Supplementary Material for

Facts, Conventions, and the Levels of Selection

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Online Appendix

Box 1: Lewontin’s three conditions

Ever since Darwin (1859), numerous authors have proposed schemes to capture the process of evolution by natural selection. The most famous of them was offered by Lewontin (1970). There are subtle differences between these schemes (see Godfrey-Smith 2007, for a review), but nearly all have the following basic structure:

> For evolution by natural selection on a trait to occur in a collection of entities, the following three conditions should be met:
>
> 1. *The entities exhibit variation on that trait*
> 2. *The variation is associated with differences in fitness*
> 3. *The variation is heritable*

This basic scheme is riddled with ambiguities and problems. For instance, one is not told what exactly is meant by ‘fitness’ beyond differences in reproductive output. The scheme is also described in a statistical rather than causal fashion. Arguably, however, natural selection is a causal process, even though there is some controversy over whether natural selection is a causal process or a statistical phenomenon (for an overview of the debate see Otsuka 2016).

To keep things simple, effective, and general, when I mention Lewontin’s conditions for a trait, I will refer to *a setting in which a collection of entities at a given level of organization 1) exhibits variation on this trait, that 2) this variation is causally responsible for or constitutes differences in fitness, which translates into differences in growth or multiplication (e.g., differences in reproductive outputs), and 3) where factors causally responsible for the trait variation are transmitted over time (e.g., from parent to offspring).* The reason I use ‘growth’ and ‘multiplication,’ which I take as synonymous, instead of ‘reproductive output’ is that these terms cover more cases, such as when reproduction and expansion are blurred (see more on the distinction between ‘reproduction’ and ‘multiplication’ in Section 5).

There exists a link between the Price equation and Lewontin’s three conditions, which is discussed in Box 5 of the Appendix.

Box 2: Why Use the Price equation to Discuss Units and Levels of Selection

The Price equation describes the average change in a character or trait— I use the two interchangeably—of a population over time—for instance, the number of stripes an individual zebra has—by decomposing this change into covariances and expected values. A short derivation of the Price equation is given in Box 4 in the Appendix.

One important reason to use the Price equation in the context of units and levels of selection is purely pragmatic. To put it simply, anyone wanting to delve into the literature on levels of selection will have to know the Price equation. Although I could, in principle, use other tools, many theorists have found the Price equation useful to discuss this topic, as well as other issues in evolutionary biology. To engage with this literature, it is thus better to retain the terminology used by those authors.

A second reason is more profound. Because the Price equation is a mathematical identity, it is nearly 'assumption free' (Walsh and Lynch 2018, pp. 146).[a] This feature gives the Price equation a level of abstractness that is particularly useful for the philosophical project of investigating conceptual issues surrounding the levels of selection. And in fact, this feature has been used to unify different parts of evolutionary theory which seemingly relied on different equations (see Luque 2017). Another advantage of the nearly assumption-free nature of the Price equation is that one can apply it to any sort of entities—whether biological or not—which form a population, at any level of organization, and over any time period. This feature is particularly useful for a philosophical project like mine.

One can also tweak the Price equation in many ways to satisfy the peculiarities of a population. For example, one might suppose that the entities of the population reproduce asexually, perfectly, and in discrete generations. These are indeed the assumptions classically used to present the Price equation. For simplicity, I make the same assumptions in this Element, unless indicated otherwise. However, one could equally assume a much messier setting in which reproduction is not asexual but complex (for instance, each offspring entity of the population has a different number of parents), inheritance has low fidelity, and generations overlap. As Price himself wrote in a piece published posthumously, he intended a general theory of selection that could be applied to systems as diverse as those studied in psychology, archeology, politics, or economics (Price 1995; Frank 1995). There is no constraint on what one can assume.

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[a] I write 'nearly' because the Price equation is not entirely assumption-free: one still needs to specify a population made of entities to apply the Price equation, and this specification is an assumption. The standard Price equation also assumes that each individual in the offspring population has at least one parent. Thus, it cannot deal with migration (for a general version of the Price equation that deals with migration, see Kerr and Godfrey-Smith 2009). This minimal assumption aside, the Price equation does not make any assumption about the *nature* of entities composing the population, hence why I say it is assumption-free. I thank Victor Luque for making this point clear to me.

Box 2: continued

The assumption-free feature of the Price equation is thus a blessing for philosophical analysis. It is, however, a mixed one. The equation's generality and abstractness mean that, like Lewontin's conditions, one can apply it to entities that have no meaning beyond that imposed by an observer such as half-organisms. These features can also lead to the erroneous belief that it delivers more than it (in-principle) can. For instance, one might think that the Price equation can tell us something about the mechanisms or causes underlying the evolutionary change observed between two times. This is not the case. The Price equation is *merely* a mathematical identity that cannot say anything more about evolution than classical algebra can, which is to say not much. It *must* always be supplemented by particular assumptions about the population studied and be *interpreted* in a causal or mechanistic way to be useful in a particular evolutionary context. Once supplemented by particular assumptions, the Price equation can illuminate things that would otherwise be harder to grasp or represent.

While some readers might be on board with the spirit of my project they might insist that the Price equation is not the most relevant tool for the task ahead of us. Although these critics might have their reasons (see, for instance, van Veelen 2005; Traulsen 2010; Nowak and Highfield 2012, pp. 100-101), I believe that using the Price approach to understand natural selection and the levels of selection is akin to learning a particular programming language. Before learning a programming language, a would-be programmer might ask why they should choose to learn one particular language over another. There might be different views on the matter. However, if one wants to work in an area in which a large number of actors use a particular language, knowing this language will facilitate understanding what is at stake and enable some progress. It is fair to say that the Price equation and related approaches have been the main language used by evolutionists to talk about levels of selection in the last 40 years. Of course, the specific use of the language might hinder some important things that another language might make more readily visible. That said, such a problem is not specific to the literature on levels of selection. It is true for any topic using a particular framework. One can just hope to be as clear as possible about separating the constraints pertaining to the language used from issues directly related to the notion of levels of selection. To be able to do so readily, one can also hope to become proficient in more than one language.

