

# Natural Selection and the Struggle for Existence

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## 1. Introduction

THE 'STRUGGLE for Existence' played an important role in Darwin's conception of natural selection. In the twentieth century, however, more than a few biologists and philosophers have sought to decouple the struggle for existence from the concept of natural selection. Consider, for example, the following statements:

It is well known that Darwin's conception of natural selection was derived from the idea of Malthus, that even the slowest breeding organisms tend to produce more offspring than can survive without eventually outrunning the food supply. . . . It was the differential mortality of the carriers of different genotypes composing a population that was supposed to make selection effective. Unfortunately, this process was also described by metaphors which were more picturesque than accurate, such as "struggle for life" and "the survival of the fittest" . . .

In reality, the essence of selection is that the carriers of different genotypes in a population contribute differentially to the gene pool of the succeeding generations. The contributions of some genotypes are relatively greater on the average than the contribution of others in the same environment.<sup>1</sup>

I have indicated above that natural selection works only among competing entities, but it is not necessary for the individuals of a species to be engaged in ecological competition for some limited resource. This requisite is often assumed, beginning with Darwin and continuing with many modern biologists. A little reflection, however, will indicate that natural selection may be most intense when competitive interactions are low.<sup>2</sup>

It is not necessary, for example, that resources be in short supply for organisms to struggle for existence. Darwin himself pointed out that "a plant at the edge of a

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<sup>1</sup>T. Dobzhansky, *Genetics and the Origin of Species* (New York: Columbia University Press, 1951), pp. 77–78.

<sup>2</sup>G. C. Williams, *Adaptation and Natural Selection* (Princeton, NJ: Princeton University Press, 1966), p. 32.



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desert is said to struggle for life against the drought.” Thus, although Darwin came to the idea of natural selection from consideration of Malthus’ essay on overpopulation, the element of competition between organisms for a resource in short supply is not integral to the argument. Natural selection occurs even when two bacterial strains are growing logarithmically in an excess of nutrient broth if they have different division times.<sup>3</sup>

The preceding quotations raise at least two issues. The first concerns how Darwin conceived of the struggle for existence. Williams suggests that Darwin had a fairly narrow conception of the struggle for existence, namely, that it referred only to direct competition between two organisms of a species for some resource essential to survival and/or reproduction. Lewontin, on the other hand, suggests that Darwin construed the struggle for existence more broadly, to include more than intraspecific competition for resources. As we shall see, Lewontin is much closer to the truth on this point.

The second issue is of greater importance: What is the proper way to conceive of the relation between the struggle for existence and the process of natural selection? The authors quoted above seem to think that the struggle for existence is not necessary for natural selection to occur; we, following Darwin, believe that (when properly understood) it is. Furthermore, we will argue that there are good reasons for distinguishing between evolutionary change that is the result of natural selection (in Darwin’s sense) and evolutionary change that results from what biologists such as Williams and Lewontin want to call ‘natural selection’.

## 2. Darwin on the Struggle for Existence and Natural Selection

The fourth chapter of *On the Origin of Species* begins with two questions, questions quite natural given the chapters which preceded it:

How will the struggle for existence, discussed too briefly in the last chapter, act in regard to variation? Can the principle of selection, which we have seen is so potent in the hands of man, apply in nature?<sup>4</sup>

The substitution of the second question for the first indicates Darwin’s intention to treat the effects of the struggle for existence on variation as the natural mechanism for achieving in natural populations what breeder selection has achieved in domestic populations.

<sup>3</sup>R. C. Lewontin, ‘The Units of Selection’, *Annual Review of Ecology and Systematics* **1**, (1970), 1–18, see p. 1.

<sup>4</sup>C. Darwin, *On the Origin of Species* (Cambridge, MA: Harvard University Press, 1964, facsimile of 1st. edn, 1859), p. 80.

In the 'too brief' discussion Darwin refers to here, he notes that heritable variation is necessary but not sufficient for adaptation and speciation:

... the mere existence of individual variability ... though necessary as the foundation for the work, helps us but little in understanding how species arise in nature. How have all those exquisite adaptations ... been perfected?<sup>5</sup>

... how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species ...?<sup>6</sup>

Darwin answers that both adaptation and speciation follow from 'the struggle for life', owing to which any profitable (i.e. better adapted) variation will tend to the preservation of its bearer, and will generally be passed on to its progeny, giving them as well a better chance at survival. Darwin concludes:

I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection.<sup>7</sup>

The usual way to read this summary is that it states a principle, and the name of that principle is 'Natural Selection'. In context, however, it is clear that the agency by which useful variations are preserved is the struggle for life. As the opening of Chapter Four makes clear, natural selection is the term for the process whereby struggle acts on heritable variation, preserving those variations which are profitable. Struggle, primarily but not exclusively intra-specific struggle, has the effect of selecting variations which contribute to the survival and reproductive activity of their bearers.

