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An analysis of aspects of economic evolution based on Price's equation

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Abstract:
This paper tries to demonstrate that the well developed analysis of directional selection within evolutionary economics can be complemented by analyses of stabilizing selection and disruptive selection. It also tries to demonstrate that the evolutionary algebra provided by Price's equation increases the intellectual coherence and power of thinking about selection and other aspects of evolutionary processes. The paper combines these aims by analysing the types of selection by means of the algebra of evolution provided by Price's equation. To prepare for this task, the paper starts by reviewing recent discussions in relation to Price's equation. This review includes the presentation of framework for analysing evolution that then is used for the definition and analysis of directional, stabilizing and disruptive selection. These types of selection are then related to fitness functions that can produce the different types of selection; and the functions are used for simple simulations of the change of the population distribution of a quantitative characteristic. Finally, Price's equation is used to decompose the statistics of the changes of the frequency distributions. The changes of mean, variance, skewness and kurtosis are all decomposed as the sum of a selection effect and an intra-member effect. It is especially the signs of these effects that serve to define and characterize the different types of selection. Both this result and the general analysis of the types of selection seem to be of relevance for applied evolutionary economics.

Keywords: Evolutionary economics; Directional selection; Stabilizing selection; Disruptive selection; Fitness functions; Price's equation; Statistics of evolution; Higher moments; Simulation of selection

Jel Codes: C65; B52; O10

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1 Introduction

When Schumpeter (2000, p. 184) in the 1930s called for "a quantitative theory of evolution", he seems to have been unaware that it had already been provided by the great statistician and evolutionary biologist R. A. Fisher (1930). One reason for Schumpeter's neglect is that he emphasized the innovative part of the evolutionary process while Fisher emphasized selection. Another reason is that the large majority of biologists was also unaware of the path-breaking approach. Since Fisher was in many respects forty years ahead of his time, the biological recognition and development of some of his major contributions took place in parallel with the emergence of modern evolutionary economics. Actually, Nelson and Winter (1982, p. 243n) remarked that their formal statistical analysis of pure selection processes "reminded us of R. A. Fisher's 'fundamental theorem of natural selection': 'The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time' " (from Fisher 1930, p. 35). However, the result of Fisher as well as that of Nelson and Winter is most obviously relevant for the study of pure selection processes. It was instead George Price who developed a general decomposition of evolutionary change that includes the effect of mutation or innovation (see Frank 1995; 1998). For the statistics of any adequately defined population of members, Price proved that

$$\text{Total evolutionary change} = \text{Selection effect} + \text{Intra-member effect} \tag{1}$$

This is the verbal version of Price's equation. The selection effect can be interpreted as the intensity of selection times the variance of the population. The intra-member effect is more difficult to interpret, but in economic evolution it includes the consequences of learning and innovation within the members of the population. Biological evolution is characterized by intra-member effects that are many times smaller than the selection effects (Frank 2012a). In contrast, applications of decomposition techniques that are mathematically identical to Price's equation on productivity data show intra-firm effects that are significantly larger than the selection effects (Foster et al. 1998; Bartelsman et al. 2004; Andersson 2006; Holm 2011, ch. 3). This result is influenced by the problematic use of firms rather than individual routine activities as the units of selection. However, it probably also reflects that even the most narrowly defined intra-member effects in economic evolution are important. These effects seem to some extent to be the consequence of boundedly rational decisions that are influenced by higher-level selection pressures. Thus there seems to be both a direct and an indirect influence of selection. This suggests that the apparently discouraging result on the nature of economic evolution does not warrant an abandonment of Fisher's and Price's focus on the selection effect of equation (1).

The importance of Price's decomposition of evolutionary change has been difficult to understand, but during the last twenty years the situation has changed radically both in evolutionary biology (Frank 1998; Rice 2004) and in evolutionary economics. With respect to the latter, Metcalfe (2002, p. 90) pointed out that "[f]or some years now evolutionary economists have been using the Price equation without realising it." It may be added to Metcalfe's observation that formulations equivalent to Price's equation have also been used in productivity studies with few relations to evolutionary economics (e.g., Foster et al. 2002; Disney et al. 2003; Foster et al. 2008). In any case, we have arrived at a situation where the Fisher principle can be appreciated (Metcalfe 1994; Frank 1997) and where we can extend the application of Price's equation in many directions.

An obvious extension for the analysis of the problem of multi-level selection was already suggested by George Price (1972). If the population consists of groups that in turn consist of group members, then the selection effect of equation (1) can be interpreted as taking place between groups. The full analysis of this evolving system presupposes that, by the recursive use of Price's equation, the intra-group effect is interpreted as consisting of a selection effect between group members and an intra-member change effect (Okasha 2006; Bowles and Gintis 2011, pp. 218–222). This extension has greatly improved the description of the possible role of group selection in the emergence of collaborative behavior, but this description of course cannot replace modeling of the evolution of cooperation (van Veelen et al. 2012). Another extension of Price's equation concerns an analysis of the joint evolution of multiple characteristics that recognize that these characteristics often covary with each other (Rice 2004, pp. 194–203). Yet another extension confronts the fact that each member normally operates in multiple selection environments. The formal development of this case might extend the analysis of firms that are simultaneously selected in the product market, the labor market and the financial market, which Metcalfe's (1997) made without explicit application of the Price equation. Later, though, he contributed to the analysis of the coevolution of market shares across input and output markets by Price's equation (Metcalfe and Ramlogan 2006).

This paper, however, is concerned with what seem to be a more fundamental extension of the application of Price's equation that has been suggested by evolutionary biologists. This extension serves to confront the limitations of the paradigm of directional evolution that evolutionary economists have derived from their basic models of evolution. From Nelson and Winter (1982) and onward, economic evolution has implicitly been defined as the change of the mean of an evolutionarily relevant characteristic of a population of firms. Evolution moves this mean in a particular direction; and when the mean does not change any more, evolution has come to a halt. This interpretation has been supported by the "Fisher principle" (Metcalfe 1994) of the distance from mean dynamics (or replicator dynamics) of a population of firms with different characteristics. Here positive directional selection can in principle always proceed, but the emergence of positive outliers is crucial. The movement of the mean characteristic is made by decreasing the variance. Thus evolution consumes its fuel; and it comes to a halt unless new variance is supplied by innovation or mutation. Evolution can also fade out if the intensity of selection moves towards zero. Thus the paradigm of directional evolution is supported by a clear principle. Furthermore, it has been formalized by many well-developed models (Nelson and Winter 1982; Metcalfe 1998; and beyond). Finally, the popularity of the paradigm is related to the (over)emphasis on productivity change within evolutionary economics. It is normally recognized that what evolves in a population of firms is ultimately a series of underlying characteristics rather than the firm-level productivities. But it is seldom recognized explicitly that these characteristics are not likely to progress in the same trendlike manner as the aggregative phenomenon of productivity. Even "evolutionary arms races" (Dawkins and Krebs 1979) cannot go on forever.

Although some concrete characteristics, during limited periods, will display a progressive evolutionary trend as depicted by the paradigm of directional evolution, we also observe two other types of evolution. On the one hand, there is stabilizing evolution that tends to remove any change away from the favored value of a characteristic. On the other hand, there are cases of disruptive evolution that in the end might split a population of firms into two separate populations. This should be obvious for any evolutionary biologist (Futuyma 2005, pp. 304–305, 345–350). Thus any biological analysis of natural selection would not be complete without considering the possibilities of directional, stabilizing and disruptive selection. Since the underlying genetics is normally unknown or complex, such analyses normally play the "phenotypic gambit" (Grafen 1984), that is, they study the change of directly observable characteristics. In the analysis of economic evolution, it is easier to apply the methods of this phenotypic approach than the methods of the traditional genotypic approach. But there are still difficult-to-detect assumptions that are not useful in economic contexts – such as the normality of population distributions and the randomness of mutations. It is, therefore, very helpful to analyze the different modes of selection within the totally general framework of Price's equation (Rice 2004, pp. 174–178). This seems the most obvious way of overcoming the one-sided paradigm of directional evolution within theoretical and applied evolutionary economics.

This paper proceeds in the following way. The next section reviews recent discussions in relation to Price's equation and presents the related framework for analyzing evolution. Section 3 uses the framework for the definition and analysis of directional, stabilizing and disruptive selection. Section 4 presents fitness functions that can produce the different types of selection. These functions are used for simple simulations of the change of the population distribution of a quantitative characteristic. Section 5 uses Price's equation to decompose the changes of mean, variance, skewness and kurtosis that are produced by the different fitness functions. It is especially the signs of the selection effects and the intra-member effect effects that serve to characterize the different types of fitness functions.