Box 3: Conventionalism

As noted by Rescorla (2019), the theme of conventionalism is recurrent in diverse areas of philosophy, from mathematics to morality through metaphysics. In general, to be conventionalist about X is to believe that X results merely from conventions, rather than from facts about the world. In contrast, to be a realist about X is to believe that X is a matter of objective facts. In philosophy of science, conventionalism is often thought to have originated in the 1902 work of Henri Poincaré *La Science et l'Hypothèse* (*Science and Hypothesis*) in which he contends that the axioms of geometry are "des définitions déguisées" (disguised definitions) (Ben-Menahem 2006; Rescorla 2019). Conventionalism is also often associated with Pierre Duhem. In his 1906 work *La théorie physique* (*The Aim and Structure of Physical Theory*), he argues that theories are underdetermined by experiments. That is, when observations do not conform to the prediction of a theory, any part of the whole set of hypotheses upon which this theory relies—which he calls 'auxiliary hypotheses'—can be amended to fit this observation without having to change the theory. It follows that if scientists choose one set of hypotheses over another, these choices are conventional rather than factual (Ben-Menahem 2006, p.36). Duhem's thesis, together with Poincaré's work on geometry shaped the conventionalism of logical positivists about diverse aspects of science such as exposed in Carnap ([1937] 2002) and Reichenbach (1938), as well as the realist responses it led to, the most famous of which being those of Quine (1936) and Quine (1960).

The topic of conventionalism crops up in different areas of contemporary philosophy and under different guises. To give one example, a fundamental question in philosophy of mathematics is whether mathematics is indispensable to empirical sciences (Colyvan 2012). Philosophers who believe so are called 'platonists' while those who believe one can dispense with mathematics are called 'nominalists' (or antirealists). The term 'nominalism' has different meanings in different contexts. However, to be a nominalist about mathematics is to believe that mathematical objects do not exist and have no causal power. There are just a set of conventions. Thus, to be a nominalist about mathematics implies a form of conventionalism. However, to be platonist does not imply one is a realist. One might believe that mathematical objects are real but that our way of describing them is conventional with potentially multiple legitimate sets of conventions. At any rate, if mathematics is conventional, then it follows that one could use another set of conventions (non-mathematical) to derive scientific theories. Field (2016) represents an attempt of this project with Newtonian mechanics. In it, Field successfully derives one part of Newtonian mechanics without reference to numbers (for an accessible introduction see Colyvan 2012). Where this example becomes interesting is that one chief reason Field finds his approach appealing is that it does not require the use of a particular coordinate frame,[a] because a coordinate frame is a conventional element within a theory. Thus, one can be a conventionalist about mathematics motivated by realism about scientific theories.

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[a] I thank Mark Colyvan for pointing this out to me.

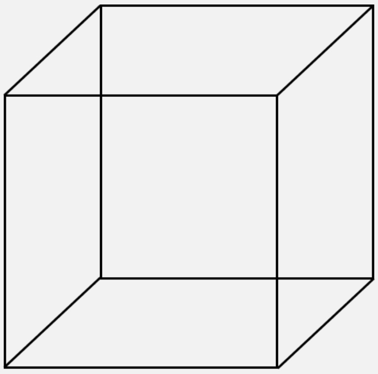
Box 3: continued

In the literature on levels of selection, conventionalist thinking is aptly illustrated by Richard Dawkins' (1982, chap. 1) Necker cube analogy. In this optical illusion (see Figure below), there is no fact of the matter as to which of the two possible orientations of the cube is *the* correct one. Similarly, evolutionary processes can be regarded from different perspectives without changing the facts. Dawkins writes:

> To return to the analogy of the Necker Cube, the mental flip that I want to encourage can be characterized as follows. We look at life and begin by seeing a collection of interacting individual organisms. We know that they contain smaller units, and we know that they are, in turn, parts of larger composite units, but we fix our gaze on the whole organisms. Then suddenly the image flips. The individual bodies are still there; they have not moved, but they seem to have gone transparent. We see through them to the replicating fragments of DNA within, and we see the wider world as an arena in which these genetic fragments play out their tournaments of manipulative skill. (pp.4-5)

Dawkins is here telling us that there is no fact of the matter concerning at which level natural selection operates. We can look at things either from the perspective of individual organisms or from the perspective of the genes without changing any fact.

A number of philosophers have defended conventionalist views about units and levels of selection (e.g., Sterelny and Kitcher 1988; Sterelny 1996; Kitcher et al. 1990; Waters 1991; Waters 2005; Sterelny and Griffiths 1999; Wilson 2003; Kitcher 2004). The term 'pluralism' has sometimes been used to refer to this position. However, I prefer the term conventionalism over pluralism in the zebra example and Necker cube analogy, because the set of conventions used to describe each scenario is the only feature that changes. The term 'pluralism' is more ambiguous in the levels-of-selection context. Other philosophers have defended, in response, explicitly realist positions (e.g., Sober 1990; Sober 2011; Okasha 2011; Lloyd et al. 2005; Lloyd et al. 2008).



A Necker cube. In this optical illusion, there are two equally valid ways of representing this cube: either the lowest of the two facing sides is in the foreground, or it is in the background.

Box 4: Simple Derivation of the Price Equation

The Price equation describes the average change of a character z between two times in a population ($\Delta\overline{z}$). I will assume here that these two times are generations, but this is for exposition purposes only. We have:

$$\Delta\overline{z} = \overline{z'} - \overline{z},$$

where $\overline{z}$ and $\overline{z'}$ are the mean values of the character in the population at the parental and offspring generation, respectively. By definition, in a population of n particles, $\overline{z}$ is equal to:

$$\overline{z} = \frac{1}{n}\sum_{i=1}^{n} z_i,$$

and $\overline{z'}$ is equal to:

$$\overline{z'} = \frac{1}{n}\sum_{i=1}^{n} \frac{w_i}{\overline{w}}(z_i + \Delta z_i) = \frac{1}{n}\sum_{i=1}^{n} \omega_i(z_i + \Delta z_i),$$

where Δz_i is the mean change in character between an entity i and that of the average of its offspring.

From there we can rewrite $\Delta\overline{z}$ as:

$$\begin{aligned}\Delta\overline{z} &= \frac{1}{n}\sum_{i=1}^{n} \omega_i(z_i + \Delta z_i) - \sum_{i=1}^{n} z_i \\ &= \frac{1}{n}\sum_{i=1}^{n} \omega_i z_i - \frac{1}{n}\sum_{i=1}^{n} z_i + \frac{1}{n}\sum_{i=1}^{n} \omega_i \Delta z_i.\end{aligned}$$

Following the definitions of covariance and expectation, we have $\mathrm{Cov}(X, Y) = \mathrm{E}(XY) - \mathrm{E}(X)\,\mathrm{E}(Y)$, where $\mathrm{Cov}(X, Y)$ is the covariance between X and Y. $\mathrm{E}(X)$ is the expectation of X which is defined as $\mathrm{E}(X) = \frac{1}{n}\sum_{1=i}^{n} X_i$.