How did Darwin think that intraspecific competition drove speciation and adaptation? To answer this, one needs a clear sense of what Darwin intended by 'the struggle for existence'. Darwin notes that the notion was a popular one in his time.<sup>8</sup> But the Darwinian concept of struggle involves two crucial innovations.

- (1) Though intraspecific, struggle should not typically be thought of as involving confrontation between species members. Even when the goal of the struggle is conceived narrowly as survival to maturity, the winner is seldom the destroyer of the loser.
- (2) But Darwin, at any rate, did not conceive the goal so narrowly:

I use the term ... Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including

<sup>5</sup>*Ibid.*, p. 60.

<sup>6</sup>*Ibid.*, p. 61.

<sup>7</sup>*Ibid.*, p. 61.

<sup>8</sup>*Ibid.*, p. 62.

(which is more important) not only the life of the individual, but success in leaving progeny.<sup>9</sup>

Perhaps even more important than either of these innovations, however, was the decision to treat the struggle for existence not as a basic principle, but as a theorem which follows from the Malthusian principle of population expansion.

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase.<sup>10</sup>

Darwin<sup>11</sup> insists this is 'Malthus applied with manifold force to the whole animal and vegetable kingdoms . . .', but in this we think he is being modest. Like Malthus,<sup>12</sup> he treats the principle of population as a counterfactual law, or what Sober<sup>13</sup> terms a 'zero-force law'; it identifies what would happen to natural populations in the absence of the various limiting forces which actually impinge upon them.<sup>14</sup> Those limiting forces Malthus refers to as 'checks'. But Darwin also transforms Malthus's ideas in two ways. First, he expands the concept of 'checks' on population growth to include virtually any factor of the environment which limits population increase. In fact, he goes out of his way to downplay the significance of resource limitations as a check.

The amount of food for each species of course gives the extreme limit to which each can increase; but very frequently it is not the obtaining of food, but the serving as prey to other animals, which determines the average numbers of a species.<sup>15</sup>

Just prior to this statement Darwin has given experimental evidence for it:

. . . on a piece of ground three feet long and two wide, dug and cleared, and where there could be no choking from other plants, I marked all the seedlings of our native weeds as they came up, and out of the 357 no less than 295 were destroyed, chiefly by slugs and insects.<sup>16</sup>

He refers to climate as 'the most effective of all checks',<sup>17</sup> notes the effects of epidemics on rapidly increasing populations,<sup>18</sup> and concludes with a long discussion of the ways in which the ecological web of relations with other

<sup>9</sup>*Ibid.*, p. 62.

<sup>10</sup>*Ibid.*, p. 63.

<sup>11</sup>*Ibid.*, p. 63.

<sup>12</sup>T. R. Malthus, *Essay on the Principle of Population* (London: J. Johnson, 1798), p. 14.

<sup>13</sup>E. Sober, *The Nature of Selection* (Cambridge, MA: Bradford Books, 1984), p. 31ff.

<sup>14</sup>Fisher seems not to have seen that this is the way both Malthus and Darwin understand the law; see R. A. Fisher, *The Genetical Theory of Natural Selection* (Oxford: Clarendon Press, 1930), pp. 46–47. Sober apparently endorses Fisher's criticism; see E. Sober, *op. cit.*, note 13, p. 194ff.

<sup>15</sup>C. Darwin, *op. cit.*, note 4, p. 68.

<sup>16</sup>*Ibid.*, p. 67.

<sup>17</sup>*Ibid.*, p. 68.

<sup>18</sup>*Ibid.*, p. 70.

species can affect the numbers of any species.<sup>19</sup> In short, the effects of limited resources are treated as the least important of checks on population expansion, whereas in Malthus they are the principle concern.

The second innovation in Darwin's mobilization of the Malthusian Principle is in its being the driving force behind adaptive change; in Malthus, it was simply the principal force acting to prevent social improvement. The tendency to population increase, embedded in a theory of fluctuating variation and gradually changing (or underexploited) environments, produced entirely different effects in Darwin's hands than it had in Malthus's.

