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The signs of change in economic evolution

An analysis of directional, stabilizing and diversifying selection based on Price's equation

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Abstract Neo-Schumpeterian evolutionary economics has, since the early works of Nelson and Winter, defined evolution as the change of the mean of a characteristic of a population. This paper trancends the previous paradigm and explores novel aspects of evolution in economics. Within the traditional paradigm change is provided by directional selection (and directional innovation). However, the full definition of evolutionary processes has to include two important types of selection that change the variance without necessarily changing the mean. Stabilizing selection removes any outlier and diversifying selection promotes the coexistence of behavioural variants. This paper emphasizes the need for an integrated analysis of all three types of selection. It also demonstrates 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. Directional, stabilizing and diversifying 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, the paper adds to evolutionary economics a novel way of using Price's equation 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 are of relevance for applied evolutionary economics.

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1 Introduction

The analysis of directional selection is well-developed in evolutionary economics where it is often applied in empirical research and simulations in relation to productivity. This paper demonstrates that these analyses can be complemented by analyses of stabilizing selection and diversifying selection. It also demonstrates 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.

Neo-Schumpeterian evolutionary economics has largely been based on the paradigm of directional 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 variance as 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 (Hanusch and Pyka 2007). 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 trend-like 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, as illustrated in Fig. 1. On the one hand, there is stabilizing evolution that tends to remove any change away from the favoured value of a characteristic. On the other hand, there are cases of diversifying evolution that promotes the coexistence of different types of behaviour within a population and may lead to the emergence of two separate populations. These
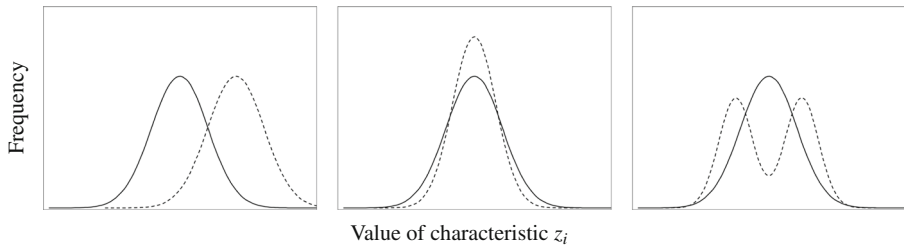
Fig. 1 Three types of pure selection. The *solid line* represent the pre-selection distribution of the characteristic and is identical across the three panels. The *dashed lines* represent the distribution of the characteristic after pure direction, pure stabilizing and pure diversifying selection respectively

two possibilities are well-established within evolutionary biology (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 diversifying selection. Since the underlying genetics is normally unknown or complex, such analyses generally 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. Even the fact that firms are diverse in a sustainable way is still not an established result within economics (Syverson 2011).

2 Price's equation and its usefulness

It is 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. However, Price's equation emerged from the statistical analysis of directional evolution. This analysis had already been developed when Schumpeter (2000, p. 184) in the 1930s called for "a quantitative theory of evolution". But he seems to have been unaware that it had already been provided by the great statistician and evolutionary biologist Fisher (1930). One reason for Schumpeter's neglect is that he emphasized the innovative part of the evolutionary process while Fisher emphasized directional selection. Another reason might have been that many biologists were 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 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 are most obviously relevant for the special case of pure selection processes. It was instead George Price who developed a general decomposition of evolutionary change that includes not only the effect of selection but also the effect of mutation or innovation (see Frank 1995, 1998). For the statistics of any adequately defined population of members, Price proved that

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

This is the verbal version of Price's equation for directional evolution. 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 selection effects that often amount to a relatively small share of total evolution (Foster et al. 1998, 2008; Disney et al. 2003; Bartelsman et al. 2004). 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 Eq. 1.

The importance of Price's decomposition of directional 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. 1998, 2002, 2008; Disney et al. 2003). 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.

It should be noted that important extensions (Metcalfe 1997; Rice 2004, pp. 194–203; Metcalfe and Ramlogan 2006; Okasha 2006; Bowles and Gintis 2011, pp. 218–222) have emerged within the directional paradigm of economic evolution. The present paper develops a very different type of extension. The background is that Price's equation can be used to decompose *any* evolutionarily relevant characteristic. The relevant characteristic for stabilizing and diversifying evolution is the

total change of the variance of the population distribution. For this case, we get the following version of Price's equation:

$$\text{Total change of variance} = \text{Selection effect} + \text{Intra-member effect} \qquad (2)$$

If the selection effect of Eq. 2 is negative, we observe stabilizing selection. If it is positive, we have diversifying selection.