Noticing that $\mathrm{E}(\omega_i) = 1$, so that its product with any term is equal to the value of the latter, and applying the definitions of covariance and expectation, the above equation can be rewritten as:

$$\Delta\overline{z} = \underbrace{\frac{1}{n}\sum_{i=1}^{n} \omega_i z_i - \frac{1}{n}\sum_{i=1}^{n} z_i \frac{1}{n}\sum_{i=1}^{n} \omega_i}_{\mathrm{Cov}(\omega_i, z_i)} + \underbrace{\frac{1}{n}\sum_{i=1}^{n} \omega_i \Delta z_i}_{\mathrm{E}(\omega_i \Delta z_i)},$$

which is Equation (2.1) in the main text, a classical form of the Price equation. For other derivations and introductions see, for instance, Okasha (2006, chap. 1), Frank (1998, chap. 2), McElreath and Boyd (2007, chap. 6), Birch (2017, Appendix), and Rice (2004, chap. 6).

Box 5: The Lewontinized version of the Price equation

Following Okasha (2006, chap. 1), we start from Equation (2.1) in the main text:

$$\Delta\bar{z} = \mathrm{Cov}(\omega_i, z_i) + \mathrm{E}(\omega_i \Delta z_i). \tag{2.1}$$

Recall that $\mathrm{Cov}(X, Y) = \mathrm{E}(XY) - \mathrm{E}(X)\,\mathrm{E}(Y)$ (see Box 4 of the Appendix). Thus, when $X = \omega$ and $Y = \Delta z$, we get:

$$\mathrm{Cov}(\omega_i, \Delta z_i) = \mathrm{E}(\omega_i, \Delta z_i) - \mathrm{E}(\omega_i)\,\mathrm{E}(\Delta z_i).$$

Noticing that $\mathrm{E}(\omega_i) = 1$, this equation simplifies into:

$$\mathrm{Cov}(\omega_i, \Delta z_i) = \mathrm{E}(\omega_i \Delta z_i) - \mathrm{E}(\Delta z_i).$$

Once rearranged we have:

$$\mathrm{E}(\omega_i \Delta z_i) = \mathrm{Cov}(\omega_i, \Delta z_i) + \mathrm{E}(\Delta z_i), \tag{A.1}$$

which is the second term on the right-hand side of Equation (2.1).

Plugging Equation (A.1) into Equation (2.1) we get:

$$\begin{aligned} \Delta\bar{z} &= \mathrm{Cov}(\omega_i, z_i + \Delta z_i) + \mathrm{E}(\Delta z_i) \\ &= \mathrm{Cov}(\omega_i, z'_i) + \mathrm{E}(\Delta z_i). \end{aligned} \tag{A.2}$$

We then define z'_i as the dependent variable of the following linear regression model:

$$z'_i = a + h^2 z_i + e_i, \tag{A.3}$$

where a is the intercept, h^2 is the slope of the regression line of average offspring character on parental character which, assuming no environmental correlation, represents the narrow-sense heritability of character z, and e_i is the residual for i, that is the deviation for i of its character value from the regression line. Narrow-sense heritability, following the standard least-square method is the regression coefficient on average offspring character on parental character and is defined as $\frac{\mathrm{Cov}(\overline{z'_i}, z_i)}{\mathrm{Var}(z)}$ with $\overline{z'_i}$ being the average offspring character of entity i, $\beta_{\omega z}$ is the regression coefficient of relative growth on character z, and $\mathrm{Var}(z_i)$ is the variance of z.

Plugging Equation (A.3) into Equation (A.2) and using the distributive property of variance, we get

$$\Delta\bar{z} = \mathrm{Cov}(\omega_i, a) + h^2\,\mathrm{Cov}(\omega_i, z_i) + \mathrm{Cov}(\omega_i, e_i) + \mathrm{E}(\Delta z_i).$$

Since a covariance between a variable and a constant such as a is nil, then by least squares theory $\mathrm{Cov}(X, Y) = \beta_{XY} Var(Y)$, where β_{XY} is the slope of the linear regression of variable X on Y (see Lynch and Walsh 1998, chap. 3), and assuming $\mathrm{Cov}(\omega_i, e_i) = 0$, we get:

$$\begin{aligned} \Delta\bar{z} &= h^2\,\mathrm{Cov}(\omega_i, z_i) + \mathrm{E}(\Delta z_i) \\ &= h^2 \beta_{\omega z}\,\mathrm{Var}(z_i) + \mathrm{E}(\Delta z_i), \end{aligned} \tag{2.7}$$

which is the Lewontinized version of the Price equation.

In fact, **Condition 1) corresponds to $\mathbf{Var}(z_i) \neq 0$; Condition 2) corresponds to $\beta_{\omega z} \neq 0$; and Condition 3) corresponds to $h^2 > 0$.** For the verbal formulation of the three conditions, see Box 1 of the Appendix.

Note that the Lewontinized version of the Price equation is more general than Lewontin's three conditions because it includes the term $\mathrm{E}(\Delta z_i)$, which is the evolutionary change due to evolutionary processes apart from natural selection. The presence of this second term can explain why, in some cases, despite the selection term being non-nil, there is no evolutionary change observed (Okasha 2006, Chap. 1). In such cases, we have $h^2 \beta_{\omega z}\,\mathrm{Var}(z_i) = -\,\mathrm{E}(\Delta z_i)$. The existence of a non-nil transmission bias term can also explain why, in other cases, the total evolutionary change goes in the opposite direction from the direction of the expected evolutionary change by natural selection only.

Note also that, contrary to the classical Price equation (Equation (2.1)), because the transmission bias is not weighted by relative growth in Equation (2.7), one needs to choose the average value of the offspring an entity would have even in the case where its relative growth is 0. Following Bourrat (2015), I choose this value as the average value of the offspring population. One can justify this convention by noticing that individuals with no offspring or offspring with the same character as the average offspring character do not produce any evolutionary change.