Darwin's theory of natural selection, then, has the following structure:

- (1) Populations have a tendency to geometric expansion which is checked by environmental forces including predation, climatic conditions, disease, dependency on other populations, and limited energetic resources.
- (2) This generates a 'struggle', primarily but not exclusively intraspecific, to survive and reproduce, among organisms with heritable variations.
- (3) This produces 'natural selection': those variants best able to avoid predation, disease, climate fluctuation, or to exploit limited resources, etc., will out-survive and out-reproduce those less well able to do so.<sup>20</sup>

For Darwin, then, natural selection refers to a process involving a quite specific type of mechanism operating on available variation—environmental checks on population expansion. For natural selection to operate, however, it was not necessary for populations to be at the 'carrying capacity' of their environment, nor was the operative check typically limited resources. Exactly how do contemporary biologists differ from Darwin in their conception of natural selection?

### 3. Contemporary Accounts of Natural Selection

Lewontin's position on the relation between natural selection and the struggle for existence is representative of the vast majority of contemporary evolutionary theorists. On the one hand, Lewontin recognizes that the struggle for existence, as Darwin conceived of it, involves more than intraspecific competition for ecological resources. However, his further comments imply that a struggle for existence, no matter how broadly construed, is not necessary for the occurrence of evolution by natural selection. Consider the scenario he mentions: two strains of bacteria growing logarithmically in a medium containing an excess of nutrient. If the two strains have different division

<sup>19</sup>*Ibid.*, pp. 71–79.

<sup>20</sup>For a detailed reconstruction of Darwin's theory of natural selection, see M. Ruse, 'Natural Selection in *The Origin of Species*', *Studies in History and Philosophy of Science* 1, (1971), 311–351.

times, then the relative proportions of bacteria of the two strains will change over time: the strain that divides more quickly will comprise a progressively greater proportion of the bacteria in the medium. Clearly, there is no 'struggle' here: both strains are reproducing as quickly as they are able. Even so, Lewontin claims that this constitutes evolution by natural selection.

Darwin presumably knew little about the reproductive habits of bacteria. Nevertheless, it seems clear that this would not count as an instance of Darwinian natural selection. Although the relative frequency of the strain that divides more quickly is increasing in the population, the rate of reproduction of both strains is not limited by environmental factors; but Darwinian selection occurs only when there is some type of environmental check on population expansion producing differential survival and reproduction.

Why might one consider this to be, *contra* Darwin, an instance of evolution by natural selection? In Lewontin's case, the answer seems to be that he simply equates natural selection with any nonrandom process that results in differential reproduction of types within a population.<sup>21</sup> On this view, the struggle for existence is not a necessary condition for natural selection. The struggle for existence pertains instead to the process of adaptation: when natural selection occurs in conjunction with a struggle for existence (i.e. checks on population growth), one will find a trend toward better adaptation of organisms to their environment. Of course, one is free to stipulate definitions for theoretical terms such as 'natural selection', 'adaptation', and so forth. But as we will argue below, defining 'natural selection' as any nonrandom process that results in differential reproduction obscures an important difference between different causal processes that are relevant to understanding evolutionary change. Before turning to that, however, it is worth considering an account of natural selection which is closer to Darwin's than is Lewontin's, an account given by Robert Brandon.<sup>22</sup>

Brandon comes as close as any contemporary writer to incorporating the struggle for existence into the theory of natural selection; however, he ultimately falls short of doing so. Understanding why this is so will go a long way toward helping us to see why contemporary accounts of natural selection count cases such as the bacteria example as instances of natural selection and to understand what is lost in those accounts.

Consider the bacteria example again. In that example, one strain of bacteria has a shorter division time than the other and hence reproduces more rapidly.

<sup>21</sup>See, for example, R. C. Lewontin, 'Adaptation', *Scientific American* **239**, (1978), 213–230, see pp. 227–228. Here Lewontin seems to be maintaining that a number of different types of nonrandom yet nonadaptive evolutionary change (direct selective change, allometry, pleiotropy) are a result, directly or indirectly, of natural selection.

<sup>22</sup>R. N. Brandon, *Adaptation and Environment* (Princeton, NJ: Princeton University Press, 1990).

Because of the difference in division time, one might characterize the first strain as 'better adapted' than the second to their common environment, an environment which contains an excess of nutrients required by both. Now suppose that one understands natural selection to be any process that produces changes in genotypic (or phenotypic) frequencies, where those changes are due to differences in the relative adaptedness (also referred to as 'fitness differences') of the different genotypes (or phenotypes). If so, then natural selection is operating on the bacteria, since the increasing frequency of the first strain is owing to its being better adapted. This is, in somewhat crude form, Brandon's account of natural selection. Let us consider that account more carefully.

