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Environments, Populations, and Natural Selection[1]

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ABSTRACT: Some biologists and philosophers hold that claims about natural selection need to be relativized to homogeneous selective environments. This classical thesis—especially in the form given to it by Robert Brandon—has been vigorously criticized by Roberta Millstein. In this paper, I assess whether the thesis resists the objections raised by Millstein and to what extent it needs to be amended in light of these objections. More specifically, my discussion shows that Millstein's critique does bring to light the fact that a delineation of the population(s) involved in the case under consideration is required for demarcating homogeneous selective environments—and in this sense, environmental homogeneity and population delineation are interconnected issues, a point that had been largely implicit before Millstein's critique. But does this entail abandoning the idea that a selective claim needs to be relativized to a homogeneous environment and replacing it with the idea that it needs to be relativized to a single population, irrespective of whether that population inhabits a homogeneous or heterogeneous environment? I show that the arguments for this latter position are not decisive, and I tentatively propose a way out of the deadlock.

KEY WORDS: Environment, environmental homogeneity, natural selection, philosophy of biology, population, Robert Brandon, Roberta Millstein.

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1. Introduction

Environment and natural selection are two intimately linked concepts in evolutionary theory. The environment is often conceived—and was

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already conceived by Darwin—as doing the "sieving" or the selecting among the variants found in a given population: if one variant is more apt at coping with the challenges raised by the environmental conditions encountered, then that variant is likely to outreproduce others and natural selection will thus be said to act in the given setup. However, not all aspects of the relationship between selection and environment have been clarified beyond dispute, and this paper focuses on one aspect that is still contentious among philosophers of biology.

Some biologists (Damuth 1985; Antonovics, Ellstrand, and Brandon 1988) and philosophers (e.g., Brandon 1990) have argued that claims about natural selection should be relativized to homogeneous selective environments. Though some decades have passed since it was proposed, this thesis has not lost its appeal for philosophers of biology, and it continues to be used as a premise in various philosophical arguments about evolutionary theory (see, e.g., Pfeifer 2005; Desmond 2022). But the thesis has not gone unquestioned, and in this paper, I will assess the objections raised by Roberta Millstein (2014) against it, objections that together constitute what is probably the most direct and the most vigorous philosophical critique that has been leveled against the thesis. Though no author defending the thesis has responded to Millstein's critique, I think it would be useful to conduct an analysis meant to assess whether the thesis survives after Millstein's critique and, if it does, to also determine whether it needs to undergo some modifications in light of Millstein's critique. To this end, I will uphold here some of the positions adopted by Robert Brandon—who has provided what is probably the most elaborated philosophical form of the thesis under consideration—and try to determine what Brandon *could* reply to Millstein's objections. My discussion will show that Millstein's critique does bring to light the fact that a delineation of the population(s) involved in the case under consideration is required for demarcating homogeneous selective environments—and in this sense, environmental homogeneity and population delineation are interconnected issues, a point that had gone largely unnoticed before Millstein's critique. But does this entail abandoning the idea that selective claims must be relativized to homogeneous selective environments and replacing it with the idea that they need to be relativized to a single population, irrespective of whether that population inhabits a homogeneous or heterogeneous environment? I show that the arguments for this latter position are not decisive, and I tentatively propose a way out of the deadlock.

In order to get there, in Section 2, I will present Robert Brandon's (1990) formulation of the thesis that selective claims should be relativized to homogeneous environments because this is the formulation that Millstein's critique mainly targets. Then, in Section 3, I will analyze Millstein's three main objections and assess to what extent they affect Brandon's thesis. Section 4 concludes.

2. The Classical Philosophical Formulation of the Relationship Between Environment and Natural Selection

Charles Darwin proposed what he termed "natural selection" as the main factor or process responsible for the "fit" between organisms and their (biotic and abiotic) environment. Later, population genetics provided a more specific meaning to the notion of "fitness": it now more narrowly referred to the reproductive values of particular types of organisms in a specified environment. The flipside to this, as pointed out by Glymour (2011), is that the precise factors that, together, constitute an environment are usually not explicitly specified in population genetics models; rather, fitness parameters are taken to also provide a global measure of the effect of the environment as a whole on reproductive values.

The classical philosophical approaches to the relationship between environment and natural selection have followed population genetics in this respect. In such philosophical frameworks, fitness is both a property of biological individuals (or types of individuals) and an indicator of the quality of the environment they experience (Glymour 2011). This is the case with one of the most sophisticated philosophical views on the selection-environment relationship, namely that provided by Robert Brandon in his 1990 book *Adaptation and Environment*. Brandon offers not only a detailed presentation of the propensity view of fitness (initially proposed in Brandon 1978 and Mills & Beatty 1979) but also the classical formulation of the account of natural selection that derives from this view of fitness. According to Brandon, fitness—or, with his term, "adaptedness"—is a dispositional property of biological individuals[2] that supervenes on the properties of these individuals within a given environment. A biological individual has a higher adaptedness than another one if it has a greater *ability* to survive and reproduce (i.e., in more common terms, if it has a higher expected fitness) in the

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[2] The term "biological individuals" is meant to signal that entities at various levels of biological organization may vary in adaptedness.

given environment.[3] And, according to the propensity view of natural selection that Brandon defends, the differences in adaptedness are the ones that explain the differences in actual reproductive output between these individuals in the given environment.