2 Price's equation and its critics

Although many presentations of Price's equation (1) are available (including Andersen 2004; Knudsen 2004), this paper presents and discusses the equation before we in the next section use it for the analysis of directional, stabilizing and disruptive evolution and selection. One reason is that the increased general use of the Price equation has led to misunderstandings and criticisms. Several criticisms have recently been summarized by van Veelen et al. (2012) and countered by Frank (2012b). We integrate a selective survey of this discussion in the following presentation of the equation. More importantly, our account for the equation may serve as an introduction to directional selection. In addition, we introduce core concepts and mathematical notation (see table 1).

Generality: In relation to an analysis of the different types of evolution, a major criticism of Price's equation (1) appears to be that it defines "total evolutionary change" as the change of the mean characteristic of a population. Thereby it per definition excludes processes that cannot be described as having a (positive or negative) direction. This apparently means that the idea of stabilizing evolution is a contradiction in terms. However, this conclusion underestimates the generality of Price's equation. It can also – as demonstrated in section 3 – be used for the analysis of an evolutionary process in which the population is brought closer to its mean by removing the outliers in a way that reduces population variance. Nevertheless, a limited interpretation of Price's equation serves to support the directional paradigm of evolutionary economics.

Importance of identities: Price's equation has been criticized for being a tautology (Nowak and Highfield 2011, pp. 100–101; van Veelen et al. 2012). But the status as a fruitful mathematical tautology is actually the main strength of the equation. Economists are accustomed to similarly tautological rewrites. For instance, any microeconomics textbook will explain how the Slutsky equation (or the Slutsky identity) serves to deepen our understanding and ease statistical analysis of the change in the demanded quantity due to a price change. The Slutsky equation does so by decomposing the change of quantity into a substitution effect and an income effect.

Since evolution is much harder to grasp than economic price changes, the services provided by Price's equation (or Price's identity) are potentially much larger than those of the Slutsky equation. Price's equation deepens our understanding and eases statistical analysis by rewriting any evolutionary change as the sum of a selection effect and an intra-member effect. Thereby, the equation has become an important part of the analytical toolbox of many evolutionary biologists and some evolutionary economists. But, like any other complex scientific tool, its use requires careful thinking.

Two censuses: Evolution is a population-level process in historical time. Price's equation allows an arbitrary specification of the population. Thus we are not restricted to analyse a population of firms. We can, for instance, analyse a population of regions, but the interpretation of the results becomes difficult unless we have a theory of the evolution of this type of population. Price's equation analyses the evolution of the population by means of data from two population censuses. We could have called them the pre-evolution census and the pre-evolution census. However, we will not use these terms since Price's equation normally focuses on selection. The first census takes place at time t and can be called the pre-selection census of the pre-selection population P. The second census at time t' can be called the post-selection census of the post-selection population P$'$. There are no constraints on the choice of t and t', but a relatively short time span seems preferable because the environment of the population as well as the evolutionary mechanism are subject to change.

It was probably not least the assumption of having two censuses that led Price (1972, p. 485) to emphasize that his equation is "intended mainly for use in deriving general relations and constructing theories, and to clarify understanding of selection phenomena, rather than for numerical calculation". This is still true. Nevertheless, the conditions for making numerical calculations have radically improved since Price's equation was formulated. We now have census data of several biological populations and some economic systems.

Mapping between P *and* P$'$: Price (1995) emphasized the necessity and difficulty of coupling the members of P and P$'$. If we consider a particular pre-selection population member indexed i, then all related members of P$'$ should also be indexed by i. In the case of firm i of P, the i-indexed representatives in P$'$ might be itself and its spin-offs. And a merged firm can be split in proportion to the initial sizes of firm i and firm j. Thus the evolutionary concept of a "member" of the post-selection population needed for the application of Price's equation is not always that of the same firm in the next period.

Firms that enter the population from the outside or are created from scratch cannot be included in the described mapping procedure – and thus need separate treatment. This treatment has been provided by Kerr and Godfrey-Smith (2009) for the case of the biological species of an ecosystem. But the solution is really quite straightforward. We

Table 1: Core variables of Price's analytical framework

Variable	Definition	Interpretation
x_i		Size of member i in pre-selection census
s_i	$x_i/\sum_i x_i$	Population share of i in pre-selection census
x_i'		Size of member i in post-selection census
s_i'	$x_i'/\sum_i x_i'$	Population share of i in post-selection census
w_i	x_i'/x_i	Absolute fitness of i
$\overline{w}$	$\sum_i x_i'/\sum_i x_i$	Mean absolute fitness
ω_i	$w_i/\overline{w} \quad (= s_i'/s_i)$	Relative fitness of i
z_i		Characteristic of member i in pre-selection census
$\overline{z}$	$\sum_i s_i z_i$	Weighted mean of z in pre-selection census
$Var(z)$	$\sum_i s_i(z_i - \overline{z})^2$	Weighted variance of z in pre-selection census
z_i'		Characteristic of member i in post-selection census
Δz_i	$z_i' - z_i$	Change in characteristic of i
$\overline{z}'$	$\sum_i s_i' z_i'$	Weighted mean of z in post-selection census
$\Delta\overline{z}$	$\overline{z}' - \overline{z}$	Change in $\overline{z}$
$Cov(w,z)$	$\sum_i s_i(w_i - \overline{w})(z_i - \overline{z})$	Weighted covariance of w_i and z_i
$\beta_{w,z}$	$Cov(w,z)/Var(z)$	Slope of simple regression of w_i on z_i
$\beta_{z',z}$	$Cov(z',z)/Var(z)$	Slope of simple regression of z' on z_i
$E(w\Delta z)$	$\sum_i s_i w_i \Delta z_i$	Expectation of $w_i \Delta z_i$

simply add an entry effect in Price's equation (1). For reasons of symmetry we may also add the exit effect:

$$\text{Evolutionary change} = \text{Entry effect} + \text{Exit effect} + \text{Selection effect} + \text{Intra-member effect}$$

Data and calculations: We now come to the data that need to be collected by the pre-selection census at time t and the post-selection census at time t' – as well as the statistical variables that we calculate from these data (see table 1). Let us briefly consider fitnesses and characteristics as well as the covariance between fitness and characteristic.

The data of the first census includes the size of each pre-population member x_i. From the data of the second census we calculate the size of each member of the post-population x_i'. Then we for all i-indexed members of the two populations calculate the population shares s_i and s_i' (in each population summing to unity). We also calculate the member's absolute fitness $w_i = x_i'/x_i$ and the population's mean fitness $\overline{w} = \sum s_i w_i$. The member's relative fitness (often called fitness) is obtained by dividing absolute fitness by the mean absolute fitness of the population: $\omega_i = w_i/\overline{w}$. Thus the mean of relative fitness $\overline{\omega} = 1$.

For each member i, the census data provide us with information on the quantitative characteristic whose evolution we want to analyse. We can study the evolution of *any* quantitative characteristic, including mathematical transformations of the data of the population. In any case, let these values of the characteristic be z_i and z_i'. The fact that members of economically relevant populations are often of very different sizes emphasizes the need of using the weighted mean characteristic $\overline{z}$ in the analysis. Price's equation decomposes the change of the weighted mean characteristic of the population $\Delta\bar{z}$. This change can come from the aggregate effect of intra-member change of characteristic Δz_i. But it can also be the result of the different fitnesses of members with different characteristics. Crucial for the latter effect is the pre-selection population variance of the characteristic $Var(z)$.

The core part of Price's partitioning of $\Delta\bar{z}$ is the statistical relationship between member fitnesses and their characteristics. Let us assume that we operate in terms of absolute fitnesses w_i. The data of the two censuses can be used to calculate $Cov(w,z)$, that is, the weighted covariance of w_i and z_i. This covariance can be interpreted as the part of evolutionary change that is caused by selection. The interpretation can be helped by the rewrite $Cov(w,z) = \beta_{w,z}Var(z)$. Here variance provides the fuel for selection while the regression coefficient is a measure of the intensity with which selection exploits this fuel. It has surprisingly been argued (van Veelen et al. 2012) that we are not facing a real covariance because of lacking explicit foundations in statistics and probability theory. But Price's equation relates to a solid expression of covariance that has deep roots the history of the biological analysis of natural selection – in the course of which even the notion of covariance was invented.

Price's equation with absolute fitness: We are now ready to consider the formally provable specification of Price's equation that was informally presented in equation (1). Since the proof of the equation is widely available (e.g., Frank 2012b), the problem is rather to recognize its different versions. Let us start with the standard version in terms of absolute fitnesses w_i:

$$\overset{\text{Total change}}{\Delta\bar{z}} = \overset{\text{Selection effect}}{\frac{Cov(w,z)}{\overline{w}}} + \overset{\text{Intra-member effect}}{\frac{E(w\Delta z)}{\overline{w}}} = \frac{\beta_{w,z}Var(z)}{\overline{w}} + \frac{E(w\Delta z)}{\overline{w}} \tag{2}$$

The left-hand side of this equation is the change of the mean characteristic of the population. The first version of the right-hand side has two terms that both have the mean absolute fitness (i.e., the reproduction coefficient of the population) in the denominator. However, the selection effect is basically expressed as the covariance between absolute fitness and characteristic. This covariance can be rewritten as the product of the selection intensity $\beta_{w,z}$ and the variance $Var(z)$. There will be no selection effect if either $\beta_{w,z} = 0$ or $Var(z) = 0$. For a given $Var(z) > 0$, the size of the effect depends on the slope of the linear regression line. The intra-member effect is more difficult to interpret because the change of characteristic within each member is multiplied by its absolute fitness. In any case, it disappears if $\Delta z_i = 0$ for all members of the population.