#### 4. Brandon on Adaptedness, Natural Selection and Evolution

According to Brandon, three conditions are necessary for evolution by natural selection:

- (1) *Variation*. There is variation in phenotypic traits among members of a population.
- (2) *Inheritance*. These traits are heritable to some degree, meaning that offspring are more like their parents with respect to these traits than they are like the population mean.
- (3) *Differential reproductive success*. Different variants leave different numbers of offspring in succeeding generations.<sup>23</sup>

The aim of Darwin's theory of natural selection, according to Brandon, is to explain Condition (3), differential reproductive success. It is here that Brandon explicitly mentions the struggle for existence: he says that the 'standard story' is that Darwin explained Condition (3) by pointing out that in the struggle for existence some organisms will be better adapted than others, and hence, will be more likely to survive and reproduce. Thus, differences in reproductive success are explained by differences in adaptedness.<sup>24</sup>

To understand Brandon's view of the relation between natural selection and the struggle for existence, it is helpful to quote him at length:

Now to return to our question: How does "the struggle for existence" or "the survival of the fittest" explain (3)? Condition (3) implies that actualized fitness is correlated with certain phenotypic traits. Why does this correlation exist? Why is there differential actualized fitness? Darwin's answer, which he arrived at after reading Malthus's *Essay on Population* (1798), was the following: since in each generation more individuals are produced than can survive to reproduce, there is a struggle for existence. In this "struggle" (which in its broadest sense is a struggle of the organism with its environment, not just with other individuals; see Darwin 1859,

<sup>23</sup>*Ibid.*, p. 7; see also R. C. Lewontin, *op. cit.*, note 21.

<sup>24</sup>*Ibid.*, p. 9ff.

p. 62) certain traits will render an organism better adapted to its environment than conspecifics with certain other traits. The better adapted individuals will tend to have greater reproductive success than the less well adapted. Why do some organisms have greater reproductive success than others? The Darwinian answer is this: they are (for the most part) better adapted to their environment.<sup>25</sup>

Clearly, Brandon recognizes that there is, at least historically, an important connection between natural selection and the struggle for existence.

Explanations of differential reproductive success (Condition (3) above) in terms of differential adaptedness are what Brandon calls 'natural-selectionist explanations'; such explanations presuppose the following 'explanatory principle' or 'law of nature', the *principle of natural selection*:

PNS: If *a* is better adapted than *b* in environment *E*, then (probably) *a* will have greater reproductive success than *b* in *E*.<sup>26</sup>

There are two points to notice about the PNS. First, the PNS does not explicitly mention the struggle for existence. Secondly, the PNS makes reference, not surprisingly, to the notion of adaptedness. More specifically, it is 'relative adaptedness', the adaptedness of one organism relative to another in a common environment, that does the work in explaining differential reproductive success. Is Darwin's struggle for existence incorporated into the PNS via the notion of relative adaptedness? To answer that, we need to consider Brandon's definitions of 'adaptedness' and 'relative adaptedness'.

The adaptedness of an organism is a function of the relation between that organism and its environment. Thus, the adaptedness of an organism can only be specified relative to a particular environment. Brandon defines 'adaptedness of organism *O* in environment *E*' in terms of the expected number of offspring of *O* in *E*.<sup>27</sup> Relative adaptedness is then defined as a relation between two organisms: one organism is better adapted than another in a common environment if and only if the expected number of offspring of the first is greater than that of the second.<sup>28</sup> What is important for our purposes is that the definition of 'relative adaptedness' is ultimately based solely on expected number of offspring and does not require that there be a struggle for existence. It does not appear, then, that Brandon has incorporated the struggle for existence into his definition of the PNS.

Another look at Lewontin's bacteria example will help to clarify further the relation between the struggle for existence and Brandon's PNS. Would the change in the proportions of the two bacteria types count as an instance of

<sup>25</sup>*Ibid.*, pp. 10–11.

<sup>26</sup>*Ibid.*, p. 11.

<sup>27</sup>See *ibid.*, p. 19.

<sup>28</sup>Brandon gives a more precise definition of 'relative adaptedness' in mathematical terms; see *ibid.*, pp. 17–20.



natural selection on Brandon's account, despite the absence of a struggle for existence? The increase in the relative frequency of the more rapidly reproducing strain could be attributed to differences in the adaptedness of the two strains: the expected number of offspring of the first strain is greater than that of the second in their common environment. Presumably, then, we could give a 'natural-selectionist' explanation of the differential reproductive success exhibited by the first strain. Thus, while Brandon sees that the struggle for existence was important for Darwin, the struggle is not explicitly incorporated into Brandon's account of natural selection. Consequently, although Lewontin's bacteria may not be a paradigmatic example of a population undergoing evolution by natural selection, Brandon's formulation of the PNS implies that it is an instance of natural selection at work.