The notion of the environment plays a crucial role in this reasoning because the adaptedness of a phenotype or genotype depends on its environment: two types of organism that vary only in their ability to withstand cold conditions will have different values of adaptedness in harsher climates (e.g., temperate or arctic ones), but they might exhibit no differences in adaptedness if we relocated them in more benign, tropical conditions. Thus, adaptedness is environment-relative, and it provides an indicator of environmental quality. But what is the relevant notion of environment for natural selection? In order to clarify this point, Brandon distinguishes between three notions:

1. *the external environment:* the totality of biotic and abiotic factors external to the biological entities under scrutiny;
2. *the ecological environment*: only those factors of the external environment (or other factors concerning population structure) that affect the expected reproductive output of a given type of biological entity;[4]
3. *the selective environment*: only those factors of the external environment (or other population-structure factors) that differentially affect the relative expected fitnesses of the types represented.[5]

Furthermore, if the types of a population *do* vary in relative expected fitness in a given environment (i.e., if we are dealing with a selective environment), we should, according to Brandon, go on and try to determine whether we are dealing with a homogeneous or a heterogeneous selective environment. If the types vary in relative expected fitness but in such a way that the relative expected fitness of each type is relatively

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[3] I will use the terms "adaptedness" and "fitness" interchangeably, but it is important to bear in mind that by "fitness," I understand "expected fitness" throughout this paper.

[4] Note that the ecological environment is not defined with respect to the entire set of entities we study but with respect to each type composing this set. This explains why the same ecological environment may be homogeneous relative to a given type (when the expected fitness of that type is constant—or relatively so—across the entire area under consideration), but it may be heterogeneous for another type belonging to the same population (if this second type varies in expected fitness in different sub-sections of the environment).

[5] As Trappes (2021) has argued (though see Baedke et al. 2021 and Walsh 2021 for partly opposing views), Brandon's notion of selective environment is intimately linked with niche construction theory, given that niche constructing involves altering one's evolutionary niche, where the latter is defined as "the sum of all the natural selection pressures to which the population is exposed" (Odling-Smee et al. 2003: 40).

constant across the given environment, the environment will count as a *homogeneous* selective one. Alternatively, if the relative expected fitness of at least one type varies significantly between different sub-sections of the environment, then the latter will count as a *heterogeneous* selective environment. Let us take as an example the two sides of a hill—the north and south sides—with the latter receiving more sun than the former. A plant population, composed of two types X and Y, occupies the entire hill. If both types are fitter on the sunny side than on the north side but in such a way that the fitness of a type relative to the other is the same on both sides of the hill, then the entire hill is a selectively homogeneous environment (though it is externally and ecologically heterogeneous). If, on the other hand, type X does slightly better than Y on the sunny side of the hill but does much better than Y on the north side, then the hill constitutes a heterogeneous selective environment (with each side of the hill being a homogeneous selective environment).

Brandon (1990) does not only argue that selective environments are the relevant environments for natural selection. Indeed, this would have been a rather circular move, given that an environment is, by definition, selective only if the relative expected fitnesses of types within it vary. Like Damuth (1985) and Antonovics, Ellstrand, and Brandon (1988), Brandon goes one step further and argues that *homogeneous* selective environments are the relevant ones for selection. In terms partly inspired by Jeler (2017), we could interpret this requirement as an "environmental homogeneity condition" (hereafter, EHC) imposed on selective claims: a selective claim will only count as "selective" if it is relativized to a single homogeneous environment. The idea behind this is simple: it is only when a set of individuals are subjected to similar selective pressures and intensity (in the form of similar environmental conditions affecting their fitnesses and, consequently, the selective coefficient) that these individuals may be said to be subjected to the same process of selection. Comparing the performances of individuals that are subjected to different selective pressures/intensities would lead to erroneous assessments of the causes of evolutionary change and to unreliable predictions. The EHC thus serves as a way of numerically distinguishing between processes of natural selection: if a set of individuals is spread over a heterogeneous environment that is composed of two internally homogeneous environments, then embracing EHC entails claiming that we have two selection processes here, one for each homogeneous environment. As will become apparent in Section 3.2 below, it is precisely this aspect of EHC that Millstein (2014) contests.

However, by endorsing EHC, Brandon did not lose sight of the fact that biologists often have to explain evolution in environments whose scale of heterogeneity is smaller than the habitat of the biological individuals under scrutiny. Brandon integrates this type of case in his framework by arguing that when the population under consideration is spread over a patchy environment, but the organisms in question move freely during their lives between patches, then this patchy environment will count as a homogeneous environment. Though it is patchy as an *external* environment, it will not be selectively patchy, given that organisms are very likely to experience the patches in the proportion in which they are represented in the global environment, so that individuals of the same type will likely have about the same relative expected fitness within this patchy environment.[6] The mobility of biological entities thus selectively "homogenizes" this externally heterogeneous environment. This kind of case involves what Levins (1968) calls fine-grained heterogeneous environments, but from Brandon's perspective, these environments constitute homogeneous selective environments.

