

## **Confounded, augmented and constrained replicator dynamics**

*Complex selection processes and their measurement*

Holm, Jacob Rubæk; Andersen, Esben Sloth; Metcalfe, J. Stanley

*Published in:*  
Journal of Evolutionary Economics

*DOI (link to publication from Publisher):*  
[10.1007/s00191-016-0477-1](https://doi.org/10.1007/s00191-016-0477-1)

*Publication date:*  
2016

*Document Version*  
Accepted author manuscript, peer reviewed version

[Link to publication from Aalborg University](#)

*Citation for published version (APA):*  
Holm, J. R., Andersen, E. S., & Metcalfe, J. S. (2016). Confounded, augmented and constrained replicator dynamics: Complex selection processes and their measurement. *Journal of Evolutionary Economics*, 26(4), 803-822. <https://doi.org/10.1007/s00191-016-0477-1>

### **General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal -

### **Take down policy**

If you believe that this document breaches copyright please contact us at [vbn@aub.aau.dk](mailto:vbn@aub.aau.dk) providing details, and we will remove access to the work immediately and investigate your claim.

# Confounded, augmented and constrained replicator dynamics

## Complex selection processes and their measurement

*J. R. Holm      E. S. Andersen      J. S. Metcalfe*

Corresponding author: J. R. Holm, [jrh@business.aau.dk](mailto:jrh@business.aau.dk). This is the final but pre-proof version for JEE.

The final and published version is DOI:10.1007/s00191-016-0477-1

### Abstract

The quantitative methodology derived from replicator dynamics for empirical studies of economic evolution is becoming increasingly well developed in theory but is rarely applied in practice. One reason is the relatively naïve nature of current methods, which focus on the evolution of a single characteristic in a single environment. This assumption constrains the analysis of real selection processes in which firms operate in several markets and their products have several characteristics that interact to determine fitness. This entails that measurement of economic selection becomes confounded: characteristics that are associated with firm growth are not becoming more frequent in the population. The reason for confounded selection is that characteristics interact to augment or constrain the rate and direction of evolution and one-dimensional, single trait replicator dynamics cannot cope with confounded selection. The contribution of this paper is to develop an approach that serves to explicitly analyse confounded selection. The primary elements of the method are the selection gradients of the characteristics and the covariance matrix of the characteristics. Based on these, the method motivates a taxonomy of selection based on the interaction of characteristics. Applying the method to a population of firms will shed light on potentially confounded selection. It will reveal the indirect effects of characteristics on selection and the augmentation and constraints created thereby.

**Keywords** Replicator dynamics; Economic selection; Price's equation; Multi-trait selection; Statistics of evolution

**Jel Codes:** B52; L11; C63

## 1 Introduction

Although economic evolution is in principle an easily understandable process, in practice it is surprisingly difficult to analyse. For practical reasons, it therefore remains necessary to develop a formal theory of economic evolution, one that addresses the key Schumpeterian questions, that is empirically robust at the relevant levels of analysis, and that might illuminate the problems faced by decision makers whether in firms or in government. Moreover, this formal theory should reconcile many different pieces and make connections with existing branches of economic theory and the pioneering insights of Schumpeter.

Within the context of how wealth is created from knowledge, the question of how innovations impact the economic system is crucial. This is not a matter of innovation alone, but of providing an explanation of how the system adapts to the possibilities immanent in any innovation and how it draws them out such that adaptation and innovation react to one another. The system must be understood as if every solution to an economic problem only serves to open up further problems somewhere in the system. The problems are dynamic, they relate to process, and it is process that we have to elucidate.

To be precise, we wish to explain the rate at which innovations are absorbed into the economic structure, displacing established methods in the process. We are addressing creative destruction in matters small and the large, and this involves structural change in the economy and differential growth in the use of innovations and their rivals. Differential growth is the essence of economic evolution, the analogue to fitness in formal biological theory.

Standard evolutionary theory gives the following formal answer for economic systems that select with respect to only one dimension:

1. Technical characteristics of innovations are converted into economic characteristics through the prevailing price system, to define effective variation in the unit costs and qualities of products and services. Formal evolutionary theory analyses the varying characteristics individually.
2. Differential effective variation is the source of economic profit in Schumpeter's sense.
3. Differential profit is the basis of the differential growth of rival methods, and hence two activities that have equal profitability are selected for at the same rate. Growth and profitability are positively correlated, and this correlation is grounded in an economic explanation of processes in single markets. This is one of the oldest ideas in dynamic economic analysis.

This standard theory is very restricted. Selection is limited to one dimension (typically the unit cost characteristic), and selection is analysed in the context of only one market process, that in the product market. The theory is of great pedagogic value, but it is far too narrow to explore the questions raised in part 1 of the above answer. One problem is that the theory emphasises differential growth of methods, which generally translates into differential growth of firms,

while firm turnover is neglected (Baldwin and Rafiquzzaman, 1995; Baldwin and Gu, 2006b). Another problem is that differential growth may be caused by structural transformations that are unrelated to differential profit (Holm, 2014). However, the main problem is that each particular process of evolution normally involves multiple technical and economic characteristics and multiple markets (such as markets for products, labour and capital).

Progress towards the analysis of these more complex forms of economic evolution thus requires two additional steps:

4. The articulation of multiple dimensions of effective economic variation.
5. The extension of the market process to cover simultaneous selection in multiple markets, adding labour and capital markets to the list.

When considering multiple characteristics, the correlation between the different characteristics is crucial for evolutionary change. Firms compete not only for customers but also for employees and access to capital. Thus labour and capital markets substantially condition the rate and direction of evolution across populations of firms. The different markets do not always select upon the same characteristics. Furthermore, some of the multiple characteristics of a firm might be strongly correlated. For instance, an innovation that changes a characteristic of positive relevance in the product market might be strongly correlated with other characteristics that are valued negatively in the labour market or capital market. Formal theory based on replicator dynamics thus not only needs to account for different markets but also for the confoundedness created by correlated characteristics.

With inspiration from Rice (2004), we show that it is possible and practically feasible to quantify economic selection in empirical studies even when simultaneous selection on multiple characteristics of firms is confounding the relationship between covarying characteristics and fitness. The confounding effects of investment behaviour and financial performance may be disentangled with this methodology. However, it also has other uses such as the study of simultaneous selection in factor and output markets. Even in a straightforward model of competition in which firms compete by undercutting one another's prices, the simple assumption that labour markets are less than perfect and that growing firms hence must offer a relatively high wage rate to attract employees, and thus have higher unit costs, entails that the relationship between profitability and growth becomes confounded (Metcalf, 1997; Baldwin and Gu, 2006a; Metcalf and Ramlogan, 2006). Once profits are imperfectly correlated with investment decisions, we must go beyond traditional versions of replicator dynamics. This is necessary because it is not assured that the most competitive firm in terms of unit costs is also the fittest firm, in the evolutionary sense of having the fastest rate of growth among its population of rivals. The contribution of the paper is to extend the usefulness of replicator dynamics in both modelling and empirical studies in a way that makes replicator dynamics able to describe economic selection when selection depends on multiple and interacting factors.