### 5. *r*- and *K*-Selection

We have claimed that Lewontin and Brandon have neglected Darwin's notion of the struggle for existence in formulating their accounts of natural selection.<sup>29</sup> We wish to recommend a different strategy, namely Darwin's: restrict the concept of natural selection to what we refer to above as Darwinian selection.<sup>30</sup> If this strategy is adopted, then changes in genotypic (or phenotypic) frequencies in cases such as the bacteria example would not be instances of natural selection since there is no struggle for existence in those cases. In such cases, evolutionary change can be attributed to what we will call 'differences in reproductive fitness', rather than to Darwinian selection. However, before discussing how that distinction might be made more precise, it is worth considering whether or not some form of the distinction has in fact already been recognized by evolutionary biologists.

Population geneticists make a distinction between two kinds of selection (also called two 'selective strategies'): *r*-selection and *K*-selection.<sup>31</sup> This distinction was first made explicit by MacArthur and Wilson in their work on island biogeography.<sup>32</sup> *R*-selection is selection favoring an increase in the 'intrinsic

<sup>29</sup>We would argue that others have done so as well, including: T. Dobzhansky, *op. cit.*, note 1; J. Endler, *Natural Selection in the Wild* (Princeton, NJ: Princeton University Press, 1986); A. Rosenberg, *The Structure of Biological Science* (Cambridge, MA: Cambridge University Press, 1985); E. Sober, *op. cit.*, note 13; G. C. Williams, *op. cit.*, note 2. Ruse goes so far as to claim that natural selection is logically independent of the struggle for existence in the *Origin*. Ruse's claim depends on interpreting the struggle for existence as a 'zero-sum game', an interpretation that we do not accept; see M. Ruse, *op. cit.*, note 20.

<sup>30</sup>For an account of natural selection that appears to be closer to ours, insofar as it emphasizes the causal role of the environment in natural selection, see L. Darden and J. A. Cain, 'Selection Type Theories', *Philosophy of Science* 56 (1989), 106-129, see pp. 112-115.

<sup>31</sup>See, for example, E. Pianka, 'On *r*- and *K*-selection', *American Naturalist* 104, (1970), 592-597; J. M. Emlen, *Population Biology: The Coevolution of Population Dynamics and Behavior* (New York: Macmillan, 1984), pp. 316-317.

<sup>32</sup>R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton, NJ: Princeton University Press, 1967), p. 149.

rate of increase' ( $r$ ) of a population; it is said typically to occur when a population is significantly below the 'carrying capacity' ( $K$ ) of its environment.  $K$ -selection, on the other hand, favors an 'increasing efficiency of utilization of environmental resources' and typically occurs when a population is at or near the carrying capacity of its environment.<sup>33</sup>

At first glance, it might appear that the distinction between  $r$ -selection and  $K$ -selection mirrors our distinction between changes in relative genotypic (or phenotypic) frequencies due to differences in reproductive fitness and changes due to Darwinian selection. However, a closer inspection will show that this is not the case. Rather, we will argue that, as characterized by Pianka, the distinction between  $r$ -selection and  $K$ -selection embodies the confusion we want to eliminate.

According to Pianka,  $r$ - and  $K$ -selection are correlated with a host of factors, including differences in climate (variable vs. fairly constant), mortality (density-independent vs. density-dependent), population size (variable vs. fairly constant), degree of competition (lax vs. keen), and length of life of the organisms (short, less than one year vs. longer than one year).<sup>34</sup> The two kinds of selection are supposed to represent a 'continuum': 'no organism is completely " $r$ -selected" or completely " $K$ -selected," but all must reach some compromise between the two extremes'.<sup>35</sup> Furthermore, on the  $r$ - $K$  continuum, the ' $r$ -endpoint represents the quantitative extreme—a perfect ecologic vacuum, with no density effects and no competition'.<sup>36</sup>

It is this last point that leads to doubts about the similarity between the  $r$ -/ $K$ -selection distinction and the distinction between changes due to differences in reproductive fitness and changes due to Darwinian selection. Suppose that  $r$ - and  $K$ -selection are in fact different kinds of selection. If so, then in certain environmental conditions, genotypes (or phenotypes) within populations that reproduce in larger numbers than their cohorts will be favored ( $r$ -selection) and in other environmental conditions, genotypes (or phenotypes) that use resources more efficiently will be favored ( $K$ -selection). The two kinds of selection could then form a 'continuum' in the following way: if actual populations are never found in either 'pure'  $r$ -selective environments or 'pure'  $K$ -selective environments, as Pianka suggests, then both kinds of selection will always be operating. Consequently, organisms must reach some sort of 'compromise between the two extremes' and this will give rise to a continuum of overall selection pressure, from high  $r$ -/low  $K$ -selection to low  $r$ -/high

<sup>33</sup>E. Pianka, *op. cit.*, note 31, p. 593.