But there are other ways in which externally heterogeneous environments may be selectively homogenized. One example provided by Brandon is that of "habitat choice."[7] Suppose we have an insect population composed of two types, A and B, distributed over a heterogeneous environment, E, composed of two internally homogeneous sub-environments, E_1 and E_2. The insects settle into one of the two sub-environments and they remain in that environment for the selectively relevant time interval. Think, for example, that insects lay their eggs on one of two plant species that cover adjacent fields (E_1 and E_2) and that the larvae hatching from these eggs will remain on a single plant for the entire larval stage (selection, let us suppose, occurs during the larval stage, operated by predators that feed on the larvae that are more conspicuous against the leaf color of the plant they feed on). But let us suppose that the distribution of types over sub-environments is not random. Rather, the A type exhibits a preference for laying eggs on one plant species, and this provides a selective advantage for its larvae

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[6] Here is Brandon's explicit statement on this: "Moths fly around and land on many different trees. Their probability of being devoured by a bird depends on the match, or lack thereof, of their color and the statistical average color of the background that they create by their behavior. Thus, if the two tree types are distributed randomly about the woods and both types of moths show no behavioral preference for one type of tree over the other, then the woods in question are selectively homogeneous" (Brandon 2005: 166).

[7] For my discussion here, I modified some aspects of Brandon's example.

(for example, 80% of the A-individuals lay their eggs in E_1).[8] On the other hand, the B-individuals exhibit no preference for any of the two potential egg-laying sites, E_1 and E_2 (i.e., 50% of the B-individuals lay their eggs in each of E_1 and E_2). Now let us further suppose that the E_1 environment is better for the insects, i.e., in E_1, the larvae of both types have a higher survival level than in E_2. However, within each of the two sub-environments, the A and B types have the same fitness.

How are we to handle a case of this sort? Will we say that there is no selection going on because within each sub-environment (E_1 and, respectively, E_2) the two types have the same fitness? Or will we say that there is selection here because in the global environment E (E_1 and E_2 put together), the A type is overall fitter due to the fact that the A type exhibits a preference for the better sub-environment E_1? Brandon argues for the latter position: there is selection going on here, and it takes place in the global environment E. Though E is an externally and ecologically heterogeneous environment, it is a selectively homogeneous one. The preference that type A exhibits for one sub-environment homogenizes E from a selective point of view. This makes sense if we do a little counterfactual reasoning: had E been populated with only one type of plant (that from E_1 or that from E_2), the two types would have had the same expected fitness because the preference of the A-type could not have led to differences in fitness (both types would have been forced to lay their eggs on the sole plant species available). The preference of the A type is only selectively relevant if there are multiple species of plants to choose between when it comes to egg-laying: the external and ecological heterogeneity of E is, therefore, a condition for there being selection in E at all. It is, therefore, only natural to conclude that E is homogeneous from a selective point of view precisely because E is externally and ecologically heterogeneous.

Finally, let us note that by endorsing EHC, Brandon did not lose sight of the fact that biologists often investigate cases in which the scale of gene flow is larger than the scale of environmental selective heterogeneity. In such cases, the target population is distributed over a global heterogeneous environment composed of internally homogeneous sub-environments; the studied organisms spend all their lives in a single sub-environment, but the types are regularly redistributed into

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[8] No deliberation on the part of the organisms in question is presupposed by Brandon here. Rather, he sees habitat choice as potentially genetically hard wired or determined by other forms of conditioning (Brandon 1990: 62).

sub-environments (for example, every generation by reproduction). This is what Levins (1968) calls coarse-grained heterogeneous environments, and I will follow suit.[9] How can this sort of case be rendered compatible with EHC? In order to accommodate such cases, Brandon introduces the term "compound natural selection," which "is a process consisting of natural selection within environments and distribution into environments" (Brandon 1990: 73). Note that selection still occurs within each selectively homogeneous sub-environment, but, in such cases, the distribution of types into environments (either during a once-per-generation dispersal stage or as an effect of rarer dispersal events) also makes an important contribution to the evolutionary outcome. In such cases, we will therefore need to take into account not only the strength of selection within and the demographic contributions of sub-environments but also the frequencies of types within each sub-environment and the way in which these frequencies are likely to change from one distribution event to the next. The more complicated cases of "compound natural selection" are contrasted by Brandon with "simple natural selection" (a term he borrows from Damuth 1985) that involves only selection within a selectively homogeneous environment (and this includes the cases of selection in fine-grained heterogeneous environments introduced above).

These precautions taken by Brandon are meant to highlight the fact that EHC is a less strict condition than it might seem at first glance, insofar as it is compatible with setups in which individuals move freely or choose between heterogeneous patches during their existence or, finally, are otherwise redistributed over heterogeneous environments once per generation or at larger intervals. While ecological and evolutionary setups are always complex—involving a plethora of factors that are never entirely invariant in space and time—these precautions taken by Brandon make sure that EHC is ready to accommodate at least some of this complexity.

3. Millstein's Critique of Brandon's EHC

A vigorous critique of Brandon's EHC has been put forth by Roberta Millstein (2014). Though Brandon did not respond to Millstein's critique, I believe it would be instructive to try to determine to what extent

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[9] As Millstein (2014: 745) notes, though there are intermediates between fine-grained environments and coarse-grained ones, for most cases, these two extremes are reasonable approximations, and we can thus leave aside from our discussion the intermediates.

her objections hit—and, respectively, miss—their target. Therefore, my main aim in the rest of this paper is to analyze the validity of Millstein's critique and especially to assess to what extent EHC must be amended in light of her points.