This paper proceeds as follows. In section 2, we highlight the proliferating use of replicator dynamics for both modelling and empirical analysis, and emphasise the limitations of current theory for analysing selection in markets. In section 3, we present a framework and a methodology for addressing the confoundedness produced by multivariate selection. In section 4 we apply the methodology to simulated data. Section 5 summarises and concludes. The paper is followed by an appendix with a guide for applying the proposed method with empirical data.

## 2 Applications of replicator dynamics

The replicator dynamics based methodology for empirical studies of economic evolution is becoming increasingly well developed theoretically. However, empirical and simulation application remains highly limited as replicator dynamics still only address a single variable at a time and hence only allows for analysis of a single characteristic in a single environment. This limits the analysis of real selection processes in which firms operate in several markets and their products have several characteristics that interact to determine fitness. Characteristics interact to augment or constrain selection, and one-dimensional, single trait replicator dynamics cannot cope with such confounded selection.

Replicator dynamics represent a basic tool in evolutionary game theory and are also widely applied in modelling in evolutionary economics (Hodgson and Huang, 2012; Safarzynska and van den Bergh, 2010; Windrum, 2007; Metcalfe, 1998). Replicator dynamics are also linked to empirical studies, as the “selection” “reallocation” or “inter-agent” term of productivity decomposition studies is often a version of replicator dynamics (Hözl, 2015; Holm, 2014; Metcalfe, 2008; Andersen, 2004). Simple replicator dynamics can be applied to numerous areas, but attempts at extending either replicator dynamics or the derived decomposition equations for empirical application have nevertheless proliferated (Andersen and Holm, 2014; van Veelen, 2011; Safarzynska and van den Bergh, 2011). Ultimately, replicator dynamics are a formalisation of the evolution of frequencies of strategies in a population. Replicator dynamics describe how the change in the frequency of one strategy depends on the frequencies of other strategies by specifying that the change in the frequency of a strategy depends on the fitness of that strategy relative to the average fitness in the population. Replicator dynamics can be formalised in a number of ways, but they share the common features of being deterministic, monotonic and, often, non-linear transformations of fitness to growth. The formalisation in equation 1 is chosen here because it relates directly to the model employed in section 4 of the current paper.

$$s'_i = s_i \frac{W_i}{\bar{W}} = s_i w_i \quad (1)$$

$s_i$  is the population share of strategy  $i$ , and  $s'_i$  is the population share at a later point in time.  $W_i$  is the absolute fitness of strategy  $i$ ,  $\bar{W} = \sum_i s_i W_i$

is the average fitness and  $w_i$  is the relative fitness. Fitness is determined in a non-linear manner based on the characteristics of the strategy, the vector  $z_i$ . In the simple case in which  $z_i$  only contains one characteristic and higher values of the characteristic monotonically translate into greater fitness, there will be positive covariance between a strategy's characteristic  $z_i$  and the change in the frequency of the strategy,  $\Delta s_i = s'_i - s_i$ . This principle is applied in empirical decompositions in the tradition of Foster et al (1998) and related approaches, where the contribution from economic selection to the change in the average characteristic in a population is quantified by equation 2.

$$\text{Selection effect} = \sum_i (\Delta s_i)(z_i - \bar{z}) = \text{Cov}(w_i, z_i) \quad (2)$$

The close relationship between the replicator dynamics of equation 1 and the selection effect of equation 2 is discussed in detail in Cantner (2014). Equation 2 is an example of what may be called positive directional selection, as the average characteristic in the population is driven continuously towards higher values by selection. Andersen and Holm (2014) derive alternative specifications for other types of selection. In the current paper we generalise the selection effect in equation 2 so that it can be applied in empirically more relevant cases where fitness can depend on more than one characteristic.

In empirical application, a strategy ( $i$ ) is normally a firm and its frequency,  $s_i$ , is the population share of the firm measured using a relevant size variable. In an empirical study of firm growth, it would not be reasonable to assume that growth depends only on one characteristic. Other characteristics, which are potentially correlated with  $z_i$ , will also affect growth and hence whether the average,  $\bar{z}$ , will tend to grow in the population. Studying the relationship between correlated characteristics and the evolution of  $\bar{z}$  leads us to a taxonomy of confounded selection, which is closely linked to our methodology for empirically accounting for such confounding effects of additional variables on the selection effect of equation 2. In order to explore and demonstrate the method and taxonomy in a controlled setting allowing for pure cases we rely on simple simulated data.

The primary elements of the method are the selection gradients of the characteristics and the covariance matrix of the characteristics. Based on these, the method motivates the taxonomy of selection based on the interaction of characteristics. This is done in a formal way but thinking in terms of confounded, augmented and constrained selection can help a variety of statistical approaches that dig deeper into the muddles of economic evolution.

### 3 Analytical framework for multivariate selection

Metcalf (1994) moved from R. A. Fisher's specific theorem of genetics-based natural selection to the general "Fisher Principle" to make the work of the great statistician and evolutionary biologist relevant for evolutionary economics. The Fisher Principle states that "in the context of a population of diverse behaviours

across which selection is taking place in a constant environment, the rate of change of mean behaviour is a function of the degree of variety in behaviour across the population.” Under such circumstances, the gradually evolving mean behaviour becomes increasingly informed about and adapted to the environment of the population. Evolutionary economists have formalised and applied this principle in the study of simple selection and evolution in simple environments in a variety of ways, which are generalised by replicator dynamics. However, the conditions of Fisher’s Principle are seldom fulfilled. First, the stability or lawful patterning of the environment of an economic population obviously cannot always be taken for granted. Second, selection can work on a number of more or less conflicting behavioural characteristics. For example, a fluctuating environment may repeatedly shift the characteristics on which selection focusses. Furthermore, the input markets and the output markets can emphasise conflicting population characteristics. Third, the importance of multiple and shifting characteristics means that it is often not obvious which characteristics of behaviour have to be recreated when old variance has been used up by the selection process.

The development of Fisher’s Principle towards an extended and more operational toolbox for theoretical and applied evolutionary economics involves a large research agenda. The turbulent environment and its shifting focus on different behavioural characteristics have, to some extent, been addressed by innovation studies. Furthermore, industrial dynamics examined the systematic change in selective focus across behavioural characteristics during the industry life cycle. However, we nevertheless lack general principles and statistical methods for coping with the selection and evolution of multiple and potentially conflicting characteristics of behaviour. The lack of analytical tools seems to have slowed the move from the well-understood univariate analysis to the general analysis of multivariate selection and evolution. In turn, the lack of multivariate analysis has decreased the analytical clarity and power of evolutionary economic studies attempting to extend Fisher’s Principle in other directions.