The paper has the aims of extending the concept of selection to include stabilizing and diversifying selection, and of demonstrating the power of Price's equation to this end. It starts by reviewing recent discussions in relation to Price's equation (Section 2). This review includes the presentation of a framework for analysing evolution that then is used for the definition and analysis of directional, stabilizing and diversifying selection (Section 3). 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 (Section 4). Finally, Price's equation is used to decompose the statistics of the changes of the frequency distributions (Section 5). Section 6 discusses the implications of the results and venues for further research.

Although many presentations of Price's Eq. 1 are available (including Andersen 2004; Knudsen 2004), this section of the paper presents the equation, discusses its use and relates to recent discussions in the literature before we in the next section use Price's equation for the analysis of directional, stabilizing and diversifying 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).

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 post-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

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 $w_i \Delta z_i$

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

Evolutionary change = Entry effect + Exit effect

+ Selection effect + Intra-member effect

Data and calculations We now come to the data that need to be collected for 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 members' absolute fitness $w_i = x_i'/x_i$ and the population's mean fitness $\overline{w} = \sum s_i w_i$. The members' 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 $\Delta\overline{z}$. 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 $\Delta\overline{z}$ 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 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 as can be seen from Table 1 the covariance element of Price's equation is not the sample covariance estimator of population covariance but rather the formula for population covariance. Thus when Price's equation is applied to population censuses rather than a sample the selection effect is population covariance divided by population fitness.

Price's equation with relative fitness We are now ready to consider the formally provable specification of Price's equation that was informally presented in Eq. 1. Since the proof of the equation is widely available (e.g., Frank 2012b), the problem is rather to identify the most useful version for evolutionary analysis. Price's equation in terms of relative fitness, ω_i, 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.

$$\underset{\Delta \overline{z}}{\text{Total change}} = \underset{Cov(\boldsymbol{\omega}, z)}{\text{Selection effect}} + \underset{E(\boldsymbol{\omega}\Delta z)}{\text{Intra-member effect}} = \beta_{\boldsymbol{\omega},z} Var(z) + E(\boldsymbol{\omega}\Delta z) \quad (3)$$

There are evolutionary problems in which population-level does matter and where it thus may be more instructive to use Price's equation in terms of absolute fitness rather than the elegant (3) but such problems are not considered in the current paper.

The left-hand side of Eq. 3 is the change of the mean characteristic of the population. The selection effect is basically expressed as the covariance between relative fitness and characteristic. This covariance can be rewritten as the product of the selection intensity $\beta_{\omega,z}$ and the variance $Var(z)$. There will be no selection effect if either $\beta_{\omega,z} = 0$ 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 relative fitness. In any case, it disappears if $\Delta z_i = 0$ for all members of the population.

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 diversifying evolution that do not change the population mean. It is not 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 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 Fig. 2. 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). It is achieved through a combination of selection favouring higher values of the characteristic and intra-member processes adding novel, higher values of the characteristic to the population. In contrast, the right panel illustrates the effect of a directional fitness function that influences both the mean and the variance of the distribution and where no novel values of the characteristic are introduced. While the left panel illustrates directional selection in its pure form, the right panel depicts the stabilizing effect of a purely directional fitness function. The concept of directional selection represents an aspect of the evolutionary process that can be combined with stabilizing selection or other types of selection (Endler 1986; Rice 2004). 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. (Endler 1986; Rice 2004). This possibility is left open if we define directional selection in terms of $\Delta \overline{z} = \overline{z}' - \overline{z}$. If $\Delta \overline{z} = 0$, there cannot be directional selection. If $\Delta \overline{z} \neq 0$, we use the covariance term in Eq. 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
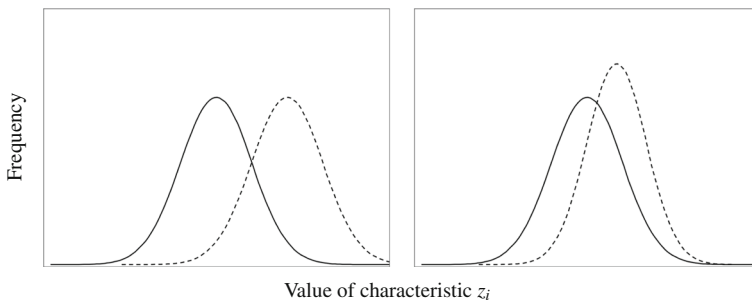

Fig. 2 Pure directional selection and the effect of a directional fitness function. The *left panel* depicts the concept of directional selection by leaving the variance unchanged. The *right panel* depicts the effect of a directional fitness function such as that of replicator dynamics, where $\Delta z_i = 0$

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 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 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 diversifying 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 Eq. 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 diversifying 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 Eq. 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 $Cov(\omega, (z - \overline{z})^2) < 0$.
– Diversifying 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 diversifying 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 $\Delta \overline{z} = 0$. In terms of Price's Eq. 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.