In order to get there, we must first distinguish between two kinds of objections that Millstein makes. One of her objections does not contest the validity of EHC itself but highlights its incompleteness. Indeed, if Brandon's criteria for delineating selectively homogeneous environments are incomplete, then EHC may remain theoretically acceptable but practically inapplicable: we may still claim that selection only acts within selectively homogeneous environments, but if we are unable to identify such environments, our claim will remain useless for any explanatory or predictive purposes. On the other hand, two objections by Millstein directly target the validity itself of EHC, arguing either that it clashes with biological practice, or that it does not conform to our deep-rooted intuitions with respect to the interactions that constitute the "struggle for existence" of biological entities. I will address these two kinds of objections in turn below.

3.1. The Incompleteness of Brandon's Criteria for Delineating Selectively Homogeneous Environments

If authors endorsing EHC do not provide us with an effective method for delineating homogeneous selective environments, insisting that selection should be relativized to such environments becomes little more than an empty claim. Millstein argues that Brandon's proposal runs precisely this risk.

Her discussion is based on the following hypothetical example: imagine a global environment *a* of a brownish background within which there is a small patch *b* of a pinkish background and five other patches (*c*, *d*, *e*, *f* and *g*) of yellow-greenish background (see Figure 1). The colors of these backgrounds are relevant to the fitnesses of differently colored variants of *Cepaea nemoralis* snails living in the area. But suppose that snails regularly move only between some of these patches: some of them move regularly between *a*, *b*, *c*, and *d*; others, between *e*, *a*, and *f*; and, finally, others only live within *g*, but not outside of it. Millstein argues that there are multiple ways in which the boundaries of the environment(s) relevant for selection could be drawn in this case, and she argues that neither Brandon nor Levins provide us with a clear solution regarding which of these demarcations is the correct one. And, in the absence of such a clear solution, we would be left with conflicting predictions and explanations of the evolutionary trajectories of the case. Millstein concludes that:

> the Brandon and Levins environment concepts are incomplete. They cannot help to settle disputes […] over which areas to include in one's data set because they are not powerful enough to determine which areas are heterogeneous and in what way. (Millstein 2014: 748)

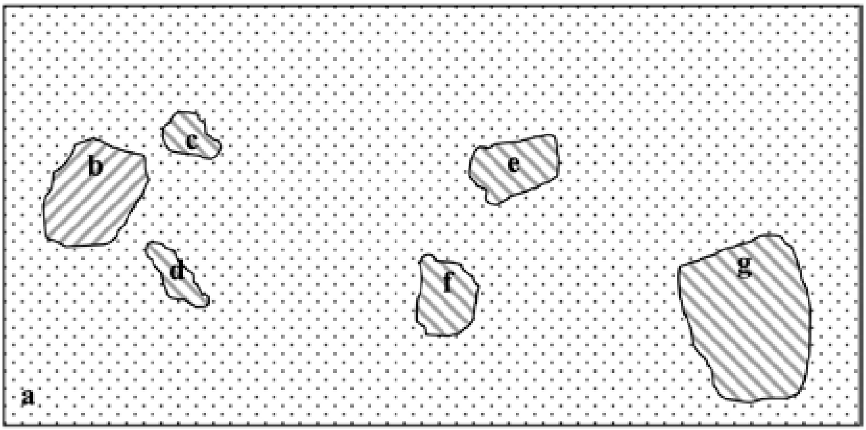

Figure 1. A patchy environment. *a* is one type of patch (with a brownish background), *b* is another type of patch (with a pinkish background), and *c*, *d*, *e*, *f*, and *g* are a third type of patch (with a yellow-greenish background). Redrawn after Millstein (2014: 747).

At first glance, this seems to be a puzzling objection because, in order to answer to it, we merely have to apply Brandon's indications (spelled out above) about how selectively homogeneous environments should be demarcated. If some snails move freely between some of the patches of the environment, then, as pointed out above, the patches in question should be taken to form a single homogeneous selective environment. Therefore, in Millstein's snail example, we have two fine-grained heterogeneous environments (in Levins' sense) that should be considered homogeneous selective environments (in Brandon's sense), namely the conjunction of *b*, *c*, *d*, and some of *a*[10] and, respectively, the conjunction of *e*, *f*, and some of *a*[11]. Finally, given that certain snails only live in *g* (but

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[10] Namely the part of *a* in which live and wander the individuals that also move between *b*, *c* and *d*.

[11] Another part of *a* is relevant here, namely the one where individuals moving between *e* and *f* wander.

do not venture into the surrounding environment of type *a*), the *g* patch is itself a homogeneous selective environment (assuming, of course, that within it, snail types have roughly constant relative fitnesses). Brandon's criteria for delineating selective homogeneous environments, therefore, do provide a manner for drawing the boundaries between the environments relevant for selection in Millstein's hypothetical example. The objection does not seem to hold.