The move from univariate to multivariate selection has already been made within evolutionary biology. The statistical procedures for theorising and data analysis can be traced back to Fisher (1930), but a very helpful advance was made by the Chicago School, a group of Chicago biologists working within quantitative genetics in the late 1970s and early 1980s (Lande and Arnold, 1983; Connor and Hartl, 2004). The Chicago approach to phenotypical selection and evolution is based on the statistical analysis of the fundamental requirements for any evolutionary process: the variance of the characteristics of the population, the covariance between characteristics and the reproduction of members, and the inter-temporal inertia of the characteristics. By focusing on these requirements for phenotypical 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; Kingsolver and Pfennig, 2007). This use has been eased by reformulations and developments by, e.g., Rice (2004) of the Chicago school approach in relation to the very general analytical framework of Fisher and George Price. With some caution and modi-

fication, the approach can also be used for the analysis of economic selection and evolution. As we have already developed the basic analytical framework elsewhere (Andersen, 2004), in the following we move quickly from Price's Equation to the Chicago novelties with respect to evolutionary economics.

### 3.1 Univariate selection as a starting point

Price (1970, 1995) worked at a deeper level than the Chicago School. He thought in terms of a population that is studied at two subsequent points of time,  $t$  and  $t'$ . He assumed that any member of the  $t'$ -population can be connected to a member of the  $t$ -population. This made it possible for him to define absolute fitness for each  $t$ -member as the number by which to multiply its size at  $t$  to determine its representation in the  $t'$ -population. Then, Price defined evolution as the change in the population mean of a characteristic between the two points in time. He also defined selection as the part of evolution that can be explained by the covariance between the characteristic values of the members of the  $t$ -population and their fitness. The residual of the evolutionary change in the mean characteristic is explained fully by mean intra-member change evaluated in the  $t'$ -population. Thus Price's Equation—or Price's Identity—can be written as

$$\text{Total evolutionary change} = \text{Selection effect} + \text{Intramember effect} \quad (3)$$

Equation 3 suggests basic analyses that apply two subsequent population censuses. As we emphasise selection, we call them the pre-selection census and the post-selection census. When necessary, we distinguish by adding a prime to variables that relate to the post-selection census. The two censuses provide the basis for calculating statistics on fitness and characteristics and the relationships between them. This procedure can be presented in three basic steps (Andersen and Holm, 2014):

- A-1 In each of the two censuses, we measure the population share of each member. Then, we calculate the relative fitness of each member as the ratio of its population shares after and before selection relative to the fitness of the population as a whole. Thus the population has mean relative fitness  $\bar{w} = 1$ .
- A-2 The censuses provide information on a focal characteristic,  $z_1$ , of the members of a population. In each census, we measure the characteristic value of  $z_1$  for each member, and we calculate the member-level change in  $z_1$  between the two censuses. We then calculate the weighted means of  $z_1$  in each of the two censuses,  $\bar{z}_1$  and  $\bar{z}'_1$ , and the change in the mean between censuses,  $\Delta\bar{z}_1$ . We also calculate the weighted mean of the member-level change in the characteristic,  $E(w\Delta z_1)$ . However, in the present paper, we focus on selection and assume that  $\Delta z_1 = 0$  for all members such that  $E(w\Delta z_1)=0$ .



A-3 We use the member-level information to calculate the covariance between fitness and the characteristic  $z_1$ ,  $Cov(w, z_1)$ , which corresponds to replicator dynamics, cf. equation 2. This covariance is equal to the product of the regression of fitness on the characteristic and the variance of the characteristic,  $\beta_{w,z_1}^{Total} Var(z_1)$ . (The superscript “Total” is used to distinguish  $\beta_{w,z_1}^{Total} Var(z_1)$  from later  $\beta$ s which are all partial regressions coefficients.)

Much can be learned by following this procedure. For example, we can turn to simple applications of Price’s Equation (4) for analysing the relative importance of the selection effect and the intramember effect with respect to individual characteristics

$$\Delta \bar{z}_1 = Cov(w, z_1) + E(w \Delta z_1) = \beta_{w,z_1}^{Total} Var(z_1) + E(w \Delta z_1) \quad (4)$$

The practical implementation of Price’s Equation (4) serves to study the process of directional univariate selection. However, the Chicago school has promoted an analytical distinction between different types of selection. Although we have already addressed this contribution (Andersen and Holm, 2014), it is worth repeating that it is important to add other types of selection to the directional selection implied by Fisher’s Theorem and Fisher’s Principle. While most thinking on selection within evolutionary economics has been dominated by the positive or negative directional selection that results in a change in the mean of a characteristic, it is possible to define other types of selection that can occur with a constant mean of the population.

### 3.2 Multivariate selection

The developers and users of the Chicago approach share an interest in the directional selection of Fisher and Price. However, they normally focus on more concrete problems connected with artificial selection and natural selection in the wild. In the context of artificial selection, the emphasis is on the selection differential, i.e., the difference between the mean value of the parents chosen for breeding and the mean value of all potential parents in the population. In other words, the selection differential is the change in  $\bar{z}_1$  that can be ascribed solely to selective reproduction and thus can be modelled with replicator dynamics. In terms of equation 4, the selection differential is  $Cov(w, z_1)$ . However, this selection differential is the combined result of direct selection on the studied characteristic and the indirect effects on that characteristic of (artificial) selection working on other characteristics. In these connections, the problems of addressing selection on multiple characteristics are obvious. For example, when breeders are performing artificial selection, they recognise that by selecting on a single characteristic, they are often co-selecting unwanted characteristics. The Chicago approach addresses this and similar problems by thinking of total evolutionary change as a vector that consists of the changes in a number of different characteristics (e.g., Lande and Arnold (1983)).

To confront such issues, the Chicago school has provided two new tools. The first tool is the vector of selection gradients, i.e., the direct effects of selection

on the different characteristics. While a selection differential includes both the direct and the indirect selection on a characteristic, a selection gradient is the partial regression of relative fitness on a characteristic. Thus the selection gradient ignores indirect selection due to other analysed characteristics and measures only the direct selection of the characteristic in question. The selection gradient in equation 4 is  $\beta_{w,z_1}^{Total}$ . As equation 4 is Price's equations for a single characteristic, there are no indirect effects and the distinction between the selection gradient and selection differential is trivial in equation 4. The second tool for coping with multiple characteristics is the matrix of phenotypic covariances between characteristics. This matrix reflects the fact that different characteristics may be interdependent. For example, we have the case in which members of the  $t$ -population that have high values of one characteristic also tend to have high (or low) values of coupled characteristics. This means that when selection acts directly on one characteristic, it also influences the population mean of more or less closely coupled characteristics. The elements of the phenotypic covariance matrix can be zero, positive, or negative.