We obtain the version of Price's equation that George Price (1972) preferred by moving the mean absolute fitness of equation (2) to its left-hand side:

$$\overline{w}\Delta\bar{z} = Cov(w,z) + E(w\Delta z)$$

Now the left-hand side is identical to the argument of the right-hand expectation operator $E(w\Delta z)$. Since we can use Price's equation on any quantitative measure of a population, we might also be able to use it for the further partitioning of $w_i\Delta z_i$. The only precondition is that each subpopulation of the analysed population have the property that w_i and z_i are themselves averages. In that case, Price's equation can be used recursively on itself. This feature makes it useful for the analysis of group selection and other types of multi-level selection. Here we end up with a decomposition of total evolutionary change into an inter-group selection effect, an intra-group selection effect, and an intra-group-member change effect (Frank 2012a).

Price's equation with relative fitness: The absolute fitnesses of equation (2) can easily be changed to the relative fitnesses (since $\omega_i = w_i/\overline{w}$):

$$\Delta\bar{z} = Cov(\omega, z) + E(\omega\Delta z) = \beta_{\omega,z} Var(z) + E(\omega\Delta z) \tag{3}$$

This version of Price's equation focuses squarely on the core issue of the analysis of evolutionary processes. The primary issue of evolutionary analysis is not the aggregate growth of the population but its structural change due to the differential growth of members with different values of the characteristic. Nevertheless, we cannot always use the effective and elegant equation (3). The reason is that population-level growth does matter for many types of evolutionary problems.

By deviating a little from Price's equation (3), it is possible to arrive at an identity that interprets the transmission bias as the pure effect of intra-member change (Heywood 2005; Okasha 2006):

$$\Delta\bar{z} = Cov(\omega, z') + E(\Delta z) = \beta_{z',z}\beta_{w,z} Var(z) + E(\Delta z) + \overset{\text{Residual term}}{Cov(\omega, \text{error})}$$

In this version of Price's equation the intra-member change is measured without fitness weights. It is the version preferred by Okasha (2006, p. 27) because it isolates the effect of fitness to the first term and thus provides a "causal decomposition" of the evolutionary process. But this also implies that the first term of the decomposition has lost its interpretation as the simple selection effect. However, if $Cov(\omega, error) = 0$, then

$$\Delta\bar{z} = \overset{\text{Change due to selection}}{\overset{\text{Fidelity}}{\beta_{z',z}} \times \overset{\text{Intensity}}{\beta_{w,z}} \times \overset{\text{Variance}}{Var(z)}} + \overset{\text{Transmission bias}}{E(\Delta z)}$$

Here $\beta_{z',z}$ can be interpreted as the degree of fidelity with which members of P' have replicated the characteristics of the corresponding members of P. This regression serves as a correction of the normal selection effect. It also serves to draw attention to the third of the three conditions for a long-term evolutionary process: variance, novelty, and replication. Thereby, this version of Price's equation helps us focusing on a core question on the research agenda of evolutionary economics. The question is whether and in which sense the fidelity of replication in different parts of economic life is sufficiently strong for generating what can be analysed as evolutionary processes. However, this important question cannot be discussed in the present paper.

Inductive and predictive uses: Now that we know which data are needed and some versions of Price's equation, it is possible to reflect on reasons for the enthusiasm and harsh criticism that are expressed, respectively, by Rice (2004) and van Veelen et al. (2012). One basic reason for the opposing views is implicit in the above presentation of the equation. It is whether the researcher is really interested in making inferences about what can be called the evolutionary transformation mechanism T. This mechanism works on the pre-selection population P to bring forth the transformed population P'. It can most easily be studied within a given state of the environment $\mathtt{R}$. We try to obtain this analytical situation by analysing relatively short periods and by correcting for the remaining environmental change. For instance, we assume that it is possible to avoid including the effect of density-dependent selection. In the given environment, $(\mathtt{P};\mathtt{R}) \xrightarrow{\mathrm{T}} (\mathrm{P}';\mathtt{R})$. Our two censuses of the population mean that we know P and P′ and can use this knowledge in the search for the T. For instance, we may ask whether we are facing directional, stabilizing or disruptive evolution.

Many researchers are more interested in the very different analytical situation in which we know P and T and want to make predictions about P′. This is, in principle, what model builders are doing. Although modellers like Page and Nowak (2002) have proven that replicator dynamics and Price's equation are, in many cases, equivalent, they also quickly recognize the "dynamic insufficiency" of the latter equation (van Veelen et al. 2012). The reason is that the $Cov(w,z)$ of Price's equation is a description of selection between t and t' and not necessarily a prediction of what will happen at time $t'', t''', \ldots$ Those interested in making predictions instead assume the existence of a permanent transformation mechanism. Replicator dynamics is an example of a deterministic fitness function that based on P iteratively can produce the subsequent populations. Many other fitness functions have been defined. While these functions can obviously be used for making predictions, they are also useful when the task is to make inferences about the transformation mechanism. We illustrate this usefulness of fitness functions in sections 4 and 5 of this paper.

From the viewpoint of inductions about T, the fact that Price's equation is descriptive and thus does not assume the permanency of fitness functions is not an error but an important feature. This permanency can seldom be assumed because the environment and the fitness function are subject to significant change. Furthermore, evolutionary economists do not yet have a theory about T that is sufficiently developed to allow quantitative predictions about P′. Therefore, we presently have to emphasize studies that provide an understanding of the mechanism of evolutionary transformation. In this respect, our situation is somewhat similar to that of many biological studies of natural selection under natural conditions. In both cases, much important research starts from general descriptions of evolutionary processes and then derives their basic mathematical properties, not least by means of statistical concepts. Thus these concepts are not treated as estimates like in ordinary statistics; they are instead representing what matters when analysing evolutionary dynamics. But they can be used in the analysis of the evolutionary change of real-life populations.

3 Three types of selection

When working with Price's equation it is tempting to define evolution solely as the change of the mean value of a directly observable characteristic of a population. This gives no problems as long as we work within the directional paradigm of evolutionary economics. But the consequence of the definition is that we exclude the pure forms of stabilizing and disruptive evolution that do not change the population mean. It is hardly useful to apply a concept of evolution that excludes the processes that keep a population near a local optimum or that bring forth the coexistence of population members with very different behaviours and characteristic values. To include these types of change we need to define evolution as *any* change of the frequency distribution of a characteristic of a population.

Evolution and pure selection: The change of the frequency distribution is the outcome of the combined effects of selection and intra-member change. The primary reason why this combination is so important in economic evolution is that the two effects here often work in the same direction. The intra-member change is not the outcome of random

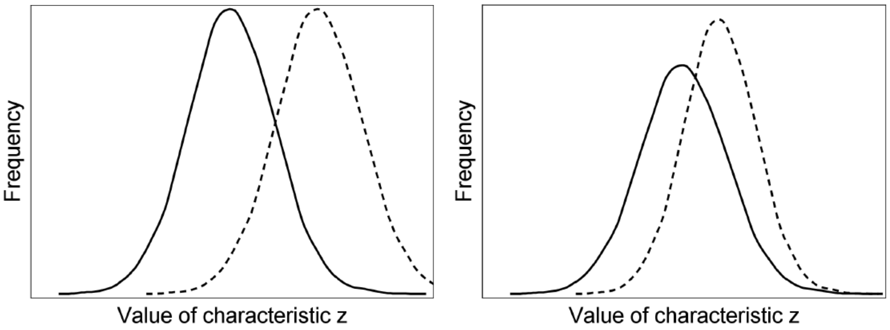

Figure 1: Pure directional selection and the effect of a directional fitness function. The left panel depicts the concept of directional selection by leaving the variance unchanged. The right panel depicts the effect of a directional fitness function such as that of replicator dynamics, where $\Delta z_i = 0$.

mutations, but of the efforts of boundedly rational firms and individuals. The recognition of this fact might give the analysis of economic evolution a "Lamarckian" flavour (Nelson and Winter 1982, p. 11). In any case, the intra-member change effect can often be interpreted as reflecting reactions to the selection pressure. This is the reason why the two effects often work in the same direction. In other words, selection produces not only the selection effect on the characteristics of the initial population; it also produces parts of the reactions that lead to the intra-member effect between the two censuses. This important problem, however, is beyond the scope of the present paper. Here we will instead focus on the ordinary selection effect.

