are the same in two subenvironments E_1 and E_2, while the absolute fitness of both types is greater in E_1 than in E_2. In other words, both a and b individuals are likely to produce more descendants starting from E_1 than E_2, although a is likely to produce more descendants than b in E_j, whether E_j is E_1 or E_2. In this case, the overall fitness of a and b depends on the probabilities of each type being found in E_1 and E_2, and not just on their relative fitnesses. If the difference in absolute fitnesses between E_1 and E_2 is great enough, then b can be fitter than a even if a is fitter than b in each subenvironment. All that's necessary is that b have a sufficiently greater probability

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[18]I read parts of chapter 1 of Brandon (1990) as concerned with token fitness, and chapter 2 seems to allude to token fitness, e.g. on page 47, when it mentions the environment of an individual. However, the primary focus of chapter 2 is on environments of populations of organisms and these environments' effects on the fitnesses of types.

than a of landing in E_1.[19]

The significance of Brandon's discussion for this paper should be apparent, but from my point of view his explicit statements, at least, do not go far enough. First, Brandon's own example shows that the concept of a selective environment is relevant to overall selection only in certain cases, since it shows that a type b can be fitter than a overall[20] even though a is fitter than b in each selective (sub)environment. Second, Brandon illustrates the case just described using an example of habitat choice, in which insects have heritable preferences for laying eggs on one kind of plant rather than other. The significance of Brandon's point goes beyond habitat choice, however. For example, if plants have heritable variation affecting the probability of seeds being blown by the wind, some types in a population may be more likely to encounter certain environmental variants than others; this is not usually considered habitat choice.[21]   Also note that parts of Brandon's discussion assume that ecological environments do not vary in extreme ways over large portions of a whole environment. However, I argued above that minute variations in circumstances within an environment can produce extreme variations in probabilities of reproductive success.[22]

4.2   What sort of grain is relevant to selection?

According to our discussion so far, natural selection occurs only when heritable types in a population are differentially reproduced because of differences in type fitness. However, as we saw in section 2, fitnesses are heritable only when environmental conditions are repeatedly encountered by the same type, as members of the population reproduce over time. Thus, there is a lower limit on the grain of environmental variations relative to which heritable fitnesses are environmentally determined. What is that limit? That is the topic of this section.

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[19]Using the first, additive model in section 3, b is fitter than a overall if

$$\mathsf{F}\,(a|E_1)P(a \text{ in } E_1) + \mathsf{F}\,(a|E_2)P(a \text{ in } E_2) \quad < \quad \mathsf{F}\,(b|E_1)P(b \text{ in } E_1) + \mathsf{F}\,(b|E_2)P(b \text{ in } E_2)\,.$$

Suppose $F(a|E_1) = 10$, $F(a|E_2) = 2$, $\mathsf{P}(a \text{ in } E_1) = .1$, $F(b|E_1) = 5$, $F(b|E_2) = 1$, and $\mathsf{P}(b \text{ in } E_1) = .9$. Then $\mathsf{F}\,(a) = 10 \times .1 + 2 \times .9 = 2.8$ and $\mathsf{F}\,(b) = 5 \times .9 + 1 \times .1 = 4.6$.

[20]That is, b could be fitter in the sense that it has a greater probability of evolutionary success, increased frequency, etc., in either/both the short term and/or the long term.

[21]To be precise, Brandon gives an example in which organisms of different types always choose specific subenvironments, thus in in effect creating a uniform "selective environment"—in that each type competes with the other relative to constant environmental conditions. However, it's not difficult to see how to extend this generalization of the concept of a selective environment to cases in which types have different non-extremal probabilities of encountering various ecological environments.

[22]Note that much of Brandon's discussion is driven by concerns other than those that are my focus.

In order for organisms that are instances of competing heritable types a_i to have fitness relative to a subenvironment E_j, instances of each type a_i must have a significant probability of experiencing the same conditions E_j. The range of conditions corresponding to a subenvironment E_j must be broad enough to allow this. But what is a significant probability of experiencing a particular subenvironment? What is the cutoff value for such probabilities? Any answer would depend on the relative strengths of selection and drift, and more specifically on fitness differences relative to a given subenvironment, as well as on effective population size. What matters is whether selection relative to a subenvironment has a reasonable chance of affecting evolution given the other evolutionary forces acting on the population.