By combining the two new tools, we can understand the strange ways in which the process of selection on coupled characteristics might operate. For instance, a change in the mean of the focal first characteristic is potentially influenced by all the studied characteristics. The selection effect in equation 3 now consists of one direct effect and multiple indirect effects. The direct effect is derived by multiplying the first element of the covariance matrix by the first element of the vector of selection gradients. Thus, we are multiplying a covariance by a partial regression coefficient. However, as we are here concerned with the covariance of the first characteristic with itself, we are actually multiplying the variance of the first characteristic by the efficiency of direct selection on that characteristic. The indirect effects might involve important covariances (and thus correlations). For example, the first indirect effect on the change in the mean of the first characteristic is obtained by multiplying the covariance between characteristics  $z_1$  and  $z_2$  by the selection gradient of characteristic  $z_2$ . Surprising observations can result from this multiplication because the covariance might be negative and the selection gradients of characteristics  $z_1$  and  $z_2$  might have opposite signs. Thus this indirect selection of characteristic,  $z_1$ , might remove or invert a positive direct selection on characteristic  $z_1$ . However, although the effects of such couplings of characteristics have been analysed intensively by evolutionary biology, discussion persists concerning the frequency of this phenomenon in nature (Agrawal and Stinchcombe, 2009).

The Chicago approach to multivariate selection can be clarified by extending the above procedure for studying univariate selection. We still have two censuses and calculate statistics on fitness and characteristics as well as the relationships between them. Furthermore, we continue to exploit the convenience of operating in the short run. In contrast to long-term analysis, this approach allows to concentrate on selection to a greater degree and thus minimise the importance of some of the huge differences between economics and biology. We also believe that the simple short-term framework helps to think clearly about concepts and measurements of selection. Finally, in numerous countries, immensely rich data

on each firm and each citizen have become available for relatively short-term social science analysis.

To apply the Chicago approach, we must redefine the three steps in the procedure.

- B-1 We extend the censuses beyond the focal characteristic to cover a set of new characteristics labelled from 2 to  $n$ . We do so by repeating steps (A-1) and (A-2) for each additional characteristic. One of the results is that we are provided with a vector of changes of mean characteristics

$$\Delta \bar{\mathbf{z}} = \begin{bmatrix} \Delta \bar{z}_1 \\ \vdots \\ \Delta \bar{z}_n \end{bmatrix}$$

The aim is to explain this vector with particular emphasis on  $\Delta \bar{z}_1$ . We have much of the information needed for this analysis, but steps (B-2) and (B-3) provide us with crucial tools.

- B-2 For the pre-selection census, we check whether the characteristics are correlated by extending step (A-3) and calculating the “phenotypic” covariance matrix

$$\mathbf{P} = \begin{bmatrix} P_{11} & \cdots & P_{1n} \\ \vdots & \ddots & \vdots \\ P_{n1} & \cdots & P_{nn} \end{bmatrix} = \begin{bmatrix} Cov(z_1, z_1) & \cdots & Cov(z_1, z_n) \\ \vdots & \ddots & \vdots \\ Cov(z_n, z_1) & \cdots & Cov(z_n, z_n) \end{bmatrix}$$

where the diagonal represents variance, because, e.g.,  $Cov(z_1, z_1) = Var(z_1)$ . The phenotypic covariance matrix is computed from a census rather than a sample, and hence it is computed as a weighted population covariance matrix. See the appendix for further computational issues. The remainder of the symmetric matrix is filled with covariances, where, e.g.,  $Cov(z_1, z_n) = Cov(z_n, z_1)$ .

- B-3 We end the census-related work by calculating the vector of partial regressions of fitness on each of the characteristics

$$\beta = \begin{bmatrix} \beta_{w,z_1} \\ \vdots \\ \beta_{w,z_n} \end{bmatrix}$$

We have an interesting case if, for example, the selection coefficient,  $\beta_{w,z_1}$ , differs from  $\beta_{w,z_1}^{Total}$ .

These redefined steps in the procedure promote the analysis of multivariate selection. We can thus use the  $\mathbf{P}$  matrix and the vector of selection gradients for the characteristics to describe the responses to selection pressures that

act simultaneously on these characteristics. In condensed matrix format, the equation is

$$\Delta \bar{\mathbf{z}} = \mathbf{P} \boldsymbol{\beta} \quad (5)$$

Let us, for example, expand the mean change in the first characteristic for the case in which there are only two characteristics, extending the assumption that  $E(w\Delta z_1) = 0$  to  $E(w\Delta z_j) = 0$ ,  $j = (1, 2)$

$$\Delta \bar{z}_1 = \beta_{w,z_1} \text{Var}(z_1) + \beta_{w,z_2} \text{Cov}(z_1, z_2)$$

Here, the evolutionary response to selection on the first characteristic has two components. First, there is the direct response to selection,  $\beta_{w,z_1} \text{Var}(z_1) = \beta_{w,z_1} \text{Cov}(z_1, z_1)$ , which consists of the change in the mean of characteristic  $z_1$  due to selection acting directly on characteristic,  $z_1$ . Second, there is the indirect response to selection due to covariance. Thus,  $\beta_{w,z_2} \text{Cov}(z_1, z_2)$  represents the indirect change in the mean of characteristic,  $z_1$ , due to its covariance with characteristic  $z_2$ .

It is, of course, possible that the change in the mean of characteristic  $z_1$  is entirely or largely due to the direct selection on characteristic  $z_1$ . Another possibility is that the correlate response to selection on characteristic  $z_2$  dominates the direct response. In the extreme case, direct selection tends to produce high levels of the first characteristic, while its mean becomes smaller due to negative covariance or to a low value of the other characteristic.

These and other possibilities are presented in table 1. Here, we distinguish among five types of bivariate directional selection (cf. Connor and Hartl (2004), p. 223). If we ignore the case in which bivariate selection reduces to two univariate selections, we can classify the outcomes in terms of the signs of the selection coefficients and the covariance of characteristics. For example, negative covariance of the characteristics and selection with opposite signs leads to the negative augmentation of direct selection. However, when covariances remain negative while coefficients have the same sign, we are facing what might be called a correlation constraint on the evolution of the characteristics.