Directional selection: The most obvious way of changing the frequency distribution is through directional selection. Two ways of approaching directional selection are illustrated by figure 1. In both panels, the pre-selection frequency distribution is to the left and the post-selection distribution is to the right. The left panel moves the frequency distribution such that the mean increases while the variance is left unchanged. Thereby it in the simplest possible way illustrates the definition of directional selection as the change of the mean characteristic (here in the positive direction). In contrast, the right panel illustrates the effect of a directional fitness function that influences both the mean and the variance of the distribution. Evolutionary economists are likely to know that replicator dynamics can lead to the change of the population distribution depicted in the right panel. This distance-from-mean dynamics implies that members with higher than mean value of the characteristic will have high relative fitness while those with low values will have lower fitness. The consequence is that the mean of the distribution increases while its variance decreases.

The movement in the left panel of figure 1 is harder to understand in terms of the underlying transformation mechanism. But the fact that the post-selection population includes member characteristics that were not present in the pre-selection population makes clear that some sort of innovation has taken place. However, such considerations are unwarranted. We are simply facing the concept of directional selection that represents an aspect of the evolutionary process that can be combined with stabilizing selection or other types of selection (Endler 1986; Rice 2004). This possibility is left open if we define directional selection in terms of $\Delta\bar{z} = \bar{z}' - \bar{z}$. If $\Delta\bar{z} = 0$, there cannot be directional selection. If $\Delta\bar{z} \neq 0$, we use the covariance term in equation (3) to determine whether this is due to directional selection. If $Cov(\omega, z) > 0$ we observe positive directional selection. If $Cov(\omega, z) < 0$, we have negative directional selection.

The Chicago approach: Although we have used Price's equation to define directional selection, this idea can be traced back to the Chicago school approach to phenotypic evolution (Lande and Arnold 1983; Conner and Hartl 2004, ch. 6). This approach can be expressed in relation to Price's equation (Rice 2004). Thus it emphasizes the variance of the characteristics of the population, covariance between characteristics and the reproduction of members, and the intertemporal inertia of the characteristics. By focusing on these requirements for phenotypic evolution rather than on the direct study of genetic evolution, this approach has been very successful for studying "natural selection in the wild" (Endler 1986; Brodie et al. 1995; Kingsolver et al. 2001; Conner and Hartl 2004, ch. 6; Kingsolver et al. 2001; Kingsolver and Pfennig 2007).

Estimating the types of selection: The Chicago approach provides a simple way of detecting the relative importance of directional selection and variance selection. This importance is estimated by multiple regressions for a large number of populations. The task is simply to estimate the relative fitness $Y_i = \omega_i = w_i/\overline{w}$ as the result of the additive effects of a linear term and a nonlinear term. The linear term is $X_1 = z_i$ and the nonlinear term is $X_2 = (z_i - \overline{z})^2$. Thus the multiple regression equation is

$$Y = a + b_1 X_1 + b_2 X_2 + \text{error} \tag{4}$$

where b_1 estimates the effect of directional selection and b_2 estimates the effect of variance selection. If b_1 is different from zero, there is directional selection. If b_2 is negative, we observe stabilizing selection. If b_2 is positive, we have disruptive selection. The two latter types of selection are often combined under the heading of variance selection (Endler 1986). We often see that variance selection coexists with directional selection. Although the formalism of equation (4) is simple, the production of studies that applies it is by no means easy. Nevertheless, the development of evolutionary economics would benefit significantly from a large number of such studies and their use for the evaluation of the relative importance of directional selection, stabilizing selection, and disruptive selection.

Defining the types of selection: Although the Chicago approach is empirically oriented, its definitions of the types of selection are what matters in the present context (Rice 2004, p. 176). The definitions can be expressed on terms of covariances or of the regression coefficients of equation (4)

- Directional selection involves a change of the mean of the frequency distribution that is explained by the covariance $Cov(\omega, z) = \beta_{\omega,z} Var(z)$. Directional selection is a nonzero linear regression of fitness on the characteristic. If $\beta_{\omega,z} > 0$, we have positive directional selection. If $\beta_{\omega,z} < 0$, we have negative directional selection.
- Stabilizing selection is a negative change of the variance of the frequency distribution produced by a negative $\beta_{\omega,(z-\overline{z})^2}$. This implies that $Cov(\omega, (z-\overline{z})^2) < 0$.
- Disruptive selection is a positive change of the variance of the frequency distribution produced by a positive $\beta_{\omega,(z-\overline{z})^2}$. This implies that $Cov(\omega, (z-\overline{z})^2) > 0$.

Directional selection is defined independently of the two other types of selection. This means that directional selection can coexist with stabilizing selection or disruptional selection.

Stabilizing selection and directional selection: Fisher (1930) started his famous book by stating that "Natural Selection is not Evolution." Here he referred to the pure directional selection. His statement emphasized that biological selection can not only cause directional change but also bring this type of change to a halt at a fitness peak. Here stabilizing selection serves to weed out mutants that do not have the locally optimal value of the characteristic. If mutations tend to push the population in a particular direction, then stabilizing selection has to be sufficiently strong to keep $\Delta\bar{z} = 0$. In terms of Price's equation (3), the balancing condition is that $Cov(\omega, z) = -E(\omega\Delta z)$. However, this is not the only way stabilizing selection can keep the population near the characteristic with maximum fitness (Frank 2012a). Since biological mutations are random, they normally increase the variance of the characteristic around the fitness peak. To avoid evolutionary chaos, stabilizing selection has to be sufficiently strong to counter this increase of variance.

Stabilizing selection represents one of the two types of variance selection (Endler 1986). In general, variance selection is defined in terms of $\Delta Var(z) = Var(z') - Var(z)$. If $\Delta Var(z) = 0$, there is no variance selection. If $\Delta Var(z) < 0$, we observe stabilizing selection. If $\Delta Var(z) > 0$, we have disruptive selection. Disruptive selection implies that pre-selection population members with extreme values of the characteristic are favoured over those with values closer to the mean. Thereby it creates a frequency distribution with two (or more) humps. In other words, two (or more) values of the same characteristic can coexist in the population.

Comparing types of selection: We have now defined directional selection in terms of the change of the mean of the frequency distribution. Similarly, we have defined stabilizing selection as the process that decreases the variance of the distribution and disruptive selection as the process that increases the variance. These definitions mean that directional selection can work together with one of the two types of variance selection. But the definitions also allow comparison between the pure types of selection. This comparison is provided by figure 2. The upper panel depicts the frequency distribution of the pre-selection population. The lower panels repeat this distribution and add the post-selection distributions. The left lower panel repeats the case of pure directional selection of figure 1. As already mentioned, it depicts a selection process in which only the mean characteristic is changing. The two other lower panels keep the mean unchanged while the variance changes. In the case of stabilizing selection the variance decreases. The variance increases with a process of disruptive selection.

Combining the types of selection: We have already noted that the directional fitness function of replicator dynamics combines directional selection with stabilizing selection. More general issues of combination can be discussed concisely if we *assume* the existence of a nonlinear fitness function for the population (Endler 1986). The upward sloping part of the function of figure 3 represents predominantly positive directional selection. Furthermore, the part of the curve around the maximum represents stabilizing selection and the downward sloping part represents negative directional selection. The effect of this function depends on the composition of the pre-selection population. The population largely faces positive directional selection if its characteristics are placed between the left dashed line and the middle dashed line. We have stabilizing selection if the population is between the middle and the right dashed line. However, the population obviously faces a mix of directional and stabilizing selection if it is placed between the two dotted lines.

We encounter similar issues if the fitness function of figure 3 is changed to including a U-shape. However, polarization cannot go on forever. Therefore, the assumed function would have to include downward bends at each of the extreme values. Assuming that the fitness function is stable, the ultimate result of this disruptive selection will be two

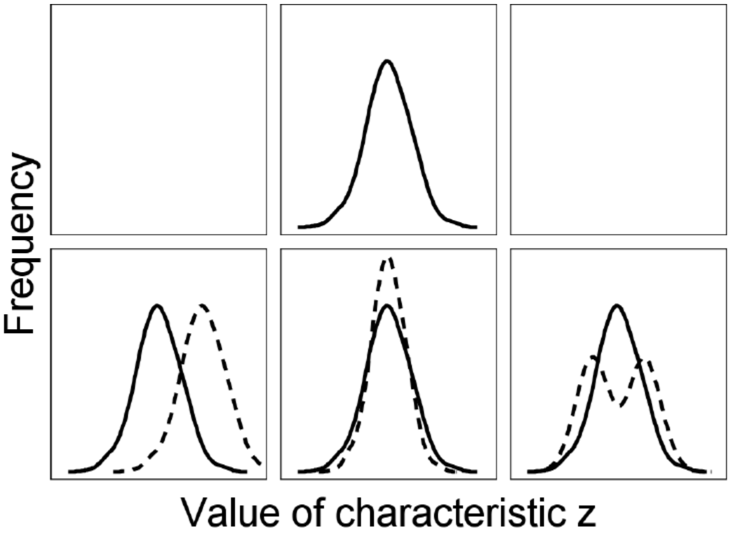

Figure 2: The three pure types of selection. The upper panel depicts the initial frequency distribution. The lower panels depicts the results of different types of selection by repeating the initial distribution and (with dashed curves) presenting the post-selection distributions. Left panel: pure directional selection. Middle panel: pure stabilizing selection. Right panel: pure disruptive selection.

separate subpopulations that are both facing stabilizing selection.