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 diversifying 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 Figs. 2 and 3. The solid lines depict the frequency distribution of the pre-selection population. The dashed lines depict the post-selection distributions. As already mentioned, Fig. 2 depicts a selection process in which only the mean characteristic is changing. The two panels of Fig. 3 keep the mean unchanged while the variance changes. In the case of stabilizing selection the variance decreases. The variance increases with a process of diversifying 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 Fig. 4 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
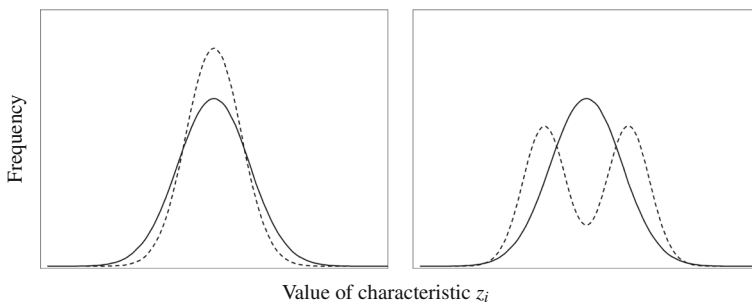

Fig. 3 The two pure types of variance selection. The *solid curve* depicts the initial frequency distribution while the *dashed curves* depict the results of different types of variance selection by presenting the post-selection distributions. *Left panel* pure stabilizing selection. *Right panel* pure diversifying selection

Fig. 4 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 to the left of the *dashed line* and stabilizing selection to the right of the *dashed line*. If the population is distributed over the entire horizontal axis we have mixed selection pressures
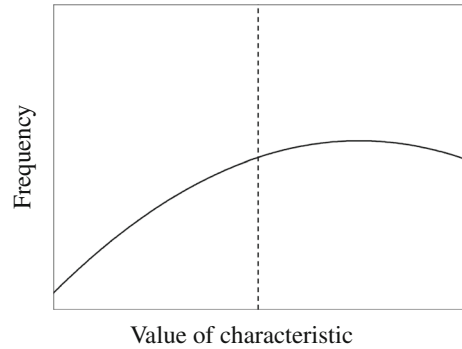
population. The population largely faces positive directional selection if the characteristics of its members are distributed to the left of the dashed line. We have stabilizing selection if the population is distributed to the right of the dashed line. However, the population faces a mix of directional and stabilizing selection if it is distributed over the entire range represented by the horizontal axis of the figure.

We encounter similar issues if the fitness function of Fig. 4 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 diversifying selection will be two 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. The result is a graph that will look familiar to 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 5 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 the origin toward the fitness maximum; but it decreases when we continue from the maximum towards the upper right corner.

Figure 5 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 generally not stable, though they may appear to be so, as they potentially move back and forth and 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 Fig. 5 is that the isofitness
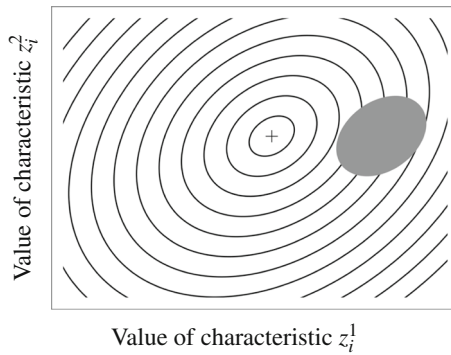
Fig. 5 Example of isofitness curves for two characteristics z_i^1 and z_i^2. The fitness peak is marked by $+$. At an earlier point of time, the isofitness curves had its peak in the middle of the *gray area*. This area represents a population that was relatively well adapted to a previous situation, 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_i^2 and a mix of directional and stabilizing selection with respect to characteristic z_i^1