The taxonomy in table 1 covers only characteristics that are subject to directional selection and only one confounding characteristic. It is this latter characteristic that augments or constrains the selection pressure that works on the focal characteristic. However, we can nevertheless use the taxonomic labels on the aggregate effects of several confounding characteristics. Even here, selection on the focal characteristic can still be augmented by selection on other characteristics. It can also be constrained. In the extreme case, a strong selection pressure on the focal characteristic can translate into zero evolutionary change due to selection on confounding characteristics. The taxonomy in table 1 concerns directional selection, but it can be generalised to also include stabilising and diversifying selection. This would not require further categories, only more careful and less elegant definitions and examples in which the selection gradients are allowed to be zero. In the remainder of the paper, we focus on

Tab. 1: Effects on evolutionary change of signs of selection coefficients and correlations of characteristics

Type of directional selection on two characteristics	Definition	Stylised example for $\Delta\bar{\mathbf{z}} = \mathbf{P}\beta$
Univariate selection	No covariance of characteristics	$\begin{bmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{bmatrix} = \begin{bmatrix} Var(z_1) & 0 \\ 0 & Var(z_2) \end{bmatrix} \begin{bmatrix} > 0 \\ > 0 \end{bmatrix}$
Positive augmentation	Positive covariance of characteristics + gradients with same sign	$\begin{bmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{bmatrix} = \begin{bmatrix} Var(z_1) & > 0 \\ > 0 & Var(z_2) \end{bmatrix} \begin{bmatrix} > 0 \\ > 0 \end{bmatrix}$
Negative augmentation	Negative covariance of characteristics + gradients with opposite sign	$\begin{bmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{bmatrix} = \begin{bmatrix} Var(z_1) & < 0 \\ < 0 & Var(z_2) \end{bmatrix} \begin{bmatrix} > 0 \\ < 0 \end{bmatrix}$
Gradient constraint	Positive covariance of characteristics + gradients with opposite sign	$\begin{bmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{bmatrix} = \begin{bmatrix} Var(z_1) & > 0 \\ > 0 & Var(z_2) \end{bmatrix} \begin{bmatrix} > 0 \\ < 0 \end{bmatrix}$
Correlation constraint	Negative covariance of characteristics + gradients with same sign	$\begin{bmatrix} \Delta\bar{z}_1 \\ \Delta\bar{z}_2 \end{bmatrix} = \begin{bmatrix} Var(z_1) & < 0 \\ < 0 & Var(z_2) \end{bmatrix} \begin{bmatrix} > 0 \\ > 0 \end{bmatrix}$

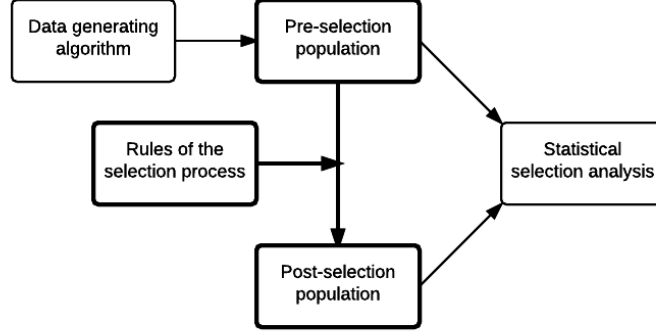


Fig. 1: The modelling strategy

the taxonomy defined in table 1 and avoid unnecessary complications following from further generalisation.

#### 4 Modelling and simulation results

In this section, we will demonstrate how selection may be confounded. The modelling strategy has two steps: a data-generating algorithm and a deterministic selection process. The data-generating algorithm is a set of rules for defining the pre-selection population. It is at this step that we may introduce correlation among the traits of business units. The selection process determines how the pre-selection population evolves into the post-selection population. At this step, we may implement different selection functions based on different assumptions regarding the characteristics of firms. Finally, the evolution from the pre-selection to post-selection population is analysed using the method presented in the current paper: the identity in equation 5. This step is merely a measurement step, and we have no influence on the results at this step. The strategy is illustrated in figure 1.

When evaluating whether selection is confounded, we compare the selection gradients with the observed evolutionary change. Selection is argued to be confounded when these have opposite signs. That is,  $\bar{z}_1 > 0$  while  $\beta_{w,z_1} < 0$  entails that selection on  $z_1$  is confounded in the sense that firms with relatively high values of  $z_1$  have decreasing population shares, despite that the mean of  $z_1$  is increasing in the population. Each simulation will be repeated 100 times for robustness and the results plotted in  $\bar{z}_1$  by  $\beta_{w,z_1}$  space.

The pre-selection population will consist of 100 firms. Each firm is characterised by a vector of three characteristics:  $z_i = (z_{1,i}, z_{2,i}, z_{3,i})$ . In a more general model, firms might enter and exit, and the characteristics of a firm would change over time through adaptation and innovation, but these complications are not included here because they are inconsequential for the aim of

the paper, as explained earlier. Thus, the evolution of the characteristics in the population,  $\Delta \bar{\mathbf{z}}$ , is described fully by  $\Delta \bar{\mathbf{z}} = \mathbf{P}\beta$ . Any change in the means of the characteristics must come from the relative growth or decline of firms.

The data-generating algorithm proceeds as follows: the three characteristics are all drawn from standard normal distributions with correlation matrix  $\rho$ . All firms have equal population shares in the pre-selection population:  $s_i = 0.01 \forall i$ .

For the rules of the selection process, we follow the general lines applied in Andersen and Holm (2014). This means that we specify a deterministic function for absolute fitness. We then transform the outcome into relative fitness and allow the population to evolve according to equation 6.

$$s'_i = s_i w_i \quad (6)$$

Relative fitness is defined as absolute fitness divided by population fitness,  $w_i = W_i / \bar{W}$ , and absolute fitness is determined by the following relationship

$$W_i = (1 + C)^{F(z_i)} \quad (7)$$

The general fitness function specified in equation 7 is an exponential function. The parameter  $C$  determines the pace of evolution in the sense that a firm will grow by  $C * 100$  per cent as many times as specified by the exponent. The specification of the exponent determines the type of selection. In the current paper, we have chosen a specification in which there is negative directional selection on  $z_1$  and positive directional selection on  $z_2$  and  $z_3$ . The exponent is determined as

$$F(z_i) = -(z_{1,i} - \bar{z}_1) + (z_{2,i} - \bar{z}_2) + (z_{3,i} - \bar{z}_3) \quad (8)$$

The rules of the selection process are uniform in all of the simulations presented in the current paper.  $C$  is fixed at 0.5. This sets a relatively high pace for evolution but allows us to disregard the possibility of multiple time periods between the pre- and post-selection populations. The data-generation algorithm is also the same in all simulations except for the value of  $\rho_{12}$  and thus also  $\rho_{21}$ : the correlation between the standard normal distributions from which  $z_1$  and  $z_2$  are drawn.

$$\rho = \begin{bmatrix} 1 & \rho_{12} & 0 \\ \rho_{21} & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \quad (9)$$

In all simulations, there will be positive directional selection on  $z_3$ , which is independent of the other characteristics. There will also be positive directional selection on  $z_2$ , but this characteristic will, to varying degrees, be correlated with the characteristic,  $z_1$ , upon which there is negative directional selection.