Box 6: Conventionalism in Social Evolution

Social evolution is the branch of evolutionary theory that studies traits that impact the reproductive output of more than one entity in the population. A debate that has raged for many years since the '60s concerns whether social traits (in particular biological altruism) evolve due to group selection or kin selection. The distinction between group selection and kin selection is an instance of the distinction between collective and particle-level selection. Some authors have argued since then that both approaches are, in fact, formally equivalent (see, for instance Dugatkin and Reeves 1994; Kerr and Godfrey-Smith 2002; West et al. 2007; Gardner 2015) and are thus conventionalists. Others disagree (see, in particular Bijma and Wade 2008; Nowak et al. 2010; Lloyd et al. 2008; Lloyd et al. 2005; Wade et al. 2010b; Sarkar 2008; Sober and Wilson 1998). For reviews of this debate see Birch (2014) and Lloyd (2017).

Under the kin selection approach, whether an individual (or particle) is evolutionarily successful cannot be judged solely based on its reproductive output. Rather, we must take into account its interactions with other individuals of the population it belongs to and their relatedness—i.e., the probability that two organisms have the same allele at a given locus (usually because they are related by descent).[a]

For instance, consider the zebra example presented in Section 2. A highly differentiated zebra's somatic cell, such as an epidermal cell or a hematocyte, produces no offspring. This cell's traits can be selected for despite it having no direct offspring. This is so for two reasons. First, this cell contributes to the success of its sister germ cells. Second, the relatedness between these cells (r) is 1. Without considering these two points, one would conclude that a trait leading to a decrease of its bearer's reproductive output is necessarily selected against when it can in fact be selected for. Whether it will be selected for will depend on whether Hamilton's rule is satisfied. This rule states that a trait that inflicts a cost c to its bearer and provides a benefit b to another individual can be selected if $c - rb < 0$. For clear introductions to Hamilton's rule see Fletcher and Doebeli (2009) and Bourke (2011, chap. 2).

Under the multilevel selection approach, which accounts for group selection, we can derive a different rule for the evolution of the same trait from a collective perspective. The multilevel approach typically uses a version of the Price equation slightly different from those encountered in Section 2 but which is presented in Section 3 (see Equation (3.1) in the main text and Box 7 fo the Appendix).

The main point made by the proponents of the equivalence thesis (i.e., conventionalists) is that, formally, the two approaches will yield the same outcome. Even though one can derive two (or more) rules for the evolution of a trait, the two rules will turn out to be equivalent if one realizes that different conventions for describing the evolution of this trait are used. As illustrated with the zebra example in Section 2, while we can look at things from the perspective of cells, zebras, or dazzles, the three approaches are formally equivalent since they merely represent different perspectives on the same evolutionary phenomenon.

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[a] In a more technical sense it is "the probability of sharing the focal gene relative to the average probability that the two organisms share the gene, which is set by the gene's average frequency in the population" (Bourke 2011, p. 31).

Box 7: Derivation of the multilevel Price equation

We start with Equation (2.5) in the main text:

$$\Delta\overline{Z} = \mathrm{Cov}_k(\Omega_k, Z_k) + \mathrm{E}_k(\Omega_k \Delta Z_k). \tag{2.5}$$

We define ΔZ_k as the average change in collective character between two generations of the collective k, the latter of which is understood as a population of particles. Using Equation (2.1) from the main text, we can write ΔZ_k as:

$$\Delta Z_k = \mathrm{Cov_k}(\omega_{kj}, z_{kj}) + \mathrm{E_k}(\omega_{kj} \Delta z_{kj}), \tag{A.4}$$

where z_{kj} and ω_{kj} are the character and relative growth, respectively, of particle j within collective k, and $\mathrm{Cov_k}$ and $\mathrm{E_k}$ represent a covariance and expected value performed within collective k, respectively.

Replacing Equation (A.4) in Equation (2.5), we get:

$$\Delta\overline{Z} = \mathrm{Cov}(\Omega_k, Z_k) + \mathrm{E}(\Omega_k(\mathrm{Cov_k}(\omega_{kj}, z_{kj}) + \mathrm{E_k}(\omega_{kj} \Delta z_{kj}))).$$

Assuming that the particles reproduce perfectly so that the transmission term within each collective is nil, we obtain:

$$\Delta\overline{Z} = \underbrace{\mathrm{Cov}(\Omega_k, Z_k)}_{\text{between-collective selection}} + \overbrace{\mathrm{E}(\Omega_k\, \mathrm{Cov_k}(\omega_{kj}, z_{kj}))}^{\text{within-collective selection}}. \tag{3.1}$$

The first term on the right-hand side, $\mathrm{Cov}(\Omega_k, Z_k)$, represents the between-collective selection term, while the second term on the right-hand side, $\mathrm{E}(\Omega_k\, \mathrm{Cov_k}(\omega_{kj}, z_{kj}))$, represents the within-collective selection term.

Box 8: Meanings of units of selection and the dispensability of replicators

Lloyd (2017) proposes that the term ‘unit of selection’ has four meanings in the literature. These are ‘unit *qua* replicator,’ ‘unit *qua* interactor,’ ‘unit *qua* beneficiary of adaptation’ (i.e., what unit—in the long-run—benefits from the process of adaptation), and ‘unit *qua* manifestor of adaptation’ (i.e., the level at which an adaptation is displayed). Among the four, the interactor notion is the most relevant for my purpose.

First, note that *adaptation* is not selection, and thus that if one strives for precision, units and levels of selection should not refer to units of adaptation. Furthermore, in this Element, I focus on selection rather than adaptation. There is a link between natural selection and adaptation, but it is less obvious than intuitively thought (for discussions of this topic see Okasha 2018; Birch 2016). Thus, the beneficiary and manifestor of adaptation meanings of the term do not correspond to what I discuss in this Element. What remains are the replicator and interactor meanings of the term. Concerning the replicator question, Okasha (2006, p. 145) rightly notes that a replicator (see below for this notion) is more akin to a ‘unit of inheritance’ than a ‘unit of selection.’ Following this reasoning, the unit of selection question should refer solely to an interactor rather than a replicator. Thus, I adopt the interactor sense of the term *unit of selection* throughout the Element, although I show in Section 5 that the question of transmission (via reproduction or, more generally, multiplication) is also relevant to the unit of selection question.