First, the interval of time over which evolutionary change might take place is relevant to what counts as a significant probability of recurrence (cf. section 1.5). Longer intervals may produce greater probabilities of recurrence, since they allow more time for a set of environmental conditions to recur. Thus probabilities of recurrence depend on what kind of time period we want to investigate (Abrams, 2009c,b). Second, if fitness differences relative to subenvironment E_j are small, then E_j must be encountered more often for these fitness differences to have a non-negligible impact on selection. Similarly, if fitness differences relative to E_j are large, then E_j can have a probable impact on evolution even if its probability of recurrence is relatively low. Third, cutoff probabilities depend on the strength of other evolutionary forces. Consider drift, for example. Effective population size determines the strength of drift. If a population is small, then the effect of minor differences in fitness will be swamped by drift. Thus for a subenvironment to be relevant to natural selection in a small population, it must encompass a broader range of circumstances, *ceteris paribus*. These relationships could be formalized in terms of a particular model, producing a formula allowing calculation of probabilities of recurrence necessary to produce a noticeable effect of selection given values for the parameters just mentioned. For a given population and environment, and a specified level of likely effect of selection, such a formula could in principle be used to estimate a *minimal environmental grain*: a specification of how fine-grained a partition of the environment can be while still making subenvironment-relative fitness differences themselves relevant to selection.

I'm not sure how useful such an estimation project would be, however. The main point is that modeling practices and empirical research are consistent with a vague boundary between subenvironments that have a significant probability of recurrence, and those that don't. Above this vague limit, researchers are free to choose a way of partitioning environmental conditions into subenvironments that is useful for their research goals.

4.3 A role for token fitness?

I think that many philosophers of biology, at least, feel that (tendential) token fitnesses must play a role in natural selection, somehow. I'm not sure that this is on the right track. However, in this section I'll explain what legitimate role token fitnesses might play in natural selection. Since token fitnesses are usually thought to depend on circumstances, we'll also see what role circumstances might have in natural selection.

Suppose that a house sparrow happens to fly across a small opening in the forest cover when a hawk happens to fly overhead. As a result the hawk chases and injures the house sparrow, causing an infection contracted when the house sparrow escapes by diving into a pond. The pond happens to contain bacteria to which the house sparrow has low resistance. The house sparrow's resistance is low because its diet has been limited to a few foods; this is in part a consequence of a recent landslide that caused rainfall to be diverted to other areas. The infection leads to the house sparrow's subsequent death.

This set of circumstances does not give this particular house sparrow low fitness in a sense that's relevant to natural selection, for this set of circumstances will never recur. That hawks are present in the region and are sometimes overhead matters to natural selection. That injuries of various sorts occur matters to natural selection. That infections of various sorts occur matters. That the water supply to nearby plants is sometimes low matters. These things matter because they recur, and they matter to a degree that's weighted by their probability of occurring in various combinations, and by the probable effects on reproductive success of each set of conditions. What matters to natural selection is not this or that organism's particular circumstances and particular fate, but the sorts of conditions that individuals in the population are likely to encounter repeatedly. Nevertheless, if outcomes relative to circumstances were probabilistically combined, they could determine fitnesses relative to more inclusive subenvironments which included those circumstances as possibilities.

Now, if the fitness of a type is defined as a simple arithmetic average of the token fitnesses of those *actual* organisms which realize the type in a particular population, as proposed in Mills and Beatty (1979) and Sober (1984), type fitnesses may fluctuate in odd ways from one time period to the next, as individuals in the population happen to experience this or that "lucky" or "unlucky" micro-habitat (Abrams, 2007). Thus it's a mistake to treat type fitness as an average of token fitness of those organisms actually existing in a population in a given period of time.[23] However, a token organism can be viewed as a real-

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[23]Recall that my focus in this paper is on tendential token fitness and parametric type fitness. It's *not* necessarily a mistake to *estimate* parametric type fitness using the average of measurable token fitnesses of actual organisms (Abrams, 2012a).

ization of a complex type including a whole genome, a phenotype produced by whatever factors contribute to development, and a set of environmental circumstances (Abrams, 2009a, 2012a). Suppose for each such complex type O_iE_j consistent with a particular heritable type a, there was an objective probability of O_iE_j occurring. Then the overall fitness of a would follow from calculations like those discussed in section 3. In this sense, token fitnesses can play a role in natural selection. Note, however, that the relevant token fitnesses are fitnesses of merely possible (i.e. probable) token organisms and circumstances. Moreover, *differences* in fitnesses relative to circumstances themselves play no meaningful role in natural selection. It is only as contributors to fitness differences in larger subenvironments that these token fitnesses play a role in natural selection per se (cf. Abrams 2009a).