Two-dimensional fitness function: Although this paper concentrates on the evolution of a single characteristic, it is helpful to consider how we can represent a two-dimensional fitness function graphically. This is not difficult for students of microeconomics. We start by constructing a two-dimensional space of characteristics. Each point in this space represents a potential location of a member of the pre-selection population. This member has the value z_i^1 of characteristic 1 and z_i^2 of characteristic 2. Then we (perhaps based on estimates) assume the fitness level that corresponds to each point in the two-dimensional space of characteristics. The result is a fitness surface. Figure 4 depicts this surface as isofitness curves in the space of characteristics. These curves represent selection as working on the combined effect of the two characteristics; and the fitness maximum is marked by $+$. Fitness increases when we move from origo toward the fitness maximum; but it decreases when we continue from the maximum towards the upper right corner.

Figure 4 allows us to understand some of the complexities of selection in a two-dimensional space of characteristics. Let us assume that the fitness maximum originally was placed in the middle of the gray area. Furthermore, we assume that the population has moved to this area, where it has been subject to stabilizing selection with respect to both of its characteristics. However, fitness surfaces are not stable. If they appear to be so, the reason is probably that they often move back and forth so that some of them from a longer-term perspective can appear to be fixed. Populations are thus facing the Sisyphus work of performing lagged adaptations to ever-changing selection pressures. The problem for the population in figure 4 is that the isofitness curves has moved so that the new maximum is the peak marked by $+$ while the heterogeneous population is represented by the gray area. While this population was relatively well adapted to a previous situation, it has become maladapted because the isofitness curves have moved. The gray pre-selection population is still subject to stabilizing selection with respect the second characteristic. But in the new situation it

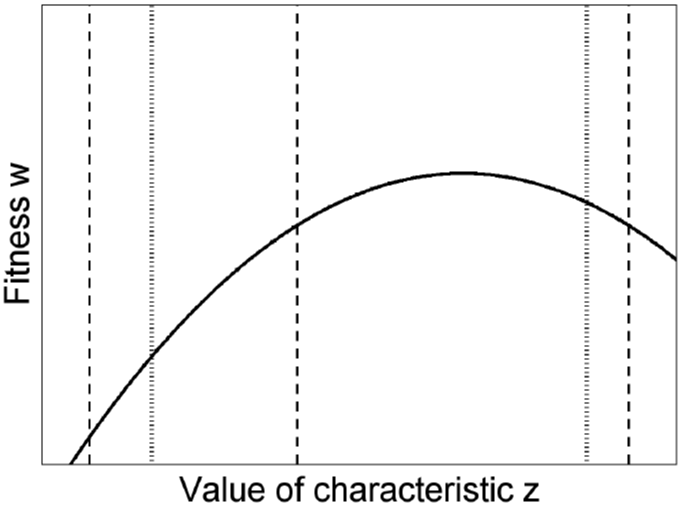

Figure 3: The population composition and the type of selection. The curve depicts a non-linear fitness function. We have directional selection if the population is placed between the first two dashed lines and stabilizing selection between the middle and the left dashed line. If the population is placed between the dotted lines, we have mixed selection pressures.

confronts a combination of directional and stabilizing selection with respect to the first characteristic.

Further discussion of the fascinating topic of two-dimensional fitness surfaces is beyond the limits of this paper. But it should be noted that although we to some extent relate to Sewall Wright's (1932) famous formalization of selection in terms of "fitness landscapes", the two concepts are not exactly the same. While each point in Sewall Wright's landscapes in principle represents the analysed mean of a small and localized population, the fitness function surfaces of the Chicago school are based on data for a single population (Conner and Hartl, 2004, pp. 210–211). However, both approaches serve to emphasize that we have to complement the well-known process of directional selection with an analysis of the processes of stabilizing selection and disruptive selection. Furthermore, we have to be very cautious when we are analyzing the evolution of a single characteristic of a population.

4 Three types of fitness functions

The understanding of the problems and methods related to the analysis of selection can be enhanced through examples of selection processes that have known properties because they are produced by explicit fitness functions. This approach has for evolutionary biology been emphasized by Endler (1986, pp. 260–271), and there is much need of producing simulated examples of selection processes in evolutionary economics. To be helpful, these examples have to be produced by simple fitness functions. In this section we define and simulate a directional fitness function, a stabilizing fitness function, and a disruptive fitness function.

Our fitness functions are all constructed so that they can produce such discrete-time simulations. To run these simulations we normally – apart from the initial population P – need the values of a couple of parameters. But the simulations are simplified by the fact that we do not provide any mechanism of intra-member change. Instead we

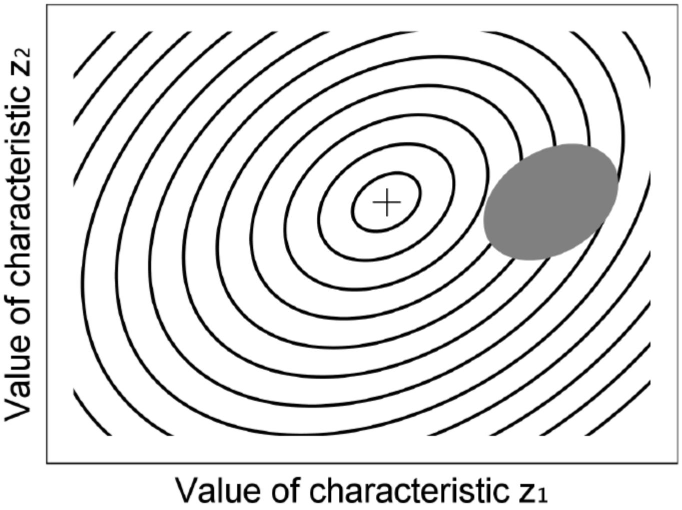

Figure 4: Example of isofitness curves for two characteristics z_1 and z_2. The fitness peak is marked by $+$. At an earlier point of time, the isofitness curves had its peak in the middle of the gray area. This area represents a population that was relatively well adapted to a previous situation, but which has become maladapted because of the exogenous movement of the isofitness curves. With the depicted position of the curves, the population faces stabilizing selection with respect to characteristic z_2 and a mix of directional and stabilizing selection with respect to characteristic z_1.

assume $\Delta z_i = 0$. The consequence is that only the selection term of Price's equation (3) needs be examined when we, in section 5, turn to the analysis of the change of mean characteristic. However, both terms of the equation are needed for the analysis of the change of variance, skewness and kurtosis of the frequency distributions.

The initial population: For the present purposes, we do not need to be realistic when defining the initial population P. On the contrary, what is needed is easy-to-understand data that provide the different types of fitness functions with lots of variance. We obtain such data by assuming a large population in which all values of the characteristic within a specified range are represented equally. Population P consists of 1000 members, and this number does not change during the simulations. Each member has a fixed value of its characteristic z_i. As the total size of the population is inconsequential to the simulations we specify each member to have an equal initial population share of $s_i = 1/1000$, and we can then refrain from considering member size, x_i, at all. For the following simulations we specify the fitness function for absolute fitness, $w_i = w(z_i)$, and the population then evolves according to $s'_i = s_i \omega_i$. The values of the characteristic are uniformly distributed over the interval $[\min(z), \max(z)]$. Thus the distance between members is $d = (\max - \min)/999$, and $z_1 = \min, z_2 = \min + d, z_3 = \min + 2d, \ldots, z_{1000} = \max$.

Standardized presentation of results: The simulation results can best be visualized as changes in the frequency distribution of the values of the characteristic. We employ a standardization of range for z_i that has become widespread in the parts of evolutionary biology which are influenced by the above mentioned Chicago school approach to phenotypic evolution. This method has several advantages, including the increased ease of comparing different types of selection. Therefore, the initial uniform distribution of the characteristic has in our simulations been defined to have mean zero and standard deviation one. Since the variance of a uniform distribution is $\frac{1}{12}(\max - \min)^2$, z_i in our initial population P has a continuous uniform distribution $\mathrm{U}(\min = -\sqrt{3}, \max = \sqrt{3})$. In terms of standard deviations this implies that our population covers about 1.7 standard deviations on each side of the mean of zero.