However, another way of interpreting Millstein's objection seems more plausible. Though Millstein does not clearly spell this out, the point of her objection may have been to show that delineating environments *requires some manner of delineating populations*. Indeed, we could not have demarcated the relevant selective environments of Millstein's hypothetical case if we had not taken into account the fact that there are three populations of snails that share different sub-sections of the global environment: one population occupies sub-sections *b*, *c*, *d* and some of *a* (with the individuals of the population moving freely between these sub-sections), another one occupies sub-sections *e*, *f* and some other part of *a* (with, again, the individuals of the population moving freely between these sub-sections) and, finally, a third population occupies sub-section *g* (with the individuals of this population not venturing outside of this sub-section). Without a demarcation of these three populations, we could not have delineated the selectively homogeneous environments relevant for a case like this one. In other words, Brandon's criteria for delineating environments implicitly rely on a demarcation of the populations of the case.

If we interpret Millstein's objection in this manner, then I believe it is sound. But note that—at least in my latter reading—the objection does not undermine the validity of Brandon's criteria for delineating selectively homogeneous environments, nor, consequently, Brandon's EHC. It merely brings to light a hitherto implicit assumption of these criteria and, therefore, of EHC.

3.2. Objections Aimed at the Validity of EHC

Millstein (2014) also puts forth two objections that directly target the validity of Brandon's EHC. I will address them in turn here, starting with the less developed one.

The scientific practice objection. A first and admittedly tentative objection is that EHC might be at odds with scientific practice. According to Millstein (2014: 751), research on the evolution of phenotypic plasticity or on the persistence of polymorphism "suggests that thinking of selection occurring across heterogeneous environments is widespread." Indeed, models that biologists use for determining the conditions under which selection may favor phenotypic plasticity or may promote polymorphism surely involve heterogeneous environments (i.e., differences in selective pressures between spatial patches or temporal periods). It, therefore, seems that biologists studying phenotypic plasticity or the persistence of polymorphism do not hesitate to relativize their selective claims to selectively heterogeneous environments, and this apparent discrepancy between Brandon's EHC and scientific practice needs to be looked into.[12]

I think there are substantive differences between phenotypic plasticity and the persistence of polymorphism, so I will treat them separately. Let us look at phenotypic plasticity first. For the purposes of this paper, we may borrow the following definition of phenotypic plasticity: "a property of individual genotypes to produce different phenotypes when exposed to different environmental conditions" (Pigliucci, Murren, and Schlichting 2006: 2363).[13] Two types of phenotypic plasticity are usually distinguished, and I will discuss them in turn. In the first type, a plastic or polyphenic genotype exhibits an "all or nothing response" to one or more environmental cues (Lively 1986: 567) or makes "irreversible developmental choices" triggered by such environmental cues (Moran 1992: 972). Once the developmental choice is made, the phenotype obtained will remain in place for the whole existence of that organism. This type of phenotypic plasticity has been called "developmental conversion" by Smith-Gill (1983: 49). So, suppose we have three genotypes, two of which are monophenic (G_{M1} and G_{M2}) and one of which (G_P) exhibits phenotypic plasticity (i.e. it is polyphenic). They are distributed in an environment E composed of patches of type E_1 and E_2, with G_{M1} being specialized for E_1 and G_{M2} being specialized for E_2. In the early stages of their life cycle, the individuals enter one of the two patches and spend the rest of their lives there (this might be the case for plants with widely dispersed seeds or for sessile invertebrates with pelagic larvae—Lively

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[12] Anderson (2019) similarly reads Glymour (2011) as claiming that models for the evolution of phenotypic plasticity involve relativizing natural selection to heterogeneous selective environments. I am not convinced that Anderson's reading is correct, but if it is, the points I will make with respect to Millstein's objection hold against Glymour as well.

[13] This definition neglects the fact that, via cytoplasmic and epigenetic factors, norms of reaction may also be affected by the environmental conditions experienced by the immediate ancestors of the organisms (Sultan 2017; Futuyma 2017). But this does not affect the conclusion of my discussion here.

1986: 562). Suppose, for simplicity, that plasticity entails no cost so that the ordinal relations of fitness in E_1 are $G_{M1} = G_P > G_{M2}$, while in E_2, it is $G_{M1} < G_P = G_{M2}$. However, overall (i.e., in the global environment E), G_P is fitter than either G_{M1} or G_{M2}, and, therefore, G_P increases in frequency in the population. Will we say that we have two processes of selection here, one in E_1 against G_{M2} and one in E_2 against G_{M1}, or will we say that we have a single selective process here, taking place in the global environment E, favoring G_P over both specialist types? Millstein suggests biologists lean towards the latter option. However, I believe this is not an argument against EHC. Indeed, though Brandon does not discuss this if we uphold some of Brandon's positions spelled out above, we can make a case that someone embracing EHC would reach the same conclusion about phenotypic plasticity as Millstein.

Recall that in cases in which a type exhibited a preference for a sub-environment (i.e., cases of "habitat choice"), this choice selectively homogenized an environment that was externally and ecologically heterogeneous. Phenotypic plasticity involving developmental choice is the same, only here the plastic type no longer chooses its habitat or environment, but, on the basis of environmental cues, "chooses" the phenotype with which to meet the environment (i.e., in Moran's terms, it makes a "developmental choice"). The plastic genotype is not adapted to E_1 or E2; it is adapted to the patchiness of the global environment E, just like a habitat-choosing type, which is adapted to the patchiness of its environment. Had E been only composed of E_1 or of E_2, the ability of G_P to *react* to environmental cues in order to produce different phenotypes would have brought no advantage; it is only the patchiness of E that occasions the developmental choice that brings about the selective advantage of G_P, just like in the case of habitat choice, where only the patchiness of the environment brought about a selective advantage for the habitat-choosing type. So it is in the global environment E that selection takes place here, favoring the plastic type G_P over the specialized types G_{M1} and G_{M2}. Thus, the presence of the plastic genotype (G_P) selectively homogenizes an externally and ecologically heterogeneous environment, just like the presence of the habitat-choosing type did in Brandon's example discussed above.