Since concepts of propensity have played a large role in philosophical discussions of fitness, it's worth noting that Abrams (2007) argued that "circumstance probabilities", such as the probabilities of O_iE_j in the preceding paragraph, are unlikely to be propensities. To my knowledge, no one has published an argument that they are propensities. On the other hand, since it is fitnesses of types, only, that are directly involved in natural selection, it may be that token fitness as such plays no role in natural selection. One can think of a population as a whole, in its environment, as a complex causal system in which organism types are realized repeatedly in response to inheritance relations between parts of the system (Abrams, 2009a,b, 2012a). The fitness of a type at a time t then corresponds to a function of probabilities of distributions of types in the population at later times t'. No reference to fitnesses of particular organisms in particular circumstances need be made. Individuals merely function as realizers of types within the entire population-environment system. Inheritance can also be conceived as a relationship between type realizations as such, rather than between concrete individuals.[24]

4.4   Gradients and recurrent properties

In many cases, conditions affecting fitness vary continuously over a whole environment. The fact that conditions relevant to fitness can vary continuously raises a potential problem for my characterization of minimal environmental grain. In this section, I present this problem and give a response to it.

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[24]For those interested in pursuing alternative interpretations of probability that may be relevant to evolutionary processes, I suggest if the complex system constituted by a biological population and its environment satisfied conditions required for what are known as mechanistic, microconstant, or natural range probabilities (Rosenthal, 2010, 2012; Strevens, 2011; Abrams, 2012b,c) it could turn out that type fitnesses would not derive from token fitnesses. This is a topic better left for later work, but I mention the possibility here for interested readers.
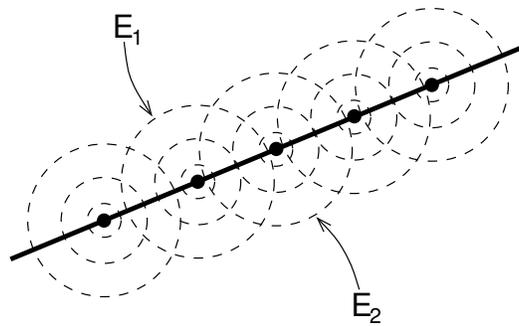
Figure 2: Schematic representation of overlapping subenvironments along an environmental gradient.

Consider an example from the literature. Thompson et al. (2004) found that the frequency of the CYP3A*5 allele of the CYP3A gene in whole-genome data from human populations increases with distance from the equator. Based on statistical patterns in the genetic data, computer simulations, and known differences in phenotypic effects of CYP3A5*3 and its allele CYP3A5*1, Thompson et al. (2004) argued that there was probably selection on these alleles which varied with temperature and humidity.

It's certainly reasonable to assume that an environmental gradient can produce different fitness values at every point along the gradient. Some models do assume this, and hypotheses about fitness gradients are not difficult to test or estimate. However, if the regions between which fitnesses have significant differences are small, it could be that no such region has a significant probability of recurring. My view seems to imply that differences in fitness at every point along a gradient do not contribute to natural selection. My proposal thus seems to rule out an idea that has clear biological sense. Here is an outline of a response. (I'll switch examples; the effect of latitudinal variation in climate on vertebrates may not be the best illustration of this possibility, since population ranges are relatively large.)

Consider a population of plants with wind-blown seeds, sparsely distributed along a the side of a mountain. Though each altitude corresponds to a range of environmental circumstances, suppose that the factors correlated with altitude—sunlight, temperature, and atmospheric density—make a large contribution to fitness of two competing heritable types. However, if the probability of seeds of each type growing at any *particular* altitude is very low, then none of the altitude-defined subenvironments are recurrent.