<sup>34</sup>*Ibid.*, p. 593.

<sup>35</sup>*Ibid.*, p. 592.

<sup>36</sup>*Ibid.*, p. 592.

*K*-selection. Pure *r*-selection and pure *K*-selection will serve as ideal endpoints of the continuum, even if neither ever actually obtains.

We have no serious objections to this characterization of *r*- and *K*-selection as two kinds of selection, as long as it is kept in mind that in both cases the environmental conditions act in some way to check unlimited population growth. However, a difficulty arises when we consider Pianka's claim that the '*r*-endpoint represents the quantitative extreme—a perfect ecologic vacuum, with no density effects and no competition'. If we now think of a pure *r*-selective environment as one in which there is 'a perfect ecologic vacuum' with 'no competition', then the bacteria described by Lewontin would seem to be in such a 'selective' environment. But if that is the case, then 'pure *r*-selection' characterizes a perfect absence of selection and hence could not be on a continuum with *K*-selection.

To sum up, if *r*- and *K*-selection do fall on a continuum, then both kinds of selection are distinct from what Lewontin wants to call 'selection' and both exemplify what we refer to as Darwinian selection. Distinguishing the two kinds of selection would then be useful in focusing attention on how different environmental conditions may have an effect on reproductive success. However, on this reading, the distinction between *r*- and *K*-selection is not equivalent to the distinction between changes due to differences in reproductive fitness and changes due to Darwinian selection.

On the other hand, if 'pure *r*-selection' is taken to occur under conditions in which the environment has no direct effect on reproduction and population growth, then 'pure *r*-selection' is not on the *r*-/*K*-selection continuum at all. In this case, 'pure *r*-selection' refers simply to changes due to differences in reproductive fitness. Understood in this way, the distinction between *r*- and *K*-selection appears to display the very ambiguity we wish to avoid, since it refers to cases of differences in reproductive fitness and cases of Darwinian selection indifferently as 'selection'.

## 6. Processes of Evolutionary Change

Virtually all contemporary evolutionary biologists recognize the need to distinguish alternative ways that evolutionary change might come about. Typically, two possibilities have been recognized: evolution by natural selection and evolution by genetic drift.<sup>37</sup> One way of thinking about these two possibilities is that the first refers to various nonrandom processes that produce evolutionary change and the second refers to a random process that produces evolutionary change. Lewontin, along with most other contemporary

<sup>37</sup>See, for example, R. N. Brandon, *op. cit.*, note 22, pp. 8–9; J. Endler, *op. cit.*, note 29, p. 5ff.

evolutionary biologists, wants to include both Darwinian selection and changes due to differences in reproductive fitness in the first alternative, evolution by natural selection. However, if one distinguishes Darwinian selection from the kinds of cases Lewontin mentions, then a threefold classification emerges:

- (1) *Darwinian selection*: Changes in genotypic (or phenotypic) frequencies<sup>38</sup> due to differential survival and reproduction of phenotypic variants better able to deal with environmental constraints.
- (2) *Changes due to differences in reproductive fitness*: Changes in genotypic (or phenotypic) frequencies due only to differences in intrinsic rates of reproduction among reproducing genotypes (or phenotypes).
- (3) *Genetic drift*: Changes in genotypic (or phenotypic) frequencies due to chance fixation and spread of variant genotypes (or phenotypes).

Thus, this classification captures a distinction between two sorts of causal processes, one a selection process, the other not, that can produce evolutionary change, rather than treating them as one in the manner of Lewontin and others. Is this just a 'semantic' issue, a disagreement over how to use the term 'natural selection'? We don't think so. There is an important difference between the two processes that can be seen by examining more carefully the causal role played by the environment in each case.

## 7. The Causal Role of the Environment

In standard cases of evolution by natural selection, where the growth of some population is checked by environmental factors and some variants are better able to survive and reproduce in the presence of those checks, the environment has an important effect on the reproductive success of the organisms in the population. That this is so is evidenced by the fact that if there were changes in the environmental factors checking population growth, either strengthening them or weakening them, the result would be changes in the reproductive success of the organisms in the population. In such cases, the environment has a 'direct effect' on the survival and reproduction of the members of the population.

In cases of evolution that are the result of differences in intrinsic reproductive rates, the environment does not affect the reproductive success of the organisms in the population in the same way. For example, in Lewontin's

<sup>38</sup>Genic selectionists would construe the relevant changes to be changes in gene frequencies; such a construal would not materially affect the distinction we wish to make here.

bacteria example, the concentration of the relevant nutrient in the growth medium might be varied without thereby affecting the reproductive success of the organisms in the population; as long as the concentration remains great enough for both strains to reproduce at their maximum rate, the environment will be causally neutral with respect to the relative reproductive success of the two strains. In such cases, the environment has an 'indirect effect' on the reproductive success of the members of the population, since it serves only as a stable causal background against which the different reproductive capacities of the organisms are realized.