The other type of phenotypic plasticity involves a more continuous phenotypic response on the part of the plastic genotype (Lively 1986: 568). In this case, the developmental choice is not irreversible, but an individual may go through multiple phenotypes depending on the successive variations of the environmental cues. This type of phenotypic plasticity has been called "phenotypic modulation" by Smith-Gill (1983: 49). Here, the individuals no longer experience a single environment during their lifetime, but each individual is likely to experience a number of environments (where environmental variation may be spatial or temporal). Monophenic genotypes (i.e., types that exhibit a single phenotype irrespective of the environment encountered) might or might not (depending on various factors that I will not detail here) be outcompeted by genotypes that are able to repeatedly track—via phenotypic responses—the various environmental conditions they are subjected to. But it is easy to see that we are dealing here with what Levins called "fine-grained environments": individuals are likely to experience the various complexes of environmental conditions in the proportion in which these complexes are represented in the global environment. In the case of spatial variation, this occurs because individuals move freely between various patches. If the variation is temporal, it is the complexes of environmental conditions that alternate at various stages of the lives of the individuals, but the effect is the same: during the course of their lives, individuals will likely encounter different environmental complexes according to the frequency of these complexes in the given setup. And given that such fine-grained environments are homogeneous selective environments in Brandon's framework, selection occurs here within the global fine-grained environment, irrespective of the number of spatial or temporal patches that it might be composed of. This fact is not changed in any way by the introduction of plastic genotypes into the picture.

Consequently, though Brandon does not directly discuss this issue, his manner of treating cases involving habitat choice or fine-grained environments allows us to conclude, against Millstein, that neither of the two types of phenotypic plasticity usually discussed by biologists undermines EHC. On the contrary, in such cases, selection arguably takes place within selectively homogeneous environments, even though these environments are externally heterogeneous.

What about studies regarding the maintenance of polymorphism? Do they undermine EHC? I think substantiating this claim would not be easy. When biologists talk about selection promoting polymorphism in coarse-grained heterogeneous environments, they *might* mean that there is a single process of selection in such a heterogeneous environment and that the various selective pressures or intensities encountered in the local sub-environments are just modulations of this single selective process. However, saying that selection promotes polymorphism in coarse-grained heterogeneous environments might *also* mean that there are multiple selection processes going on in the local sub-environments and that, therefore, differences in selective pressures or intensities indicate numerically distinct selective processes. The first interpretation is not compatible with EHC, but the second one is. The mere fact that biologists talk about selection in heterogeneous setups can, therefore, not constitute, in itself, an argument against EHC. When we look at some of the models for the maintenance of polymorphism, we see that many of them—even among those put forth by biologists quoted by Millstein (2014: 746)— explicitly involve selection within patches followed by dispersion in various degrees, of types into patches; in other words, many of them are perfectly consistent with Brandon's compound natural selection. This is the case for the first model for the maintenance of polymorphism in heterogeneous environments, proposed by Levene (1953). In this model, "after fertilization, the zygotes settle down at random in large numbers into each of the niches and are thereafter immobile. There is then differential mortality ending with a fixed number of individuals in each niche" (Levene 1953: 331). The model is, therefore, compatible with Brandon's compound natural selection, involving random mating followed by settlement in one patch (where selection occurs).[14] This model was later expanded by Levins and MacArthur (1966) and Gillespie (1974).[15] More arguments would, therefore, be needed if one wanted to substantiate the claim that models that investigate the maintenance of polymorphism by selection in heterogeneous environments are incompatible with the EHC.

To sum up, I have shown that neither the models for the evolution of phenotypic plasticity nor those concerning the maintenance of polymorphism seem to unequivocally clash with the EHC.

The interactions objection. Millstein's last objection is also the most radical. It consists of nothing less than arguing that Brandon's environmental homogeneity condition for selective claims should be replaced with what we might call a "population homogeneity condition" based on Millstein's (2009, 2010) "causal interactionist population concept" (hereafter, CIPC). In order to better grasp this last objection, we need to take a look at this population concept:

> *Populations* (in ecological and evolutionary contexts) consist of at least two conspecific organisms that, over the course of a generation, are *actually* engaged in survival or reproductive interactions or both;

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[14] The same holds for Spieth (1979).

[15] For a review of the issue, see Hedrick (2006).