Note, however, that subenvironments corresponding to larger ranges of altitudes may nevertheless be recurrent. And for each point on the environmental gradient there is a series of larger and smaller regions around it, each of which overlaps similar regions centered on other nearby points (Figure 2). These are just subenvironments in the usual

sense, even if they overlap with other subenvironments with similar ranges of variation. Moreover, fitness differences relative to overlapping recurrent subenvironments can be considered to play a direct role in natural selection. Thus fitness differences in both of the overlapping subenvironments E_1 and E_2 schematically represented in Figure 2 can be viewed as relevant to natural selection. The fact of the gradient is nevertheless captured by the series of overlapping, recurrent subenvironments.

5   Conclusion

I've argued, first, that fitnesses of types are fundamental to natural selection, and that views that treat differences of fitness for actual token organisms as fundamental cannot make sense of selection's basic character. In part this is because the fully-detailed circumstances of each individual's life can generate significant variation in probabilities concerning reproduction and persistence of descendants. As a result, token fitnesses are often not heritable to the degree required for natural selection.

Second, I've presented a view of fitness as a possibly complex function of reproductive probabilities in subenvironments, and probabilities of an organism experiencing each subenvironment. This scheme allows an environment to be partitioned into subenvironments in various ways, and allows subenvironment-relative fitnesses to be derived from narrower component subenvironments.

Third, I argued that subenvironments that are unlikely to be experienced repeatedly don't determine a sense of fitness that allows comparisons between competing types. That a is fitter than b in a nonrecurrent subenvironment is by itself irrelevant to selection, since this relationship is not heritable. Only fitness differences relative to recurrent subenvironments matter, in the end. I noted that environmental gradients which produce fitness gradients seem to conflict with this picture, since a point on a gradient might be unlikely to recur—in the sense that no two organisms are likely to experience it. I argued, however, that fitness gradients can be understood in terms of overlapping recurrent subenvironments.

My view is that researchers have various constrained choices about what aspects of an evolving population to ask questions about, but given those choices, there are objective answers determined by the world (Abrams, 2012a). Researchers can choose what competing heritable types to focus on, what set of organisms to treat as a population, and over what period of time evolution matters. These choices implicitly specify a whole environment relevant to evolution in that population during that period of time (Abrams, 2009c) and specify what fitness consists in (Abrams, 2009b). The choices delimit a part of the world,

with respect to which the facts about whether and how natural selection takes place are objective. Researchers also have constrained choices about how to divide up a population into subpopulations, and about how to divide the environment into subenvironments. These choices will usually be designed to capture different kinds of variation thought to be causally relevant to the evolution of the whole population or of subpopulations.

I see environments as defined by probabilities of the occurrence of subenvironments over time as a result of interactions involving members of a population and other natural processes (Abrams, 2007, 2009c,b,a). As a result, I see the views presented in this paper as consistent with interactions between organisms affecting each others' fitnesses, as the house sparrow example in section 1.2 suggested; with organisms affecting the environment, as in niche construction (Odling-Smee et al., 2003); and with a focus on the role of organism-environment interactions in development (cf. Oyama et al. 2001).

I believe that my perspective applies equally well to the biological evolution of humans and their ancestors. There is a common view that the biological evolution of humans has stopped because culture and individual learning allow humans to adapt to new environmental conditions without natural selection on biologically heritable traits (e.g. Dawkins 1976; Barkow et al. 1992). What the present view suggests is a way of framing this claim. I see no reason to think that social and cultural variation, combined with individual differences, do not also affect probabilities of survival and reproduction. Thus there is a sense in which humans experience complex environmental variation that could be relevant to natural selection. If human biological evolution has stopped because of the utility of individual learning and culture, it it is because sociocultural environmental variation experienced by humans is insufficiently recurrent: Even if there are patterns to social and cultural conditions, what is stable does not last long enough for selection on genetically-influenced types to act in a consistent manner over many generations. It may be, however, that despite the appearance of rapid sociocultural change, there are higher-order patterns in sociocultural variation which recur sufficiently often that biological natural selection can sometimes respond to it (cf. Richerson and Boyd 2005). Natural selection for genes affecting lactase digestion in response to cattle husbandry has often been mentioned as an instance of natural selection in response to cultural conditions (e.g. Richerson and Boyd 2005). However, there is a growing body of evidence from whole-genome data suggesting that natural selection has had numerous effects on human populations in the last few tens of thousands of years (e.g. Thompson et al. 2004; Moreno-Estrada et al. 2009; Klimentidis et al. 2011; Scheinfeldt et al. 2011). Perhaps some of these effects are the result of higher-order stable patterns in social and cultural conditions.

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