The replicator/interactor distinction is a famous one in the units-of-selection literature. It was proposed by Hull (1980) to describe the process of natural selection in the abstract. Note that ‘vehicle’ is the term used by Dawkins (1976) in lieu of interactor, which for my purpose is equivalent. Hull (1980, p. 318) defines two types of entities and the role they play in a selection process as follows:

> *replicator*: an entity that passes on its structure directly in replication
>
> *interactor*: an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential
>
> With the aid of these two technical terms, the selection process itself can be defined:
>
> *selection*: a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them

Box 8: continued

Although the replicator/interactor distinction has been very influential and useful in many respects, it is clear that replicators are dispensable in evolutionary theory (Godfrey-Smith 2009, pp. 31-36; see also Godfrey-Smith 2000). Evolution by natural selection can occur even if there is no replication occurring at any level of organization. In many cases, we do not even need to mention them to have a clear understanding of a given evolutionary setting. Note here that I do not think this is so if by 'evolution by natural selection' one refers *solely* to the change due to natural selection. When entities reproduce unfaithfully, some mutations are introduced in the population leading to a case of mixed evolution by natural selection and by mutations (see Bourrat 2019a). This point is consistent with the idea illustrated in Figure 2 in the main text, that the fidelity of transmission from parents to offspring might be quite low, and yet the transmission bias in the Price equation is nil. There are other reasons why the distinction should not be regarded as fundamental in evolutionary theory, for an overview see Okasha (2006, pp.16-17).

If evolution by natural selection can occur in the absence of replication, interactors exhibiting different rates of extinction and proliferation, as well as some heritable variation, is all that is required for evolution by natural selection to occur in a realist sense. However, this reasoning seems to lead us back to Lewontin's three conditions and its conventionalism. We should notice, however, that the notion of interactor emphasizes—with the ideas of 'interacting directly' and 'cohesive whole'—that a selection process occurs on functional units. This is something that we do not find in Lewontin's three conditions. Half an organism, and even a dazzle, do not count as interactors precisely because neither interacts as a cohesive whole with the environment. The idea that functional organization is associated with the notion of unit of selection can also be found in Williams (1966).

Box 9: Disaggregation & Independent Character Values

The idea of a particle trait being measured independently once the collective has been disaggregated is at the core of Section 4. How to make sense of it precisely and operationalise it? It depends on the type of collective and trait in question. Many collective traits are the result of interactions occurring in the short term between the constituent particles of a collective. In those situations, when the functional integration of the collective is not too high, we can imagine that this collective is instantaneously and physically decomposed into its component particles. Next, some measures are performed on the isolated particles and, finally, the collective is reaggregated seamlessly. For instance, we could take a swarm of bees, disaggregate it, measure the behavioural traits of the bees that compose it, and aggregate it again. In other situations, this would not be possible: the process of disaggregation would destroy the particles. Yet in other cases, the collective character either results from interactions between the particles of the collective over much more extended time periods, or it is the result of developmental processes. Here again, instantaneously disaggregating the collective would not allow us to determine what the value of the trait is when measured independently. Think, for instance, if you were instantaneously physically disaggregated into your cells. There is little chance that any of your cells' characteristics would change in the short term, assuming they are cultured for some time.

In these cases, 'measured independently' should be understood as a measure of the character in the closest possible counterfactual situation, in which each particle is able to live independently of others in the collective. One way to implement these counterfactual situations, in some cases, is to compare the value of a character of related particles which are 'free-living' from the character value of particles which live within a collective. This approach has been developed by Michod and collaborators using different species of Volvocine algae (for an overview of this research see Herron 2017).

In the Element, for ease of exposition, I only cover situations in which physical disaggregation is possible, and the collective trait results from short-term interactions between the particles constituting the collective.

Box 10: Interventionism, Substitution, and Plucking out

In Section 4 I refer to two procedures performed on particles: 'plucking out' and 'substituting' a particle to observe the difference made on the particle character and the collective character, respectively. These two ideas are related to the notion of causation following the interventionist account of causation (see Woodward 2003; Woodward 2010; Pearl 2009; Spirtes et al. 2000; Griffiths et al. 2015; Bourrat 2019b). However, the way they relate to this notion of causation is different.

In the literature on interventionism, causation from a variable X to another variable Y is established if an intervention—which amounts to changing the value of X at a particular time without changing any other variable at that time—is associated with a change in the value of Y. An intervention is like an ideal controlled experiment where all confounds have been eliminated.

Plucking out a particle to see what difference it makes to its character is like intervening on the variable 'presence/absence of a collective.' If this intervention does not lead to any change in the particle character, then we can conclude that the collective level is not a difference maker or cause of the particle character; rather, the collective character is aggregative. If, on the other hand, it does lead to a difference, we can conclude that the collective level is a cause of change in the character, and the collective character is non-aggregative.

Note importantly that the idea of 'plucking out' an individual and measuring the value of its character should only be regarded as accurately representing a value of the character 'measured independently' in simple situations. More specifically, it is accurate only when the value of the character does not vary in 'biologically normal' non-collective environments (which would involve some pragmatic considerations). For traits that can vary in non-collective environments, knowing this value would involve measuring the trait in the range of possible normal non-collective environments a particle can be found in. One would then have to attribute a probability for each of these environments so that a probability distribution for the character value in the absence of a collective is obtained. Such a distribution would then have to be compared to the one obtained in a collective context to assess whether the two are statistically different. Doing so would permit us to distinguish situations in which a character is exhibited in a non-collective context but could also be exhibited in a collective context, from situations in which it is only exhibited in a collective context. Only the latter situations could lead us to attribute non-aggregativity to a collective. For purposes of simplification, I only consider characters that do not vary when measured independently. Note also that the plucked-out character is equivalent to the notion 'basal reproductive output' if the character is reproductive output.

Box 10: continued

The idea of allelic substitution found originally in Fisher (1930; 1941, see also Williams 1966) is also similar to an intervention. The view that an allelic substitution can be approached from an interventionist perspective has been made explicit by Lee and Chow (2013). It can also be related to the mutation test found in Nunney (1985) and Okasha (2006, pp. 192-197). Extending this notion to *particle* substitution in a collective, substituting a particle for another (assuming they have different character values), is unlike intervening on the variable 'presence/absence of a collective' as in the case of plucking out a particle. Instead, it is similar to intervening on the variable 'value of the particle character,' assuming the context of the collective is always present. If the substitution makes no difference to the collective character, the conclusion that the particles do not affect the collective character is not warranted—it is still possible that plucking out the particle from the collective in this setting would produce a change in the collective character. However, if the substitution makes a difference, then we can conclude that the particle composition affects the collective character. Furthermore, if the substitution of a particle with a character value v_1 by another with character v_2, for any composition of the collective, produces a change proportional to $v_1 - v_2$ to the collective character—or, in other words, a linear change—then the collective character is a contextual additive collective character (see Section 4).