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

Further discussion of the 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 Wright's (1932) famous formalization of selection in terms of "fitness landscapes", the two concepts are not exactly the same. While each point in 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 diversifying 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 diversifying 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 assume $\Delta z_i = 0$. The consequence is that only the selection term of Price's Eq. 3 needs to 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 are needed are the simplest data 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. 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 $z_1 = \min(z)$, $z_2 = \min +d$, $z_3 = \min +2d, \ldots, z_{1000} = \max(z)$. For the following simulations we specify the fitness function for absolute fitness, $w_i = w(z_i)$, and the population then evolves according to:

$$s_i' = s_i \frac{w_i}{\overline{w}} = s_i \omega_i \tag{5}$$

By using Eq. 5 we are assuming that the change in population share of member i is entirely determined by relative fitness but in empirical applications it is likely that population shares exhibit persistence. This could be explicitly modelled by allowing s_i' to be the weighted average of s_i and $s_i \omega_i$. However, as our simulations are meant to provide simple illustrations of the evolutionary processes the only consequence would be that we would have to run the simulations for additional rounds for the results to stand out clearly. Results can be seen after just 1 round of simulation with Eq. 5 and after 4 rounds they stand out very clearly.

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 the 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 $U(\min = -\sqrt{3}, \max = \sqrt{3})$. 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 $\overline{z}$. The logic of this fitness function is that $\omega_i = 1$ if $z_i - \overline{z} = 0$; but if $z_i - \overline{z} > 0$, then $\omega_i > 1$; and if $z_i - \overline{z} < 0$, 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:

$$\omega_i = \frac{z_i + k}{E(z_i + k)} = \frac{z_i + k}{\overline{z_i} + k} = \frac{w_i}{\overline{w}} \tag{6}$$

The constant k is added to avoid negative fitness values and to avoid dividing by zero. The results of simulating the directional fitness function of Eq. 6 are depicted in the upper panel of Fig. 6, page 14. 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 result of the first round of selection is 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 $\overline{z} > 0$. The fourth round is based on an even higher $\overline{z}$. Its result is shown by the full line of the panel. However, it should be noted that a directional fitness function cannot on its own produce pure directional selection as selection necessarily consumes variance. 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. As an example, assume that we are studying work organisation in a large factory paying a piece rate. Workers have complete discretion in organising their work so whatever practices result in a higher physical efficiency will spread to other workers (assuming that there is no collusion among workers). If workers can be more productive by stacking their goods higher then the average hight of the stack of goods next to each worker's station will evolve according to a directional fitness function. This process obviously cannot go on for ever but, as already mentioned, this is a typical element of directional selection.

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

Fig. 6 Effects of one and four rounds of selection by different fitness functions. The *upper panel* is produced by the directional fitness function (6), the middle panel by the stabilizing function (7) with $z^* = 0$, and the *lower panel* by the diversifying function (8) with $\bar{z} = 0$. 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 the minimum and maximum. From the viewpoint of evolutionary modelling this behaviour can be considered an artefact that should be ignored
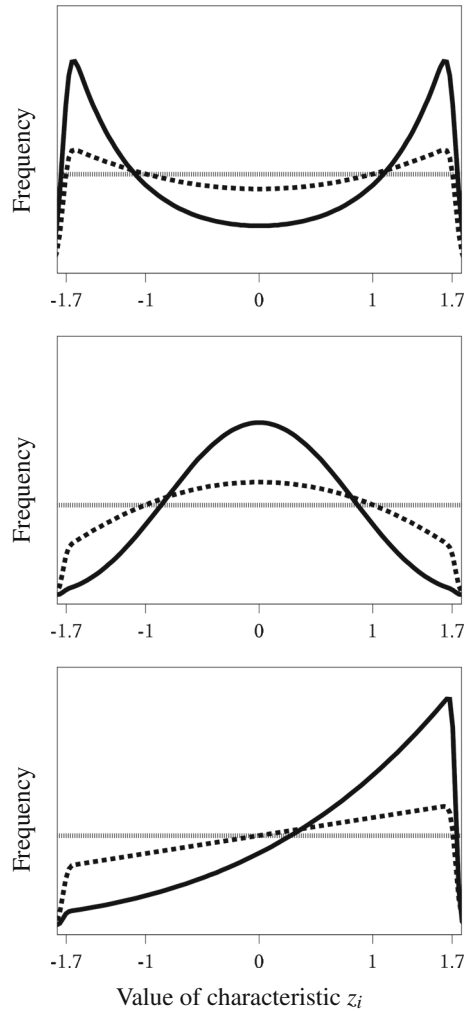
be decreasing in some relation to the numerical distance $|z_i - z^*|$. These requirements for a stabilizing fitness function is fulfilled by a second degree polynomial with maximum at z^*; that is $w_i = -z_i^2 + 2z^*z_i + k$.