If this distinction between the two causal roles played by the environment is sound, then it should be recognized at some level within evolutionary theory. This can be accomplished by distinguishing clearly between selective and nonselective (yet nonrandom) processes that can produce evolutionary change (i.e. by distinguishing between (1) and (2) above). We will pursue this suggestion in more detail in Section 8 below.

Would it be possible to accommodate this distinction within the context of a general account of the Darwinian theory of natural selection such as that given by Brandon? There are at least two ways of doing so. First, Brandon's PNS could be reformulated to read:

PNS\*: Under conditions in which there are checks on population growth, if  $a$  is better adapted than  $b$  in environment  $E$ , then (probably)  $a$  will have greater reproductive success than  $b$  in  $E$ .

In essence, the range of application of Brandon's PNS is simply being restricted. Of course, the notion of 'checks on population growth' will need to be made more precise, in the same way that Brandon needed to spell out the notion of  $a$  being better adapted than  $b$  in environment  $E$ . In particular, one would need to take into account such factors as: limited food supplies, climatic conditions, predator-prey relationships, etc.

Alternatively, one might focus on the definitions of 'adaptedness' and 'relative adaptedness'. For example, instead of defining 'the adaptedness of organism  $O$  in environment  $E$  in terms of the expected number of offspring of  $O$  in  $E$  for any specifiable  $E$ , we might place restrictions on the possible environments within which one can define the adaptedness of an organism. We might do so by restricting such definitions to those environments that have a 'direct effect' on the reproductive success of the organism in question, on the grounds that the notion of adaptedness only makes sense within an environment where the reproductive success of the organism is directly dependent on features of that environment.

There are two things worth noting here. First, both potential modifications of Brandon's account of the Darwinian theory of natural selection involve placing restrictions on the use of the notion of the environment in his

definitions. Secondly, modifying his account in either way would give rise to a less general theory of natural selection; we will return shortly to the notion of generality and its importance in evaluating our proposal.

### 8. Generality and Causal Processes

Before discussing some of the virtues of our proposal, it is worth considering why the distinction has not been clearly recognized. In Lewontin's case, one reason seems to be fairly clear: he wants to separate the process of evolution by natural selection from the process of adaptation.<sup>39</sup> For Lewontin, adaptations are the result of selection under conditions of a struggle for existence; but evolution by natural selection can occur without a struggle for existence and thus without giving rise to adaptations (or increasing the overall adaptedness of a population). Consequently, natural selection and the struggle for existence are separated.

Another possibility is that the use of mathematical models of selection in population genetics interferes with the recognition of this distinction. Mathematical models of selection typically begin with a model of a population in Hardy-Weinberg equilibrium and then introduce a selection parameter ( $s$ , also called the 'selection coefficient'), which is used to relativize the fitness values of the different genotypes to one another.<sup>40</sup> For example, in a model of a single-locus two-allele system exhibiting complete dominance, the fitness of the dominant homozygote and heterozygote is assigned a value of 1 and the fitness of the recessive homozygote is assigned a relative fitness of  $1-s$ . Thus, in models of selection in population genetics, the selection coefficient is simply a variable used to describe the changes in relative genotypic frequencies. More importantly, the same mathematical model can be used to describe changes due to Darwinian selection as well as changes due to different reproductive rates in the absence of environmental checks. But the fact that both types of change can be modelled in the same way does not imply that the causal factors underlying the changes are one and the same.

Brandon, on the other hand, does not want to separate the process of evolution by natural selection from the process of adaptation.<sup>41</sup> What he wants to do is to develop a general account of the Darwinian theory of natural selection.<sup>42</sup>

<sup>39</sup>See R. C. Lewontin, *op. cit.*, note 21, p. 227ff.

<sup>40</sup>See any standard textbook on population genetics, e.g. J. Roughgarden, *Theory of Population Genetics and Evolutionary Ecology: An Introduction* (New York: Macmillan, 1979).

<sup>41</sup>Quite the opposite; see R. N. Brandon, *op. cit.*, note 22, p. 39ff.

<sup>42</sup>Others have done so in somewhat different ways; see, for example, M. B. Williams, 'Deducing the Consequences of Evolution', *Journal of Theoretical Biology* 29, (1970, 343-385; A. Rosenberg, *op. cit.*, note 29; D. L. Hull, 'Individuality and Selection', *Annual Review of Ecology and Systematics* 11, (1980), 311-332.