It should be clear that whether a trait is contextual additive is 'tested' by 'substitution' while aggregativity is tested by 'plucking out.'

Box 11: Comparison of the Non-aggregative Account of Levels of Selection with Other Approaches

Shelton and Michod (2014, see also Shelton and Michod 2020) arrive at a similar equation to Equation (4.6) in the main text (their Equation 9) by decomposing ω into two components: one they call ‘counterfactual fitness’ and another which is a deviation from the actual fitness.[a] They define counterfactual fitness as “the fitness that groups would have if the trait in question had no group-dependent [read ‘collective-dependent’] fitness effects” (p. 466). Thus, rather than decomposing z into an aggregative and a non-aggregative component, and assessing the extent to which each component affects ω, Sheldon and Michod make this decomposition on ω itself.

This last feature can be problematic since the potential effects of particles on the collective phenotype are left undefined. As noted by Bijma (2014, p. 67) within the context of the debate in social evolution about the level of selection (see Box 6 of the Appendix): “A fundamental principle in genetics, however, is that the genotype affects the phenotype and the phenotype subsequently affects fitness.” Bypassing the effects of the character of other individuals on the character of the focal individual, Bijma argues “may also obscure the mechanisms underlying the fitness effects of competition and cooperation among individuals” (*ibid.*). He then goes on to provide a few examples where this is the case. This problem also applies to Shelton and Michod’s model. Furthermore, I note that there are great risks in playing with the fitness term, for despite being a fundamental term in evolutionary theory, it is also a very slippery one. Leigh Van Valen is only one of many evolutionary theorists to have noticed that “fitness is the central concept of evolutionary biology, but it is an elusive concept. Almost everyone who looks at it seriously comes out in a different place” (Van Valen 1989, pp. 2-3). Michod is certainly aware of this since he devotes a chapter of his book (see Michod 1999, chap. 8) to the numerous philosophical issues surrounding this concept.

Another difference between Shelton and Michod’s model and my own is that their equation is applied at the particle level, while mine is at the collective level. There is, however, another much more substantial difference between Shelton and Michod’s model and my own. This difference will be a recurring one in the different approaches reviewed in this box. Shelton and Michod do not provide any criteria for determining what should count as a collective. This decision seems to be left entirely to the observer. In that respect, their approach risks mistaking arbitrary collectives for genuine ones. This misidentification is, arguably, particularly important in the context of evolutionary transitions in individuality. In contrast, I have argued that to count as genuine collectives, collectives identified by an observer in a population of particles should satisfy the property of compositional stability. There is scope, however, to supplement Shelton and Michod’s model in order to apply it exclusively to genuine collectives using the condition of compositional stability. On balance, I thus prefer to use my partitioning than that of Shelton and Michod, even though, again, the two are conceptually very similar.

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[a] The notation used by Shelton and Michod is different. I use here my notation for their equivalent terms.

Box 11: continued

There is an important connection between my decomposition of collective characters into aggregative and non-aggregative components, on the one hand, and the decomposition proposed in the literature on indirect genetic effects (IGEs) in quantitative genetics. An IGE is an effect on a character due to the interaction(s) between the character's bearer and other individuals of its group. For instance, the level of aggression of an individual can depend on the behaviour of other individuals with which the focal individual interacts. Thus, a breeder selecting only the less aggressive individuals, which is referred to as 'individual selection' in this literature, might not end up with a less aggressive cohort if IGEs affect the trait significantly. To reduce the overall level of aggression, one must instead select the groups of individuals that are less aggressive, since this will take into account IGEs. This selection process is called group selection in this literature. Contrary to Shelton and Michod's model, the focus is on traits rather than fitness which is an advantage.

A real example in which IGEs play an important role occurs in poultry farming. It was demonstrated that selecting the groups of hens (cages) with the highest yield in terms of eggs, rather than individuals with the highest yields (often more aggressive and as a result monopolizing food), leads to a much higher overall yield after a few generations (Craig and Muir 1996; Wade et al. 2010a; Wade 2016).

Historically, this approach was first developed by Griffin (1967, see Wade 2016; Bijma 2014). Since the '80s, a number of experiments and theoretical works have supported the role of IGEs in evolution (e.g., McCauley and Wade 1980; Wade 1978; Wade 1985; Goodnight et al. 1992; Goodnight and Stevens 1997; Bijma and Wade 2008; Bijma et al. 2007; Bijma 2010; Hadfield and Wilson 2007). Reviews of this literature are presented in Walsh and Lynch (2018, chap. 22; see also Wolf et al. 1998; Bijma 2014; for a less mathematically involved presentation of the main findings, see Wade 2016). An important point to note is that much of the debate surrounding the status of kin selection and group selection can be resolved using the IGEs framework (see Bijma and Wade 2008; Walsh and Lynch 2018, p.824; and Box 6)

Despite the similarities between the quantitative genetics approach to IGEs and my own, there are two key differences. First, although in some IGE models the direct effect of a character does not depend on collective size (Walsh and Lynch 2018, p. 778), it is unclear whether this independence refers to contextual additivity or aggregativity. It seems plausible, however, that IGEs models could be interpreted as referring to aggregativity. Charles Goodnight (personal communication) proposed to define a quantity he terms 'extended breeding value' (or 'global breeding value'), which is uniquely defined in a population of collectives. A breeding value is an additive component. He distinguishes this value from 'local breeding values' (Goodnight 1995), which are values obtained within each collective. Since both types of breeding values are defined relative to a population in context, they must refer to a notion of contextual additivity, but a global breeding value should have a close value to the functional aggregative breeding value.

The second difference is that a collective (or group) in the IGE literature is, following a textbook treatment, "[the] set of individuals that interacts with the focal individual" (Walsh and Lynch 2018, p. 773). This definition of a collective is too loose to capture the notion of a functional unit or an interactor. As such, it would only satisfy the condition of non-aggregativity, but not necessarily that of compositional stability. In this respect, IGEs are thus on par with Shelton and Michod's proposal. That being said, here again, IGEs models could be supplemented to accommodate the interactor requirement (e.g., with the compositional stability condition).