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

Again it is necessary to add k for computational reasons. This stabilizing fitness function resembles the directional fitness function of Eq. 6. But whereas (6) is linear, Eq. 7 has a maximum at $z_i = z^*$ and decreases symmetrically for higher and lower values of z_i.

The discussion in relation to Fig. 4 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 (7) does not change the mean of the frequency distribution.

The middle panel of Fig. 6 depicts the result of using Eq. 7 with $z^* = \bar{z}$ on the uniformly distributed pre-selection population specified above. This fitness function gradually brings the population closer to its fitness maximum by decreasing the variance and increasing the kurtosis 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^*. As an example consider again the large factory paying a piece rate and assume that a 5 minute break after an hour's work results in the highest physical efficiency. A shorter break means that the worker becomes tired and works slower towards the end of the day while a longer break entails squandering working time. So the mean break length per hour of work will converge on 5 minutes throughout the factory in a process of stabilizing selection.

Diversifying fitness function In principle, the specification of a diversifying 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 it is sufficient to know the location of the fitness minimum at $\tilde{z}$. We specify our diversifying fitness function in a way that is closely related to the specification of Eq. 7. This diversifying function is

$$\omega_i = \frac{z_i^2 - 2\tilde{z}z_i + k}{E(z_i^2 - 2\tilde{z}z_i + k)} = \frac{w_i'}{\bar{w}} \tag{8}$$

Equation 8 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 Eqs. 6 and 7.

The diversifying fitness function produces pure diversifying 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 Eq. 8 are shown in the lower panel of Fig. 6. 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 kurtosis. For an example of diversifying selection return once again to our factory. Workers have a choice of two different methods for fitting together two components. Some workers will initially be switching back and forth for a bit of variation but unless a worker uses the same method each time she misses out on the opportunity of specialisation. So over time the probability that any one methods is used across the factory will evolve in accordance with a diversifying fitness function.

Mixed selection The simulations of the quadratic fitness functions have served to illustrate pure forms of stabilizing selection and diversifying selection. A quick glance on these illustrations might give the impression that Eqs. 8 and 7 will always produce pure forms of selection. This impression is false for both equations, but we will emphasize the stabilizing fitness function. Figure 4 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 Fig. 5) move the fitness function. In the univariate case of Eq. 7, we obtain a similar result by changing from $z^* = 0$ to $z^* = 0.7$ (so that $\overline{z} < z^*$). The consequences are shown in Fig. 7 on page 16. 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 kurtosis.

5 Analyzing the fitness functions through Price's equation

After having discussed Price's equation and types of selection, the remaining task is to demonstrate and analyse the relationship between the types of selection and the fitness functions defined above by application of Price's equation. It is demonstrated in this section how Price's equation provides an exact and fruitful way of analysing the dynamics created by the fitness functions. We have in Section 2 seen how Price's Eq. 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
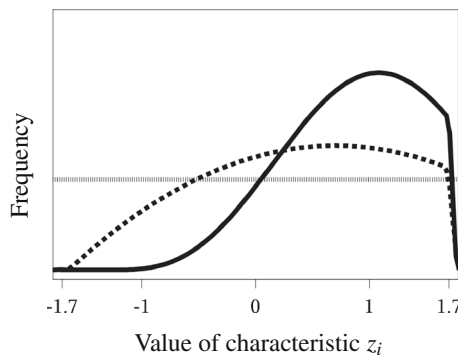

Fig. 7 Effects of one and four rounds of selection by the stabilizing fitness function with changed fitness maximum. The results are produced by Eq. 7 with $z^* = 0.7$. Characteristics data are standardized to have a mean of zero and a standard deviation of unity initially. The *curve* is constructed as a kernel density estimate over z_i in the simulated data and thus the distribution appears rounded near the minimum and maximum. From the viewpoint of evolutionary modelling this behaviour can be considered an artefact that should be ignored

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 distributions' 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 Figs. 6 and 7.

Statistics of the distributions The figures of Section 4 visualize how the different types of selection can be represented by different changes in the initial population's frequency distribution of the characteristic z. Table 2 presents the statistics needed for comparing the distribution in P with the different distributions in 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 kurtosis of the distribution.