Directional fitness function: It is possible to define an unrealistic directional fitness function in which a particular value of the characteristic z_i under all circumstances gives the same absolute fitness w_i. However, we normally think of a process of positive directional selection in which the relative fitness ω_i of a member with characteristic z_i depends on its distance from a changing population mean $\bar{z}$. The logic of this selection function is that $\omega_i = 1$ if $z_i - \bar{z} = 0$; but if $z_i - \bar{z} > 0$, then $\omega_i > 1$; and if $z_i - \bar{z} < 0$, then $\omega_i < 1$. Furthermore, ω_i should be proportional to the distance from the mean. What is called replicator dynamics or distance-from-mean dynamics has these properties. Thus we can use the following directional fitness function:

$$\omega_i = \frac{z_i + k}{E(z_i + k)} = \frac{z_i + k}{\overline{z_i} + k} = \frac{w_i}{\overline{w}} \tag{5}$$

The constant k is added to avoid negative values and to avoid dividing by zero. The results of simulating the directional fitness function of equation (5) are depicted in the upper panel of figure 5, page 26. The dotted line represents the frequency distribution of the initial population (that was described above). The standardized mean is zero. This implies that the right half of the population has above mean fitness and the left half has below mean fitness. The results of first round of selection are indicated by the dashed line. This round increases or shrinks the member shares in proportion to the distance from the mean of zero. The second round of selection is not depicted but it is based on $\bar{z} > 0$. The fourth round is based on an even higher $\bar{z}$. Its result is shown by the full line of the panel. However, it should be noted that the directional fitness function does not produce pure directional selection. Compared with the initial uniform distribution, the four rounds of applying the directional function have moved the mass of the distribution so that increasing mean and kurtosis is one consequence and decreasing variance and skewness is another consequence.

Stabilizing fitness function: Let us consider the properties of simple fitness functions that are able to produce stabilizing selection. The basic requirement is that there is maximum fitness related to a particular value of the characteristic, z^*. The logic of stabilizing fitness functions is that ω_i has its maximum if $z_i = z^*$. Furthermore, if $z_i < z^*$ or if $z_i > z^*$, then ω_i is smaller than its maximum. Finally, ω_i should be decreasing in some relation to the numerical distance $|z_i - z^*|$. These requirements for a stabilizing fitness function is fulfilled by a second degree polynomial with maximum at z^*; that is $w_i = -z_i^2 + 2z^* z_i + k$. This quadratic fitness function has the same format as equation (5):

$$\omega_i = \frac{-z_i^2 + 2z^* z_i + k}{E(-z_i^2 + 2z^* z_i + k)} = \frac{w_i}{\overline{w}} \tag{6}$$

Again it is necessary to add k for computational reasons. This stabilizing fitness function resembles the directional fitness function of equation (5). But whereas equation (5) is linear, equation (6) has a maximum at $z_i = z^*$ and decreases symmetrically for higher and lower values of z_i.

The discussion in relation to figure 3 suggested that the outcome of applying a stabilizing fitness function depends on the localization of the characteristics of the population relative to the fitness maximum, z^*. We get pure stabilizing selection if the population is located symmetrically around the mean $\bar{z}$. The other possibility is that $z^* \neq \bar{z}$, and this possibility will be discussed below. Presently we consider the case in which $z^* = \bar{z}$. Given that $\Delta z_i = 0$ for all members, this implies that equation (6) does not change the mean of the frequency distribution.

The middle panel of figure 5 depicts the result of using equation (6) with $z^* = \bar{z}$ on the uniformly distributed pre-selection population specified above. Here it is obvious that this fitness function gradually brings the population closer to its fitness maximum by decreasing the variance and increasing the peakedness of the frequency distribution. After many more rounds of simulation, the distribution will end up as being concentrated on the characteristic with maximum fitness, z^*.

Disruptive fitness function: In principle, the specification of a disruptive fitness function assumes that there are two values of the characteristic that have maximum fitness, a lower value and a higher value. However, if these maxima are located outside the range of characteristic values that are represented in the population, then we only need to know the location of the fitness minimum at $\tilde{z}$. We specify our disruptive fitness function in a way that is closely related to the specification of equation (6). This disruptive function is

$$\omega_i = \frac{z_i^2 - 2\tilde{z}z_i + k}{E(z_i^2 - 2\tilde{z}z_i + k)} = \frac{w_i'}{\overline{w}} \tag{7}$$

Equation (7) produces a U-shaped parabola with minimum when $z_i = \tilde{z}$. Thus fitness increases on both sides of this fixed location of minimal fitness. To ensure comparability, we apply the positive constant k that was used in equations (5) and (6).

The disruptive fitness function produces pure disruptive selection if the population is located symmetrically around the mean and this mean is equal to the minimum fitness $\tilde{z}$. This is the case for the above specified initial population. The results of one and four rounds of using equation (7) are shown in the lower panel of figure 5. In our standardized presentation of the data $\tilde{z} = \bar{z} = 0$. The shares of members near the mean steadily decrease while the fitness of those with extreme characteristics increase. Compared with the initial one, the distribution after four rounds is characterized by an increase of variance and a decrease of peakedness or kurtosis.

Mixed selection: The simulations of the quadratic fitness functions have served to illustrate pure forms of stabilizing selection and disruptive selection. A quick glance on these illustrations might give the impression that equations (7) and (6) will always produce pure forms of selection. This impression is false for both equations, but we will only consider the stabilizing fitness function. Figure 3 demonstrated that such a function can produce stabilizing selection, directional selection, and a mix between the two. In this figure the varying results depend on the composition of the population. But we can also (as in figure 4) move the fitness function. In the univariate case of equation (6), we obtain a similar result by changing from $z^* = 0$ to $z^* = 0.7$ (so that $\bar{z} < z^*$). The consequences are shown in figure 6 on page 27. Here the stabilizing fitness function has produced a mix of stabilizing selection and directional selection. More specifically, the function moves the frequency distribution closer to the maximum of 0.7 by increasing the mean, decreasing the variance, decreasing the skewness, and increasing the peakedness.

Table 2: Statistics of the standardized distributions of figures 5 and 6

	Initial distribution	After four rounds of			
		Directional	Stabilizing	Disruptive	Mixed
Mean of z	0.00	0.69	0.00	0.00	0.59
Variance of z	1.00	0.68	0.45	1.56	0.39
Skewness of z	0.00	-0.85	0.00	0.00	-0.27
Kurtosis of z	1.80	2.93	2.48	1.37	2.40

Note: The table presents statistics of the initial distribution and of the distributions produced by four rounds of the different types of fitness functions. Directional is the distribution produced by the directional fitness function (5). Disruptive is produced by the disruptive fitness function (7). Stabilizing and Mixed are produced by stabilizing fitness function (6) with two locations of maximum fitness, $z^* = 0$ and $z^* = 0.7$. It should be noted that the paper analyses the *changes* of these statistics. For instance, in the mixed case $\Delta\bar{z} = 0.59 - 0.00 = 0.59$ and $\Delta Var(z) = 0.39 - 1.00 = -0.61$.

5 Analyzing the fitness functions through Price's equation

After having defined and applied the three fitness functions, the remaining task is to demonstrate that Price's equation provides an exact and fruitful way of analyzing these dynamics. We have in section 2 seen how Price's equation (3) can be used to decompose the total change of the mean characteristic of the population. However, Price (1995, p. 391) pointed out that his equation can be used for the analysis of any "change produced by the selection process in a *population property* X related to property x of individual set members. (For example: X might be the arithmetic mean of the x_i or their variance, and correspondingly for X' and the x_i' values.)" This comprehensiveness of Price's equation is crucial for the analysis of the dynamics of the different fitness functions. This analysis is supported by the additional use of the equation to decompose the frequency distribution's change of variance, change of skewness, and change of kurtosis. As an introduction it is helpful to consider the descriptive statistics of the frequency distributions presented in figures 5 and 6.

Statistics of the distributions: The figures of section 4 visualize how the different types of selection can be represented by different changes in initial population's frequency distribution of the characteristic z. Table 2 presents the statistics needed for comparing the distribution of P with the different distributions of P$''''$. The statistical characteristics of the initial distribution are given in the first data column of table 2. The following columns present the statistics of the new distributions after four rounds of using the fitness functions.

By subtracting the first from the second data column of table 2, we see that the directional fitness function has complex effects. In four rounds it has moved the mean in the positive direction by 0.69 standard deviations. At the same time it has decreased the variance of the frequency distribution by nearly a third, provided a strong negative skewness, and increased the peakedness of the distribution.

The third and fourth data column show the results of using the stabilizing fitness function (6) with $z^* = 0$ and the disruptive fitness function (7) with $\tilde{z} = 0$. By subtracting the first column from each of them we see that these fitness functions work only through the change of variance and kurtosis. The difference is that while stabilizing selection decreases variance and increases kurtosis, disruptive selection increases variance and decreases kurtosis. These results are based on the locations of the maximum fitness of the stabilizing function z^* and the minimum fitness of the disruptive function $\tilde{z}$. Both were placed at the mean of the distribution $\bar{z}$.