#### 4.1 Baseline simulation ( $\rho_{12} = 0$ )

In the first simulation, the three traits of the firms are uncorrelated;  $\rho_{12} = 0$  in equation 9 above. The pre-selection population is described by the vector of

$$\begin{bmatrix} \Delta \bar{z}_1 \\ \Delta \bar{z}_2 \\ \Delta \bar{z}_3 \end{bmatrix} = \begin{bmatrix} -0.376 \\ 0.469 \\ 0.350 \end{bmatrix} = \begin{bmatrix} -0.139 \\ 0.613 \\ 0.242 \end{bmatrix} - \begin{bmatrix} 0.239 \\ 0.145 \\ -0.108 \end{bmatrix} = \begin{bmatrix} 1.174 & 0.042 & 0.190 \\ 0.042 & 1.108 & 0.051 \\ 0.190 & 0.051 & 0.929 \end{bmatrix} \begin{bmatrix} -0.406 \\ 0.418 \\ 0.436 \end{bmatrix}$$

Fig. 2: Result from a baseline simulation

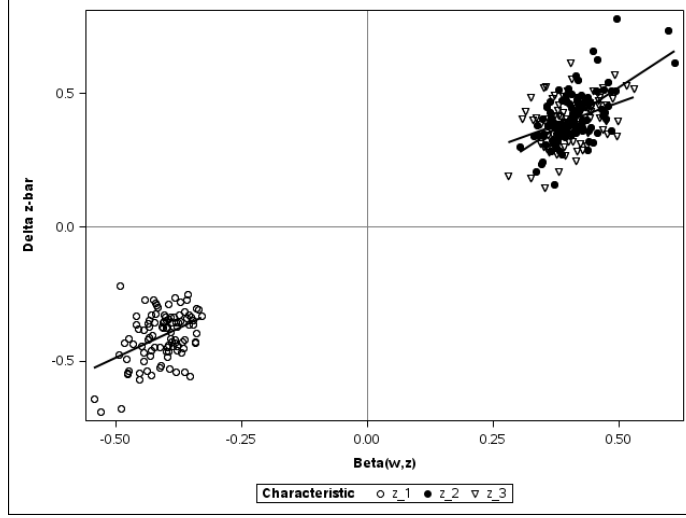


Fig. 3: 1000 baseline simulations

mean characteristics,  $\bar{\mathbf{z}}$ . After having been subject to the deterministic selection process described in equations 6 through 8, the post-selection population is created, and it is described by  $\bar{\mathbf{z}}'$ . The evolution of the population is described by the change in mean characteristics,  $\Delta \bar{\mathbf{z}}$  (step B-1). This evolution is then decomposed into the variance-covariance matrix of the characteristics (step B-2) and the vector of selection gradients (step B-3). In a typical baseline simulation, the results look as presented in figure 2. The mean of the characteristic  $z_1$  has decreased by 0.376, while the means of the remaining two characteristics have increased by approximately the same magnitude. This is in accordance with the assumed directional selection processes. The final product on the right is the decomposition of the selection differential,  $\mathbf{P}\beta$ . The selection gradients reflect the assumed selection processes and correspond to the observed evolution in means:  $z_2$  and  $z_3$  have positive selection coefficients (0.418 and 0.436, respectively), while  $z_1$  has a coefficient of  $-0.406$ .

Figure 3 plots the results from figure 2 along with 99 additional simulations with the baseline specification. The values of the  $(\beta_{w,z_1}, \Delta \bar{z}_1)$  pairs cluster in the bottom left while the values of  $(\beta_{w,z_2}, \Delta \bar{z}_2)$  and  $(\beta_{w,z_3}, \Delta \bar{z}_3)$  cluster at the top right corner.



Figure 3 also includes three regression lines, one for each characteristic. All three have a positive slope, indicating that there is a positive relationship between the gradient and the change in mean. The slope of the regression line and the clustering of the data points show that selection is not confounded: observing that a characteristic is becoming more (less) frequent in the population allows us to assume that it is positively (negatively) related to firm growth. In a population where the change in the average characteristic is greater, we may even assume that the significance of the characteristic for firm growth is also greater.

## 4.2 Simulations with positive correlation ( $\rho_{12} > 0$ )

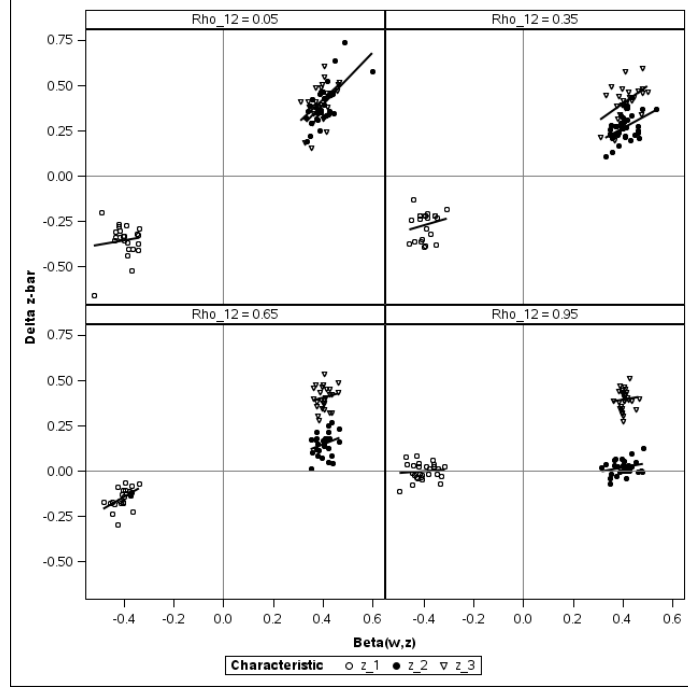
In this section, we will present the results from assuming that  $\rho_{12} \neq 0$ . Specifically, we will let the correlation approach unity in a stepwise manner that can be illustrated in a series of simulations. Adding correlation between  $z_1$ , upon which there is negative directional selection, and  $z_2$ , upon which there is positive directional selection, is expected to lead to confounded selection, as the selection mechanism will drive  $\bar{z}_1$  down and  $\bar{z}_2$  towards ever higher values, while they are positively correlated at the firm level. In the taxonomy introduced in section 3, this is a case of gradient constraint selection. The correlation between  $z_1$  and  $z_2$  constrains  $\bar{z}_1$  from decreasing, and it constrains the growth in  $\bar{z}_2$  to be lower than would otherwise be the case.

The results from specifying  $\rho_{12} = 0.05$  to  $\rho_{12} = 0.95$  in increments of 0.3 are shown in figure 4. This yields a total of four different parameterisations. Compared to figure 3 (where  $\rho_{12} = 0$ ), it does not make a substantial difference if instead  $\rho_{12} = 0.05$ . However, as the correlation increases, the data points describing the evolution of  $\bar{z}_1$  and  $\bar{z}_2$  cluster closer and closer to the horizontal axis. In this region, selection is confounded:  $\Delta\bar{z}_1$  is positive, while  $\beta_{w,z_1}$  is negative, meaning that the average of  $z_1$  is increasing in the population but firms with high values of  $z_1$  have relatively low growth. The reason that this can happen is that  $z_1$  is correlated with  $z_2$ , upon which there is positive directional selection, vice versa for the evolution of  $\bar{z}_2$ .