The third and fourth data column show the results of using the stabilizing fitness function (7) with $z^* = 0$ and the diversifying fitness function (8) 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, diversifying 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 diversifying function $\tilde{z}$. Both were placed at the mean of the distribution $\overline{z}$.

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

Table 2 Statistics of the standardized distributions of Figs. 6 and 7

	Initial	After four rounds of			
	distribution	Directional	Stabilizing	Diversifying	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

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 (6). Diversifying is produced by the diversifying fitness function (8). Stabilizing and Mixed are produced by stabilizing fitness function (7) 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 $\Delta \overline{z} = 0.59 - 0.00 = 0.59$ and $\Delta Var(z) = 0.39 - 1.00 = -0.61$

direction. Then four rounds of using Eq. 7 produce results that are rather similar to those produced by the directional function (6). 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 mth central moment of the distribution is defined as

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

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 $(z_i - \overline{z})^2$ gives the expectation $\sum (z_i - \overline{z})^2 = Var(z)$. In the case of skewness, the characteristic is $(z_i - \overline{z})^3/\sigma_z^3$ since the expectation is the skewness of the distribution. In the case of kurtosis, the characteristic is $(z_i - \overline{z})^4/\sigma_z^4$ since the expectation is the kurtosis of the distribution. Thus we can use Price's Eq. 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

$$\Delta Var(z) = Cov\left[\omega, (z - \overline{z})^2\right] + E\left[\omega\Delta(z - \overline{z})^2\right]$$
$$= Cov(\omega, \upsilon) + E(\omega\Delta\upsilon) \tag{9}$$
$$\Delta Skew(z) = Cov\left[\omega, (z - \overline{z})^3/\sigma_z^3\right] + E\left[\omega\Delta((z - \overline{z})^3/\sigma_z^3)\right]$$
$$= Cov(\omega, \gamma) + E(\omega\Delta\gamma) \tag{10}$$
$$\Delta Kurt(z) = Cov\left[\omega, (z - \overline{z})^4/\sigma_z^4\right] + E\left[\omega\Delta((z - \overline{z})^4/\sigma_z^4)\right]$$
$$= Cov(\omega, \kappa) + E(\omega\Delta\kappa) \tag{11}$$

By moving from decomposing the change of the mean in Price's Eq. 3 to decomposing the change of the variance in Eq. 9, we have started the analysis of the recursive process of selection. The original Price's equation deals only with the change from the pre-selection population to the post-selection population, but Eq. 9 provides us with a measure of the fuel that this change leaves for the movement of the mean between the post-selection population 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 that 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 $(z_i - \overline{z})^3$ and $(z_i - \overline{z})^4$. 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 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 Eq. 10 for skewness and Eq. 11 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 analysis of these changes by means of Price's equation: 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 diversifying 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 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 diversifying selection are solely produced by the covariance term.

Table 3 Statistical components of the selection dynamics in Figs. 6 and 7

Statistical change that is decomposed	Term in Price's equation	After four rounds of			
		Directional	Stabilizing	Diversifying	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

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: $-0.61 = -0.26 + (-0.35)$

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 (6) and the stabilizing fitness function (7) 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 diversifying function with optima at $\overline{z}$. The pattern of signs is opposite. With respect to change of variance, the results of the stabilizing function have a negative covariance term while the diversifying 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 the stabilizing function and the negative expectation term of the diversifying function.

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

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

Statistical change that is decomposed	Term in Price's equation	Type of fitness function			
		Directional	Stabilizing	Diversifying	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

The signs are from Table 3

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 discussion of the current section highlights how quick recognition of the traces of the different fitness functions is facilitated 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 diversifying 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 diversifying 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 diversifying 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 diversifying 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 diversifying selection in economic evolution. The reason is that this estimation is an empirical problem beyond the scope of the current paper.

The second aim of this paper was to demonstrate the surprising analytical power of Price's equation, and a main contribution thus is 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 contributed to surmounting 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 require the use of mathematical notation, and we largely used the standard notation that has developed in relation to Price's equation.

Although our exposition includes a number of 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 helps 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. The third condition for a long-term evolutionary process, besides from variance and replication, is novelty. In economics this generally means learning and innovation and it has here been confined to the intra-member effect but such processes also contain an element of selection among alternatives.

It remains to be seen whether the concepts of directional, stabilizing and diversifying evolution can also help the analysis of learning and innovation. If this is the case, there might be a chance of analyzing systematically broad ideas such as techno-economic paradigms, regimes and trajectories of evolution, and the distinction between radical and incremental innovation.

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