The last column of table 2 shows the result of the stabilizing fitness function when the maximum fitness z^* is moved 0.7 standard deviations in the positive direction. Then four rounds of using equation (6) produce results that are rather similar to those produced by the directional function (5). The mean is moved by 0.59 standard deviations, variance is decreased, we see negative skewness, and kurtosis is increased. This similarity emphasizes that caution is needed when we try to characterize overall fitness functions as representing different types of selection.

Moments of the distributions: The method of moments was introduced by the statistician and evolutionary biologist Karl Pearson (by a concept borrowed from physics). We consider the central moments of frequency distributions with characteristic z at the random variable. Then the m^{th} central moment of the distribution is defined as

$$E\left[(z_i-\bar{z})^m\right]=\sum_i s_i(z_i-\bar{z})^m$$

The second central moment ($m=2$) is the variance of the distribution. When the third central moment is divided by σ_z^3, we get the statistical concept of the skewness of the distribution. When the fourth central moment is divided by σ_z^4, we get one of the statistical concepts of kurtosis. The central moments characterize different aspects of the shape of the distribution. Odd moments ($m=3,5,\ldots$) measure the asymmetry of the distribution while even moments ($m=2,4,\ldots$) measure the symmetric spread around the mean. With increasing m the importance of outliers increases. Since outliers are crucial for evolutionary processes, the higher moments here have an importance that is not found in non-evolutionary uses of statistics (emphasized by Metcalfe 1994; and Rice 2004, p. 227).

Change of moments and Price's equation: As already mentioned, Price's equation can be used for the partitioning of the change of the mean of any quantitative characteristic C. The only requirement is that we define the member values of the characteristic C_i such that $\overline{C}$ is the mean and $\Delta\overline{C}$ is the change we want to decompose. In the case of variance, the characteristic $(z_i-\bar{z})^2$ gives the expectation $\sum(z_i-\bar{z})^2=Var(z)$. In the case of skewness, the characteristic is $(z_i-\bar{z})^3/\sigma_z^3$ since the expectation is the skewness of the distribution. In the case of kurtosis, the characteristic is $(z_i-\bar{z})^4/\sigma_z^4$ since the expectation is the kurtosis of the distribution. Thus we can use Price's equation (3) to decompose the change of the variance, skewness and kurtosis of the frequency distribution. The decompositions of the change in the distribution's variance, skewness and kurtosis are thus provided by

$$\Delta Var(z)=Cov\left[\omega,(z-\bar{z})^2\right]+E\left[\omega\Delta(z-\bar{z})^2\right]=Cov(\omega,\upsilon)+E(\omega\Delta\upsilon) \tag{8}$$

$$\Delta Skew(z)=Cov\left[\omega,(z-\bar{z})^3/\sigma_z^3\right]+E\left[\omega\Delta((z-\bar{z})^3/\sigma_z^3)\right]=Cov(\omega,\gamma)+E(\omega\Delta\gamma) \tag{9}$$

$$\Delta Kurt(z)=Cov\left[\omega,(z-\bar{z})^4/\sigma_z^4\right]+E\left[\omega\Delta((z-\bar{z})^4/\sigma_z^4)\right]=Cov(\omega,\kappa)+E(\omega\Delta\kappa) \tag{10}$$

By moving from decomposing the change of the mean in Price's equation (3) to decomposing the change of the variance in equation (8)), we have started the analysis of the recursive process of selection. The original Price equation deals only with the change from the pre-selection population to the post-selection population, but equation (8) provides us with a measure of the fuel that this change leaves for the movement of the mean between the post-selection popu-

Table 3: Statistical components of the selection dynamics in figures 5 and 6

Statistical change that is decomposed	Term in Price's equation	After four rounds of			
		Directional	Stabilizing	Disruptive	Mixed
Δ Mean	$Cov(\omega, z)$	0.69	0.00	0.00	0.59
	$E(\omega \Delta z)$	0.00	0.00	0.00	0.00
Δ Variance	$Cov(\omega, \upsilon)$	0.16	-0.55	0.56	-0.26
	$E(\omega \Delta \upsilon)$	-0.48	0.00	0.00	-0.35
Δ Skewness	$Cov(\omega, \gamma)$	1.26	0.00	0.00	0.83
	$E(\omega \Delta \gamma)$	-2.11	0.00	0.00	-1.11
Δ Kurtosis	$Cov(\omega, \kappa)$	0.40	-1.31	1.51	-0.65
	$E(\omega \Delta \kappa)$	0.72	1.98	-1.94	1.25

Note: The total change of the different statistics can be found in table 2. For instance, in the mixed case $\Delta Var(z) = -0.61$. This change is the sum of the covariance term and the expectation term: $-0.61 = -0.26 + (-0.35)$.

lation and the post-post-selection environment. If the amount of fuel is being gradually reduced the selection process will after many rounds of selection come to a halt – unless a change of the environment changes the fitness function or new fuel is provided by mutation or innovation.

There are three aspects of the selection process are not adequately covered by the analysis of the change of the variance of the distribution. First, the outliers of the distribution of characteristics are crucial and they can be emphasized more than in the measure provided by the squared distances from the mean. We can also study higher central moments such as those dependent on $(z_i - \bar{z})^3$ and $(z_i - \bar{z})^4$. Second, the asymmetry of the distribution, as reflected by moments with odd powers, is also of importance for the selection process. Third, some types of selection can only be defined by reference to changes in the higher moments of the distribution. In general, we as already mentioned have to recognize that the statistics of the higher moments play a much larger role in evolution than in most other subjects. Therefore, it is important that we can use Price's equation to decompose the change of all these moments as demonstrated by equation (9) for skewness and equation (10) for kurtosis.

Analysing the change of the distributions: The mean, variance, skewness and kurtosis of the initial distribution and the distributions produced by four rounds of applying the different fitness functions were shown in table 2. The overall changes of these statistics have already been discussed. Now we turn to the Price equation analysis of these changes as the sums of covariance terms and expectation terms. The results are shown in table 3. Let us start by the decomposition of the change of the mean. Since $\Delta z_i = 0$, the expectation term is zero and the whole change of 0.69 standard deviations produced by the directional fitness function is accounted for by the covariance term. The same is the case for the mixed type of selection produced by the stabilizing fitness function with maximum fitness different from the mean. In contrast, the pure types of stabilizing and disruptive selection do not change the mean.

The decompositions of the changes of variance are more interesting. From table 2 we know that the directional fitness function produces an overall change of the variance of -0.32. However, the covariance term of table 3 shows a positive selection effect of 0.16 while the expectation term shows a negative intra-member effect of -0.48. We have

Table 4: Signs of the components of the analysed examples of selection dynamics

Statistical change that is decomposed	Term in Price's equation	Model of selection dynamics			
		Directional	Stabilizing	Disruptive	Mixed
Δ Mean	$Cov(\omega, z)$	POS	0	0	POS
	$E(\omega\Delta z)$	0	0	0	0
Δ Variance	$Cov(\omega, \upsilon)$	POS	NEG	POS	NEG
	$E(\omega\Delta\upsilon)$	NEG	0	0	NEG
Δ Skewness	$Cov(\omega, \gamma)$	POS	0	0	POS
	$E(\omega\Delta\gamma)$	NEG	0	0	NEG
Δ Kurtosis	$Cov(\omega, \kappa)$	POS	NEG	POS	NEG
	$E(\omega\Delta\kappa)$	POS	POS	NEG	POS

Note: The signs are from table 3.

accounted for the overall change of variance since $-0.32 = 0.16 - 0.48$, but we now recognize the complexities of the process produced by the directional fitness function. We also recognize the difference between the directional function and the stabilizing function that has a maximum different from the mean. The latter also has an overall negative change of variance, but this change is produced by two negative terms ($-0.61 = -0.26 - 0.35$). In contrast, the changes of variance by pure stabilizing and disruptive selection are solely produced by the covariance term.

The concepts of pure directional and pure stabilizing selection do not include the skewness of the frequency distribution. However, a change of skewness is found in the distributions produced by the directional fitness function (5) and the stabilizing fitness function (6) with maximum different from the mean. They both produces a negative change of skewness that is caused by a positive covariance term that is smaller than the negative expectation term.

The signs of change: Although the details of the statistics of the decomposed overall changes of mean, variance, skewness and kurtosis are important, the different fitness functions can to a large extent be characterized by the signs of the covariance terms and the expectation terms. These signs are presented in table 4. Let us start by comparing the results of applying the stabilizing function and the disruptive function with optima at $\bar{z}$. The pattern of signs is opposite. With respect to change of variance, the results of stabilizing function have a negative covariance term while the disruption function produces a positive covariance term. The same is the case for the covariance terms of the change of kurtosis. However, the change of overall kurtosis is also influenced by the positive expectation term of stabilization and the negative expectation term of disruption.