Box 11: continued

Finally, the aggregative/non-aggregative distinction should be compared to contextual analysis (see Section 3.2). It might be argued that if contextual analysis, if not identical to the aggregative/non-aggregative version of the Price equation, is nevertheless similar to it. First, note that both IGEs models and contextual analysis are multilinear regression models. They are both attempts to capture, in different ways, the effect of a collective (or group) on individuals or groups. There is thus a clear link between the version of the Price equation I developed and the contextual analysis. However, as noted in Section 3.2, contextual analysis, in and of itself, does not pose any restriction on what a collective can be. This means, for instance, that a particle could belong to more than one collective, without violating the assumption of contextual analysis. Thus, contextual analysis does not permit us to define an interactor. Nevertheless, there would be ways, as with IGEs models and Shelton and Michod's, to supplement contextual analysis with the condition of compositional stability.

However, the notion of additivity which is operating in contextual analysis is contextual additivity, not functional aggregativity. This is so because both the particle and contextual character are defined in the context of a collective. Concretely, this means that the two approaches would radically depart in some critical situations. For instance, we could suppose that a population of collectives becomes increasingly functionally integrated, in the sense that the non-aggregative component of a collective trait radically increases as a result of selection. However, at the same time, the aggregative component decreases with the same magnitude. This would produce a situation in which the collective-level character (Z) does not, overall, change for any of the collectives. Using Equation (4.6), following my interpretation, despite no observed changes *in situ*, there would nonetheless be a change in the levels at which selection is considered to operate. Namely, a shift would occur from the lower level to the higher. Using contextual analysis, however, the answer would be that natural selection operates consistently with the same magnitude at both levels.

One might retort that such situations are irrelevant because they would be rare in nature. However, I used this extreme example only to illustrate a conceptual point. Less extreme situations would lead to similar conclusions. Second, it might be argued that such situations would be hard to distinguish from those in which there is no selection using any framework, and so we should not worry about it. Yet, while it might be the case that distinguishing these situations is empirically challenging, this possibility is not relevant when it comes to *defining* rather than *detecting* units and levels of selection in a biological population.

In sum, the main difference between my approach and those presented in this section is that mine is grounded in the notion of an interactor. A partitioning of selection between the particle level and the collective level is only applied once interactors have been defined. My approach is thus more causal than others with respect to the notion of 'collective.'

Box 12: MLS1*/MLS2* and Evolutionary Transitions in Individuality

The MLS1*/MLS2* distinction discussed in Section 5 intersects with the literature on evolutionary transitions in individuality (ETIs) (Griesemer 2000; Michod 2005; Okasha 2006; Bourrat in press; Bourke 2011; Clarke 2014; Clarke 2016; Clarke 2013; Black et al. 2020; Godfrey-Smith and Kerr 2013; De Monte and Rainey 2014; Doulcier et al. 2020). ETIs are closely related to the major transitions in evolution (Maynard Smith and Szathmary 1995; Calcott and Sterelny 2011; Jablonka 1994) and predated by the work of Bonner (1974) and Buss (1983; 1987). ETIs, as mentioned several times in the main text, are events during which a particular level of description (e.g., collective level), which is not initially a level of selection, progressively becomes one. A level of selection refers here to entities that are both functional units and units of multiplication. Bourke (2011, pp. 11-15) distinguishes six types of evolutionary transitions in individuality that have occurred during evolution. These are the transitions from separate replicators to cells enclosing genomes, from separate unicells to symbiotic unicells (eukaryotic cells), from asexual unicells to sexual unicells, from unicells to multicellular organisms, from multicellular organisms to eusocial societies, and from separate species to interspecific mutualisms.

Okasha (2006, see also Okasha 2009) and Michod (2005) both have proposed that what explains why collective-level entities become units of selection, with the ability to multiply in their own right, is that fitness either shifts levels or is transferred from one level to the other (see also Folse and Roughgarden 2010; Rainey and Kerr 2010). They follow the fitness decoupling model and the traditional way of understanding the MLS1/MLS2 distinction criticized in Section 5.[a] In particular, Okasha (2006, chap. 8) proposed a model in which, at the beginning of an ETI, collective fitness is measured by the number of particles produced. It is thus an MLS1 process. In contrast, at the end of the ETI, collective fitness is measured by the number of collectives produced, which corresponds to an MLS2 process. In between these two stages, there is, using Okasha's own words, "a sort of grey area between MLS1 and MLS2" (Okasha 2006, p. 237). I criticized this model in Section 5.1 on the basis that, except under very unrealistic assumptions, the fitness of a collective and that of its constituent particles cannot be decoupled if they refer to the same material substrate.

The MLS1*/MLS2* distinction is a possible alternative to the fitness decoupling model. An ETI can be regarded as a transition in which, starting from a population of particles, any partitioning of particles into collectives is initially arbitrary. At that stage, collectives are merely instruments for generating book-keeping descriptions of a population's evolutionary dynamics. A transition begins when some functional non-aggregativity is produced by the particles, such that functional units start to be delimited. In these cases, collective-level selection is of the MLS1* sort. From there, new mutations produce functional non-aggregative characters, such as allocation mechanisms, which are directly implicated in collective-level multiplication. These characters transform functional units into units of multiplication. At that point, collective-level selection transitions into an MLS2* process. This type of scenario is explored in more detail in Bourrat (in press). [b] Of course, the same trait could be responsible both for a collective becoming a functional unit and for it becoming a unit of multiplication at the same time.

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[a] In more recent works, it appears that Michod has moved away from the fitness transfer model, or has given it a different meaning in terms of counterfactual fitness (see Box 11 of the Appendix, Shelton and Michod 2014; Shelton and Michod 2020).

[b] Note that the experimental designs proposed by Hammerschmid et al. (2014, see also Rose et al. 2019) and Ratcliff et al. (2012) have the potential to permit us to experimentally test some predictions of this scenario.