> The boundaries of the population are the largest grouping for which the rates of interaction are much higher within the grouping than outside. (Millstein 2010: 67)

I do not intend to discuss the CIPC at length here, nor to defend or reject this manner of understanding what "population" means in evolutionary or ecological contexts (for discussions, critiques, and refinements, see Matthewson 2015; Stegenga 2016; Baraghith 2020). Instead, I will only highlight the two points that are of interest for my present aims. First, according to the CIPC, it is survival and reproductive interactions between individuals that help define and delineate a population. Second, a grouping of individuals counts as a population if there are no large differences in the survival and interaction rates within and between the subsets of that grouping. If we take one such subset and discover that its members have a much higher interaction rate between themselves than with members of the other subsets of the grouping, then we can conclude that the grouping at hand is not a population (rather, as Millstein criteria suggest, it is a metapopulation). But this is tantamount to claiming that if a grouping is to be a population, the rate of survival and reproductive interactions within and between its subsets need to be roughly homogeneous. (The term "roughly" is meant to capture the fact that some differences between rates of interactions within and between subsets are accepted, as long as these differences are not very large.[16])

Millstein's suggestion in the last part of the paper is that of "using the CIPC as an environment delineator" (Millstein 2014: 751). This does not mean using the CIPC to complete Brandon's criteria for delineating a homogeneous selective environment (as was the case in the first objection discussed above); rather, it means replacing Brandon's EHC with a different condition based on Millstein's population concept. Millstein's argument for this begins by drawing attention to populations whose individuals may be spread over a heterogeneous environment, yet the level of survival and reproductive interactions between individuals on different sides of the borderline between sub-environments might be similar or identical to the level of interactions between individuals belonging to the same sub-environment. And the argument continues:

> These sorts of survival interactions—examples of Darwin's "struggle for existence"—are part of the process of natural selection. It thus does not make sense,

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[16] Millstein's CIPC, for example, allows for "patchy populations" in which the rate of interactions between subsets is lower but not significantly lower than the rate of interactions within subsets (Millstein 2010: 76–78).

> in situations such as those described here, to say that there are two separate selection processes when in fact all of the organisms in both patches are engaged in a struggle for existence and in reproductive interactions (also part of natural selection) with one another. Of course, it is also possible that there are cases where few or no interactions occur across patches, or where those interactions were very much fewer than the interactions within the patches; in those cases, there would be two separate selection processes going on in two separate environments. These considerations vindicate the CIPC approach to environment delineation. (Millstein 2014: 752)

Two strong claims transpire from this fragment.

a) When we are dealing with a single population (in the CIPC sense), we should conclude that there is a single selection process going on; when, on the other hand, we are dealing with two populations (again, in the CIPC sense), then, as the last part of the quotation emphasizes, we should conclude that there are two selection processes taking place in our setup. This is tantamount to embracing the view that selective claims need to be relativized to individuals belonging to a single population. Moreover, a grouping of individuals should only be considered a population (from an ecological and evolutionary point of view) if there is homogeneity (or near homogeneity) of survival and reproductive interactions within and between its subsets. Though Millstein does not spell this out herself, by putting these two ideas together, we can see that the thesis advanced by Millstein here is that selective claims need to meet a "population homogeneity condition" (for short, PHC), i.e., they need to be relativized to a population that is homogeneous in the relevant sense.

b) But note that the CIPC demands that a population be *the largest* grouping exhibiting (near) homogeneity of interactions between and within its subsets (Millstein 2010: 67). Stating that selective claims need to be relativized to a single population thus entails that, even when that population is spread over a heterogeneous selective environment in Brandon's sense, we should still conclude that we are dealing with a single selective process because we are dealing with a single population. The first part of the quotation above highlights this point, but Millstein also clearly states it elsewhere in her article:

> Note that using the CIPC (…) to delineate the boundaries of the selective environment entails that selection can occur across a heterogeneous environment, contra the view of Brandon and others that selection should be understood within homogeneous environments only. (Millstein 2014: 751)

We can thus conclude that Millstein's PHC is meant to replace Brandon's EHC: selective claims should not be relativized to homogeneous selective environments but to groupings of individuals exhibiting homogeneity of interactions within and between their subsets, i.e., to populations in the CIPC sense. Or, to put it otherwise, it is the number of populations in a scenario that determines the number of selection processes, and not the number of homogeneous selective environments as Brandon had claimed.

But what is Millstein's argument for replacing EHC with PHC? When a single population (in the CIPC sense) is spread over two (or more) patches of a heterogeneous environment, the density of survival and dispersal interactions is roughly homogeneous within and between patches. These sorts of interactions are "examples of Darwin's 'struggle for existence'" or "part of natural selection" (Millstein 2014: 752). Thus, the argument goes, homogeneous rates of interactions within and between patches suggest a common evolutionary fate of the individuals in both patches.

While the argument seems correct, it does not provide sufficient reasons to support the conclusion that there is a single selection process ranging over both patches here. Indeed, Millstein's argument does nothing to deny the fact that the interactions *with the environment* that the individuals of two adjacent patches engage in *remain different* to a larger or smaller extent (otherwise, the relative fitness of one or more types would not vary across patches) and *this is also evolutionarily significant*. Organisms also struggle for existence with or against their environment—as Darwin famously noted[17]—and therefore interactions with the environment—or with various environmental factors from their habitat—are equally "part of the process of natural selection." And the fact that these interactions with the environment are different between the two patches—leading to different expected relative fitnesses for at least one type—is not at all indifferent to the evolutionary fate of the population spread over the two patches. So why should we only take into account the (near) homogeneity of the survival and reproductive interaction rates within and between the subsets of individuals found in the two patches and not the heterogeneity in the interaction of these individuals with the environmental conditions of their respective patches? Millstein's argument provides no answer to this question.