Figure 5 shows one of the results from the bottom-right panel of figure 4 in greater detail. The selection gradients, the final element on the right, take approximately the same value as in figure 2. This is because evolution follows the exact same deterministic fitness function. Any variation is due to the stochastic data-generation algorithm. The observed evolution, however, differs from figure 2:  $\bar{z}_2$  has only increased slightly (0.127) despite the strong selection on the characteristic, and  $\bar{z}_1$  has even increased (0.079) despite strong negative selection.

## 5 Conclusions

Economic evolution is the combined result of innovation in firms and selection within and between them. Selection is often modelled using replicator dynamics, and this entails assuming that selection is based on a single characteristic

Fig. 4: Four different parameterisations for  $\rho_{12}$ 

$$\begin{bmatrix} \Delta \bar{z}_1 \\ \Delta \bar{z}_2 \\ \Delta \bar{z}_3 \end{bmatrix} = \begin{bmatrix} 0.079 \\ 0.127 \\ 0.583 \end{bmatrix} = \begin{bmatrix} -0.042 \\ 0.005 \\ 0.656 \end{bmatrix} - \begin{bmatrix} -0.121 \\ -0.122 \\ 0.073 \end{bmatrix} = \begin{bmatrix} 1.036 & 1.029 & 0.266 \\ 1.029 & 1.122 & 0.264 \\ 0.266 & 0.264 & 1.375 \end{bmatrix} \begin{bmatrix} -0.513 \\ 0.482 \\ 0.431 \end{bmatrix}$$

Fig. 5: A result from a simulation with  $\rho_{12} = 0.95$

reflecting a single uniform selection environment in which all firms are treated equally. This assumption constrains the analysis of real selection processes in which the firm operates in several markets and has products with several characteristics. From a simplified perspective, this means that we are facing confounded selection that cannot be addressed by standard replicator dynamics. This paper develops a statistical approach that serves to analyse confounded selection explicitly and illustrates the proposed method by means of simulation.

The results show how observed evolutionary change may not convey the suspected information about selection gradients. As an example, consider a population in which there is selection on, *inter alia*, firms' wage costs and the adaptability of the work force. For the former, there is negative directional selection: lower costs mean higher growth; for the latter, there is positive directional selection: firms that can easily adapt their workforce grow more than others. However, the correlation between these two variables – labour turnover entails a loss of tacit knowledge and incurring retraining costs – means that we would not be able to infer the importance of either characteristic for firm growth from the observed change in the mean characteristic at the population level. In this example, it is plausible that neither characteristic's mean would change at all, despite that a micro-level regression analysis would show that both are important for firm growth. As in this example, the simulations show quantitatively how population dynamics constrain the evolution of aggregate variables towards values that would be deemed "optimal" in an atomistic study of firm behaviour. A regression analysis does not, on the contrary, necessarily allow for forecasting of evolutionary change. Even if the regression analysis shows that a characteristic has a large effect on firm growth, the characteristic will not become more frequent in the population if selection is confounded.

Despite this comparison it is important to keep in mind that methodologies for decomposing evolutionary change are very different from regression analysis. Regression analysis attempts to identify the effect of a characteristic on firm growth while decomposition analysis charts the role of differential growth on the change in average characteristic. Decomposition analyses rely on two or more full population censuses to quantify population dynamics, whereas regression provides estimates of effects at the level of population members from a sample of data.

Correlation is vital in evolution. It determines the direction of change in the characteristics of a population, but we may be mistaken if we interpret observed change as indicating correlation, as the correlation between a characteristic and fitness can be mediated by other characteristics, and hence the determinants of fitness fail to actually correlate with fitness.

The simulations and the above example were constructed around a process exhibiting gradient-constrained selection, but we could easily have included the other types of confounded selection defined in table 1. Positive or negative augmented selection would be created by setting  $\rho_{23} > 0$  or  $\rho_{12} < 0$ , respectively. Correlation-constrained selection could have been included by setting  $\rho_{23} < 0$ . It is even possible to go beyond directional selection processes and incorporate stabilising or diversifying selection in the simulations by adapting the  $F(\cdot)$  func-

tion of equation 8. It is relatively simple to illustrate confounded selection as augmenting or constraining when selection is directional, but the phenomenon of confounded selection is not restricted to such cases.

In this paper we have developed an approach that serves to explicitly analyse confounded selection. The central elements are the selection gradients and the covariance matrix of the characteristics. Based on these, the method motivates a taxonomy of selection. The method is relatively formal but thinking in terms of confounded, augmented and constrained selection can be useful in a variety of different approaches to economic evolution. The discussions in this paper focus on the evolution of a characteristic in a population of firms, but the method is equally applicable to studies of populations of industries, regions, countries, etc. Future research applying the methodology will invariably also contribute to further generalisation of the method. Such research must necessarily consider that, for the methodology and its interpretation to be applicable, it is necessary to assume that the data are census data for the units of selection and that the measured characteristics are stable over time. Firms, or more generally business units, have characteristics that may be assumed to be stable. When instead studying a population of regions or industries, such an assumption becomes increasingly problematic, but it more likely that the data can be assumed to be a complete census. Further studies applying the methodology will have to discuss these assumptions and demonstrate the robustness of conclusions to the assumptions.

## Acknowledgements

We thank participants in the 2014 Conference of the International Schumpeter Society for very helpful comments on a draft version of this paper, as well as the editors of this journal and two anonymous reviewers. Remaining errors are our own.

## Appendix – Guide for empirical application

The starting point for any decomposition of evolution is the absolute size of members and their characteristics,  $x_i$  and  $z_{ij}$ , where  $i$  denotes the members and  $j$  indexes the characteristics. The population share of a member is defined as  $s_i = x_i / \sum_i x_i$ , and selection can then be discussed in terms of absolute fitness,  $W_i = x'_i / x_i$ , or relative fitness,  $w_i = W_i / (\sum_i s_i W_i) = s'_i / s_i$ . Recall that applying a decomposition requires the use of two censuses at each time  $t$  and  $t'$ , with  $t < t'$ , and that the prime is also used to distinguish between values taken from each census. Relying on relative fitness rather than absolute fitness does not make the computations more arduous, but it facilitates interpretation, and at least in our case, it makes the decomposition equation more parsimonious.

Table 2 contains an overview of the computations necessary to conduct the decomposition of the evolution of a vector of characteristics. A superscript  $T$  indicates a transpose and  $\bullet$  is the dot product. When performing the computa-

tions, one must note that  $Var(z)$  is the population, not the sample, variance-covariance matrix and that the vector of selection gradients,  $\beta$ , is computed in a regression that also contains an intercept, although the intercept is not included in  $\beta$ , and that this is a WLS regression.

With the elements defined in table 2, it holds as an identity for any size of the population  $m$  and any number of characteristics  $n$  that

$$\Delta \bar{z} = Var(z)\beta + E(w\Delta z) \quad (10)$$

As we assume in the expositions presented in the main text that there is no change within members,  $\Delta z = 0$ , the identity becomes  $\Delta \bar{z} = Var(z)\beta = P\beta$  as in section 3 of the main text.