The comparison of the changes in the distribution produced by the directional function and the stabilizing function with a displaced maximum contains more elements. However, they have the same signs except in the case of the decomposition of the overall change of kurtosis. For the directional function the covariance term and the expectation term are both positive. However, for the mixed function of stabilization only the covariance term is positive while the expectation term is negative. We have not reported results for simulating negative directional selection but changes in the distribution of the characteristic induced by negative directional selection would not be identical to those induced by positive directional selection. In the case of negative rather than positive directional selection the mass of the distribution would shift towards the left tale rather than the right. The decompositions of the changes in mean and skewness would show the opposite signs when compared to positive directional selection. The decompositions of the changes in variance and kurtosis, however, would show the same signs.

The quick recognition of the traces of the different fitness functions is obviously eased by focusing on the pattern of signs of the two terms of Price's equation. However, further simulations are much needed for producing closer approximations to real evolutionary processes. First, different fitness functions might concurrently contribute to more realistic cases of selection. Second, real selection normally works concurrently on several characteristics of the members of the population. Third, we have to analyse the consequences of abandoning the assumption that $\Delta z_i = 0$.

6 Conclusion

The research underlying this paper had two closely connected aims. The first aim was to demonstrate how the well developed analysis of directional selection within evolutionary economics can be complemented by analyses of stabilizing selection and disruptive selection. The second aim was to demonstrate that the evolutionary algebra provided by Price's equation increases the intellectual coherence and power of thinking about selection and other aspects of evolutionary processes.

The first aim of the paper serves to counter the predominant directional paradigm within evolutionary economics that has led to a neglect of processes of evolution that are influenced by stabilizing selection and disruptive selection. Actually, these types of selection still lack generally acknowledged definitions. We suggested that – like in evolutionary biology – they should be defined by their influence on the variance of the population distribution of the values of a characteristic. Stabilizing selection is the negative change of this variance and disruptive selection is the positive change of variance. In contrast, directional selection is defined as the positive or negative change of the mean.

These definitions do not necessarily represent what is normally thought of as the different types of selection. This is one of the reasons why we complemented the basic concepts with the definitions of fitness functions that can produce the different types of selection. For instance, replicator dynamics provides a fitness function that is normally considered a core example of directional selection. It nevertheless not only influences the mean but also the variance. Similarly, the fitness functions that best represent stabilizing selection and directional selection only produces a change in variance without influencing the mean when we assume that it is very special characteristic values that produce maximum fitness and minimum fitness in these functions. Actually, the three fitness functions can produce so many patterns of change that there is a strong need of finding methods for detecting which processes have produced a particular pattern of change. We produced detectable patterns by using Price's equation to decompose the change produced by the different types of fitness functions with different parameters. Then the possible fingerprint is the set of eight signs of the two Price equation effects for the change of the mean, variance, skewness and kurtosis produced under different conditions by the different types of fitness functions.

The paper could not confront the more important issue of using the basic definitions of the types of selection to estimate the relative importance of directional selection, stabilizing selection and disruptive selection in economic evolution. The obvious reason it that this estimation requires actual censuses of a large number of pre-selection populations and post-selection populations.

The second aim of this paper was to demonstrate the surprising analytical power of Price's equation. If the paper has any value, this is largely due to the combination of discipline and flexibility that we got from thinking in terms of this equation. However, our review of recent controversies on Price's equation serves to emphasize the difficulties involved in its comprehension and application. We tried to overcome some of these by reviewing the different versions of Price's equation as well as specifying the analytical framework in which it can be used. This framework includes two censuses of a population, a mapping between the members of the pre-selection population and the post-selection population, the analysis of changes in the frequency distribution of a selected characteristic, the calculation of fitnesses, the decomposition of the changes of the distribution into the sum of selection effects and intra member effects, and the analysis of these effects. The handling of these and other issues requires the use of mathematical notation, and we largely used the standard notation that has developed in relation to Price's equation.

Although our exposition seems to include a few novelties, we have basically been presenting the state of the art. The most concrete contribution to the literature is the analysis of the signs of the Price equation decomposition of the change of skewness and kurtosis. In any case, a main conclusion of this paper is that Price's algebra of evolution seems to help in improving the intellectual coherence and power of thinking about selection processes in economic life. Through multi-level analysis it can also help to disentangle parts of evolution that are not immediately revealed as being based on selection. It remains to be seen whether alternative versions of Price's equation can also help the analysis of learning and innovation.

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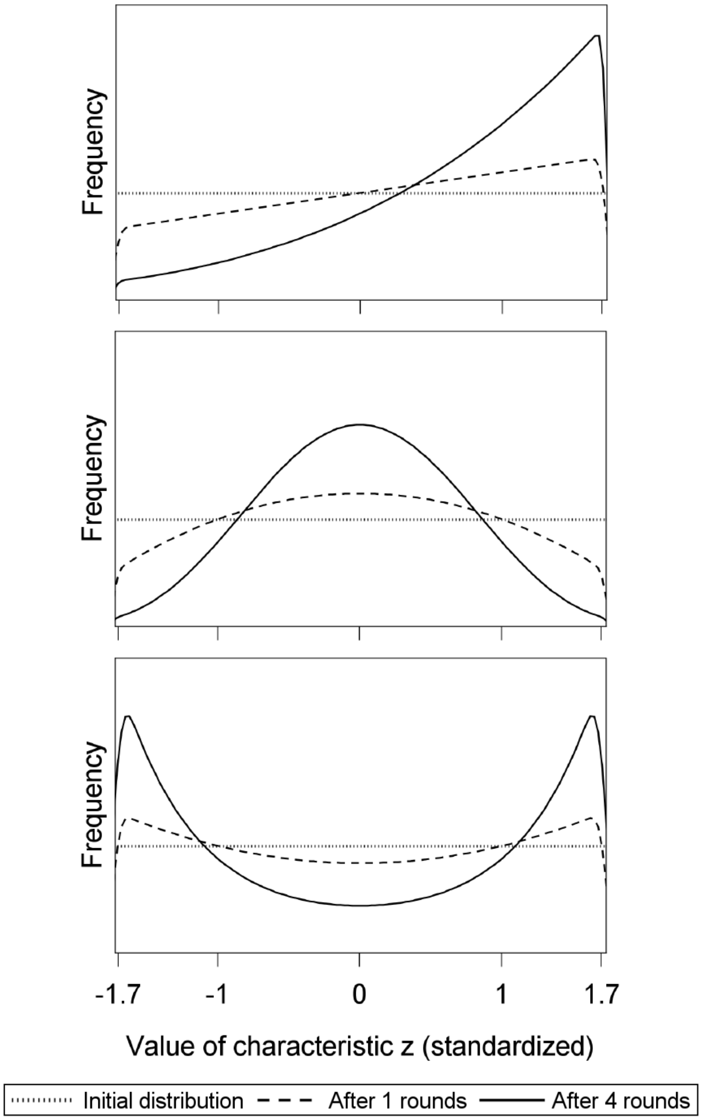

Figure 5: Effects of one and four rounds of selection by different fitness functions. The upper panel is produced by the directional fitness function (5), the middle panel by the stabilizing function (6) with $z^* = 0$, and the lower panel by the disruptive function (7) with $\tilde{z} = 0$. Characteristics data are standardized to have a mean of zero and a standard deviation of unity initially. The curves are constructed as kernel density estimates over z_i in the simulated data and thus the distributions appear rounded near min and max. From the viewpoint of evolutionary modelling this behaviour can be considered an artefact that should be ignored.

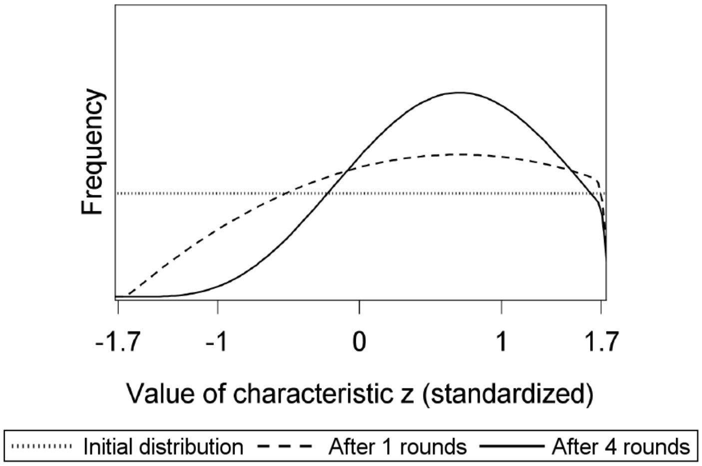

Figure 6: Effects of one and four rounds of selection by the stabilizing fitness function with changed fitness maximum. The results are produced by equation (6) with $z^* = 0.7$. Characteristics data are standardized to have a mean of zero and a standard deviation of unity initially. The curve is constructed as a kernel density estimate over z_i in the simulated data and thus the distribution appears rounded near min and max. From the viewpoint of evolutionary modelling this behaviour can be considered an artefact that should be ignored.