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[17] "Two canine animals, in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture" (Darwin 1872: 50).

3.3. A Reconciliatory Proposal

That being said, I would like to end this paper by pointing out that there might be a middle way here, a way in which EHC might be rendered compatible with an admittedly weaker version of PHC. Let me begin outlining this tentative solution by noting that Millstein's PHC is a fairly restrictive condition to impose upon selective claims. Indeed, to maintain that selective claims need to be relativized to populations in the CIPC sense sets a rather heavy practical burden on researchers in the field. In many cases, there might be serious pragmatic obstacles that prevent the researcher from studying an entire population (the sheer size of the population might be such an obstacle, as would the distribution of the population across political borders). But even if one studies just part of a population (in the CIPC sense), this would still not invalidate one's claims that selection is acting in that sub-population and that selection favors a particular variant over others, etc. These pragmatical considerations do not undermine the CIPC as a definition of populations and as a way to demarcate them; instead, these considerations suggest that Millstein's PHC might be too stringent a condition to impose upon selective claims.

I therefore propose a version of the PHC that is weaker than Millstein's. My weaker version consists in maintaining that selective claims need *not* be relativized to *the largest* grouping whose subsets exhibit roughly homogeneous rates of survival and reproductive interactions within and between them but simply to *a* grouping whose subsets exhibit such roughly homogeneous rates of interactions within and between them. One could thus make selective claims about sub-populations, i.e., about parts of a CIPC population (which would themselves be homogeneous in the relevant sense). One could adopt my weaker version of PHC and still support EHC. Two examples will clarify this. First, imagine we have two groupings of individuals living in a homogeneous selective environment (in Brandon's sense), but there are much fewer survival and reproductive interactions between the groupings than there are within them. Adopting my weaker version of PHC would allow us to conclude that we have two selection processes here (one for each grouping), even though the two groupings occupy a homogeneous selective environment. Of course, adopting Millstein's stronger version of PHC discussed above would lead to the same conclusion; but this is precisely the point: in cases where multiple populations (in the CIPC sense) are distributed over a single homogeneous environment, we lose nothing by adopting my weaker PHC instead of Millstein's stronger one.

Second, imagine a population (in the CIPC sense) distributed over a heterogeneous selective environment (in Brandon's sense). An empirical example is provided by McNeilly (1968), who studies a population of the grass *Agnostis tenuis* in a valley where an abandoned copper mine is located. The population is composed of two types of *Agnostis tenuis*, one that tolerates high levels of copper in the soil and a normal, non-tolerant type. On the soil contaminated with copper from the old mine, the tolerant type is strongly favored by selection, while on the surrounding non-contaminated soil, selection is weaker and goes in the other direction, favoring the normal type: the contaminated area and the non-contaminated one thus constitute two selectively homogeneous subsections that make up a selectively heterogeneous environment. Moreover, the wind makes sure that gene flow is strong between the contaminated and non-contaminated areas of the valley. Here, adopting Millstein's strong version of PHC would lead to the conclusion that there is a single selection process ranging over the whole valley—and this is because *the largest* grouping exhibiting roughly homogeneous survival and reproductive interaction rates within and between its subsets is the whole set of individuals distributed over the two heterogeneous patches. We would thus be forced to reject EHC, and, as shown in my discussion above, this is precisely what Millstein does. But what if we embraced my weaker version of PHC? We would start by noting that the groupings of individuals inhabiting the contaminated and, respectively, the non-contaminated area exhibit roughly homogeneous rates of survival and reproductive interactions within and between their subsets: indeed, if the whole population exhibits roughly homogeneous interaction rates within and between its subsets, then the parts of that population (inhabiting the contaminated and, respectively, the non-contaminated soil) will exhibit the same rough homogeneity. And since my weaker PHC entails that selective claims need to be relativized to *a* grouping whose subsets exhibit such homogeneity, we would conclude that natural selection acts within each of the patches of the environment, i.e., within the contaminated area, on the one hand, and within the copper-poor area, on the other hand. This verdict would thus be compatible with the idea that selective claims need to be relativized to homogeneous selective environments. My weaker version of PHC thus seems to be compatible with EHC, and I hope this tentative suggestion might help move the discussion forward.

4. Conclusion

One of the take-away points from Millstein's critique of EHC is the idea that environmental demarcation requires some manner of delineating populations. And, of course, Millstein's own population concept—the CIPC—is a good candidate for this, especially after Baraghith's (2020) spelling out of the exact rules that should be followed when one wants to delineate CIPC populations. Millstein's critique makes it clear that EHC is inapplicable if our criteria for environmental demarcation are not complete, and they can only be complete by taking population delineation into consideration.

However, I argued that Millstein's other lines of critique against EHC are unconvincing. I thus showed that EHC is not necessarily incompatible with scientific practice. Moreover, I argued there are not enough reasons to replace EHC with a "population homogeneity condition" (PHC) imposed upon selective claims based on Millstein's population concept. However, I argued that there might be a way for reconciliation here: I thus proposed a weaker version of PHC that is compatible with EHC. Adopting both of these conditions would mean maintaining that selective claims need to be relativized both to homogeneous environments and to groupings that are roughly homogeneous with respect to the rate of survival and reproductive interactions within and between their subsets.

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