In any empirical application, the expectation term would have to be included, and in many cases so would entry and exit in some manner. The vector of selection gradients would be computed as

$$\beta^* = \begin{bmatrix} \beta_0 \\ \beta_1 \\ \vdots \\ \beta_n \end{bmatrix} = \begin{bmatrix} \beta_0 \\ \beta_1 \\ \vdots \\ \beta_n \end{bmatrix} = \left( \hat{z}^{*T} \hat{z}^* \right)^{-1} \hat{z}^* \hat{w} \quad (11)$$

where  $z^*$  is the  $m \times (n+1)$  matrix

$$z^* = \begin{bmatrix} 1 & z_{11} & \cdots & z_{1n} \\ \vdots & \vdots & \ddots & \vdots \\ 1 & z_{m1} & \cdots & z_{mn} \end{bmatrix} \quad (12)$$

and hats denote weighted data, i.e.,

$$\hat{z}^* = (\sqrt{s} \bullet I_m) z^* \quad (13)$$

Tab. 2: Computations for empirical applications

Element	Dimensions	Definition
$z_{ij}$		Value of $z_j$ for member $i$ in the early census. $i = (1 \cdots m)$ , $j = (1 \cdots n)$
$z$	$m \times n$ matrix	Values of the $n$ characteristics for the $m$ members in the early census
$s$	$m \times 1$ vector	Population shares for the $m$ members
$w = s'/s$	$m \times 1$ vector	Relative fitness (i.e. growth) for each member
$\bar{z} = E(z) = z^T s$	$n \times 1$ vector	Population mean values for the $n$ characteristics
$\Delta \bar{z} = \bar{z}' - \bar{z}$	$n \times 1$ vector	Change in the $n$ population level means from $t$ to $t'$
$Var(z) = (z - \bar{z}^T)^T ((z - \bar{z}^T) \bullet s) = P$	$n \times n$ matrix	Weighted population variance-covariance matrix of the $n$ characteristics
$E(w \Delta z) = (w \bullet (z' - s))^T s$	$n \times 1$ vector	Intra member change (generally assumed to be zero in simulations; as in the main text)
$\beta$	$n \times 1$ vector	Slopes from the WLS regression $w = \beta_0 + \sum_j z_j \beta + error$ with $s$ as weights

## References

- Agrawal AF, Stinchcombe JR (2009) How much do genetic covariances alter the rate of adaptation? *Proceedings of the Royal Society B* 276(1659):1183–1191
- Andersen ES (2004) Population thinking, Price's equation and the analysis of economic evolution. *Evolutionary and Institutional Economics Review* 1(1):127–148
- Andersen ES, Holm JR (2014) The signs of change in economic evolution: An analysis of directional, stabilizing and diversifying selection based on Price's equation. *Journal of Evolutionary Economics* 24(2)
- Baldwin JR, Gu W (2006a) Competition, firm turnover and productivity growth. Statistics Canada, Economic Analysis Research Papers 11F0027MIE No. 042
- Baldwin JR, Gu W (2006b) Plant turnover and productivity growth in Canadian manufacturing. *Industrial and Corporate Change* 15(3):417–465
- Baldwin JR, Rafiquzzaman M (1995) Selection versus evolutionary adaptation: Learning and post-entry performance. *International Journal of Industrial Organization* 13(4):501–522
- Brodie ED, Moore AJ, Janzen FJ (1995) Visualizing and quantifying natural selection. *Trends in Ecology and Evolution* 10(8):313–318
- Cantner U (2014) Evolution in markets. Paper presented at the Economic Change and Evolution conference, Rome, Italy, November 10 - November 11
- Connor JK, Hartl DL (2004) *A Primer of Ecological Genetics*. Sinauer, Sunderland, Mass
- Endler JA (1986) *Natural Selection in the Wild*. Princeton University Press, Princeton
- Fisher RA (1930) *The Genetical Theory of Natural Selection*. Oxford University Press, Oxford
- Foster L, Haltiwanger J, Krizan CJ (1998) Aggregate productivity growth: Lessons from microeconomic evidence. NBER Working Paper Series 6803
- Hodgson GM, Huang K (2012) Evolutionary economics and evolutionary game theory: are they different species? *Journal of Evolutionary Economics* 22(2):345–366
- Holm JR (2014) The significance of structural transformation to productivity growth: How to account for levels in economic selection. *Journal of Evolutionary Economics* 24(5):1009–1036

- Hölzl W (2015) Sunk costs and the speed of market selection. *Journal of Evolutionary Economics* 25(2):323–344
- Kingsolver JG, Pfennig DW (2007) Patterns and power of phenotypic selection in nature. *BioScience* 57(7):561–572
- Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gibert P, Beerli P (2001) The strength of phenotypic selection in natural populations. *American Naturalist* 157(3):245–261
- Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. *Evolution* 37(6):1212–1226
- Metcalf JS (1994) Competition, Fisher’s principle and increasing returns in the selection process. *Journal of Evolutionary Economics* 4(4):327–346
- Metcalf JS (1997) Labour markets and competition as an evolutionary process. In: Arestis P, Palma G, Sawyer M (eds) *Markets, Unemployment and Economic Policy: Essays in Honour of Geoff Harcourt*, vol 2, Routledge, London and New York, pp 328–344
- Metcalf JS (1998) *Evolutionary Economics and Creative Destruction*. Routledge, London and New York
- Metcalf JS (2008) Accounting for economic evolution: Fitness and the population method. *Journal of Bioeconomics* 10(1):23–49
- Metcalf JS, Ramlogan R (2006) Creative destruction and the measurement of productivity change. *Revue de l’OFCE* 97(5):373–397
- Price GR (1970) Selection and covariance. *Nature* 227:520–521
- Price GR (1995) The nature of selection. *Journal of Theoretical Biology* 175(3):389–396
- Rice SH (2004) *Evolutionary Theory: Mathematical and Conceptual Foundations*. Sinauer Associates, Inc. Publishers, Sunderland, M. A.
- Safarzynska K, van den Bergh JCJM (2010) Evolutionary models in economics: a survey of methods and building blocks. *Journal of Evolutionary Economics* 20(3):329–376
- Safarzynska K, van den Bergh JCJM (2011) Beyond replicator dynamics: Innovation-selection dynamics and optimal diversity. *Journal of Economic Behaviour and Organization* 78(3):229–245
- van Veelen M (2011) The replicator dynamics with  $n$  players and population structure. *Journal of Theoretical Biology* 276(1):78–85
- Windrum P (2007) Neo-Schumpeterian simulation models. In: Hanusch H, Pyka A (eds) *Elgar Companion to Neo-Schumpeterian Economics*, Edward Elgar, Cheltenham and Northampton, pp 405–439