In what sense has Brandon developed a general account of the Darwinian theory of natural selection? Earlier, we mentioned that most contemporary evolutionary theorists recognize two processes that can result in evolutionary change: natural selection and random genetic drift. If one takes these two processes to exhaust the possibilities, as Brandon apparently does,<sup>43</sup> then a general theory of natural selection must include all nonrandom causal processes that can produce evolutionary change.

One reason for developing a general theory is that it can lead to what Kitcher calls 'explanatory unification'.<sup>44</sup> Brandon in fact sees this as one of the virtues of his account: it enables one to give a 'selectionist-explanation' for a wide range of evolutionary phenomena. However, Brandon recognizes that one might also want what he calls a 'causal-mechanical' explanation, whereby one explains some phenomenon by describing the underlying causal mechanisms that have effected it. Furthermore, he thinks that these two approaches are components of an 'ideally complete' explanation. With respect to many evolutionary phenomena at least, that is true: where the underlying causal mechanisms are all of the same type, the two approaches are 'two sides of the same coin'.<sup>45</sup> For example, in standard cases of evolution by natural selection, where there is some environmental check on population growth, the interaction between organism and environment may differ in some particulars (e.g. the check might be limited food resources, predation, etc.) but always involves some direct effect of the environment on reproductive success. Thus, the underlying causes of evolutionary change are of the same type and a more specific description of those causes fills out the more general 'selectionist-explanation.' But where the underlying causal processes are of different types, then there are tradeoffs between these two explanatory ideals. An overly abstract theory may obscure differences between types of causal processes

<sup>43</sup>R. N. Brandon, *op. cit.*, note 22, pp. 8–9.

<sup>44</sup>See P. Kitcher, 'Explanatory Unification', *Philosophy of Science* 48, (1981), 507–531; P. Kitcher, 'Explanatory Unification and the Causal Structure of the World', in P. Kitcher and W. C. Salmon (eds), *Scientific Explanation* (Minneapolis: University of Minnesota Press, 1989), pp. 410–505. Explanatory unification was also an ideal in Darwin's original theory; see P. Kitcher, 'Darwin's Achievement', in N. Rescher (ed.), *Reason and Rationality in Natural Science* (Lanham, MD: University Press of America, 1985), pp. 127–189. For a discussion of Darwin's strategy as an application of *vera causa* reasoning, see M. J. S. Hodge, 'The Structure and Strategy of Darwin's "Long Argument"', *British Journal for the History of Science* 10, (1977), 237–246; M. J. S. Hodge, 'Darwin's Theory and Darwin's Argument', in M. Ruse (ed.), *What the Philosophy of Biology Is: Essays Dedicated to David Hull* (Dordrecht, Boston: Kluwer Academic Publishers, 1989), pp. 163–182; M. Ruse, 'Darwin's Debt to Philosophy: An Examination of the Influence of the Philosophical Ideas of John F. W. Herschel and William Whewell on the Development of Charles Darwin's Theory of Evolution', *Studies in History and Philosophy of Science* 6, (1977), 159–181.

<sup>45</sup>R. N. Brandon, *op. cit.* note 22, p. 159ff.

underlying evolutionary phenomena, differences that are relevant to a satisfactory explanation of those phenomena. On the other hand, if one distinguishes the types of causal processes underlying the phenomena and exploits these differences in giving explanations, it may no longer be clear whether the explanations fall within the domain of a single, general theory. To achieve such generality, one needs an account of why different causal processes should be treated as theoretically unifiable, rather than as demarcating distinct theoretical domains. Thus, generality is achieved only at a price and, in the case of the standard approach to natural selection, the price is a failure to recognize important differences between types of phenomena that need to be recognized if one is properly to understand those phenomena. We feel the price is too high.

### 9. Conclusion

It remains to point out certain virtues of our proposal. First, the theory of natural selection remains Darwinian in essence, incorporating Darwin's insight about the role of the environment in checking geometrical population expansion. Secondly, the use of the term 'selection' retains a close connection to its common meaning: selection involves discriminating between different types on the basis of some criterion (or set of criteria). In the case of Darwinian selection, the environment 'discriminates' between different phenotypes according to their ability to overcome the obstacles to survival and reproduction present in that environment.

Finally, the theory of evolution by natural selection will be given increased causal/biological content. Distinguishing between different ways in which the organism/environment interaction can have an effect on reproductive success gives the theory greater explanatory power. The notion of 'checks on population growth' remains fairly general; the variable, 'check', can take a limited variety of values in different applications, but it will always refer to an environmental factor able to differentially preserve or eliminate certain variations. In this respect at least, we aim to put Darwin back into the Darwinian theory of natural selection.

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