Box 12: continued

Note that I have described ETIs in this box as though they are the outcome of particle activities, without mentioning any role played by the environment. Particles may indeed produce new variation by mutations directly leading to some functional non-aggregative phenotype. However, this type of explanation, in which the explanans of an ETI are fully located in the properties of the particles constituting collectives, is only one of two possible generic explanations. An alternative is that ecology creates boundaries between particles, which results in the *de facto* production of collectives (Clarke 2014; Clarke 2013). Now, these collectives might not be *functional* initially in the sense that they would disappear as soon as the environmental conditions change but might behave *as if* they are functional units and units of multiplication. They are unit-*like*. Similarly, ecology could explain how the production of new collectives is established over a longer timescale than the time over which a cell reproduces. It would create a collective-*like* life cycle. Rather than explaining ETIs purely from particle-level properties, this explanation externalizes the origins of collective-level properties. This 'externalist' view on ETIs has been underexplored in comparison to the 'internalist' one. However, it represents a *prima facie* equally viable starting point. An externalist model of ETIs is proposed in a recent publication with collaborators (see Black et al. 2020).

Online Glossary

Additivity *See* functional aggregative character & contextual additive character

Arbitrary entity Entity (e.g., collective) delimited by an observer in a population of lower-level entities (e.g., particles) that does not correspond to a functional unit. An entity might be arbitrary because there are no interactions between lower-level entities (cross-level by-product), because the population structure is viscous, or because the higher-level entities are gerrymandered. See Figure 4 in the main text

Collective In a two-level abstract hierarchy, a collective represents the highest level. Collectives are composed of particles. They might also be units of selection or multiplication, or they might instead be arbitrary units (e.g., half an organism) defined by an observer. *See also* particle

Compositional stability Property of exhibiting the same collective-level character. Two or more collectives defined by an observer have this property when they exhibit the same collective-level character. This property is attributed to collectives that are non-aggregative and share the same particle composition (measured independently). It allows us to establish that a collective character is a *functional non-aggregative* one. *See also* functional aggregative character, non-aggregative character & functional non-aggregative character

Contextual additive character Character of an entity that exhibits a linear relationship when the lower-level entities that compose it are substituted for lower-level entities that belong to the same class but have different character values. *See also* functional aggregative character

Conventionalism In the context of levels of selection, it is the view that describing an evolutionary sequence by reference to a particular level of selection is just a matter of convention, as opposed to objective facts. If one accepts this view, then the sequence can be described by referring to entities at different levels of organization, without one description having a greater claim to objectivity than the other. *See also* Realism

Fitness Property of an entity which determines, in part, its actual evolutionary success. It is usually measured or conceptualized as the *expected* reproductive output. In this book, I prefer to use the term 'expected growth,' since growth refers not only to reproduction but also multiplication. *See also* growth

Fitness decoupling Proposed evolutionary process by which the fitness of the entities at two levels of organization become independent of one another. *See also* fitness & multilevel selection 1 & 2 (MLS1 & MLS2)

Functional aggregative character character of an entity which is obtained by aggregating some of the characters of its components when they are measured independently. For instance, if a collective character is a functional aggregative character, it means that, although this character is measured in *situ*, the same value would be obtained had the properties of its particles been measured independently and aggregated. *See also* non-aggregative character & functional non-aggregative character

Functional non-aggregative character Non-aggregative character of a functional unit. A functional non-aggregative character is one that satisfies the condition of compositional stability. *See also* non-aggregative character, functional aggregative character &

Functional unit Entity (e.g., collective) of which the components (e.g., particles) interact in such a way that they form a bounded system. Boundaries might be spatial, but not necessarily so. More abstractly, they are causal: the nature of the interactions between the components of a token functional unit occurring *within* it are different from those occurring with components of other functional units. Potential units of selection in a realist sense are functional units. I consider the term functional unit to be equivalent to the term 'interactor' used by Hull (1980). *See also* level of organization

Gerrymandered entity Entity (e.g., collective) delimited by an observer in a population of lower-level entities (e.g., particles), which results from a level of description that does not correspond to a level of organization. I use this term to refer to the specific situations in which collectives described by the observer do not correspond to functional units, while a different way of partitioning particles into collectives would have yielded collectives which are functional units

Growth Outcome of multiplication after some time (persistence, developmental growth, and reproduction). If it is preceded by the word 'relative,' it means it is measured relative to other entities of a population. The growth of an entity is determined by both its fitness and its environmental circumstances. *See also* fitness

Interactor *See* functional unit *See also* level of organization

Level of description A way of partitioning a system (e.g., population) into components (e.g., particles, collectives). This partitioning may correspond to a level of organization or selection, or it may be more arbitrary. If arbitrary, the set of entities it delimits neither represent functional units nor units that are gerrymandered. In this book, when I talk abstractly about different levels of description, organization, or selection, I refer to particles and collectives, where collectives are composed of particles

Level of organization In this book, I use this term to refer to a level of description at which one can define a type of functional unit or a type of unit of multiplication. I consider the term 'level of organization' to be equivalent to the term 'level of interaction' used by Hull (1980)

Level of selection The definition depends on whether one has a conventionalist or realist approach to multilevel selection. If the former, a level of selection is merely a level of description at which Lewontin's three conditions are verified for the entities defined at that level. If the latter, it represents a level of description which is also a level at which the entities described are functional units or units of multiplication

Lewontin's three conditions See Box 1

Multilevel selection 1 & 2 (MLS1 & MLS2) Two different approaches to conceptualizing the evolutionary dynamics of a multilevel setting. Suppose an abstract two-level setting of particles organized into collectives. From an MLS1 perspective, both particle-level and collective-level fitness are measured by the number of particles produced. From an MLS2 perspective, particle-level fitness is measured by the number of particles produced, while collective-level fitness is measured in terms of collectives produced. This difference in perspective is often associated with the notion of fitness decoupling. *See also* multilevel selection 1* & 2* (MLS1* & MLS2*), fitness & fitness decoupling

Multilevel selection 1* & 2* (MLS1* & MLS2*) Two different types of evolutionary dynamics in a multilevel setting. Assume a setting of particles organized into collectives. The MLS1*/MLS2* distinction is intended to supplant the MLS1/MLS2 distinction by preserving only the dichotomy between collective multiplication that is a by-product of particle multiplication, and that which is genuine, respectively. If the former, the setting is of the MLS1* sort; If the latter, it is of the MSL2* sort. *See also* multilevel selection 1 & 2 (MLS1 & MLS2)

Multiplication Process by which an entity produces more entities of its class. It generalizes the notion of reproduction in which the entities produced become independent from their parent(s), to situations in which the entities produced remain attached to their 'parent(s)'. In this latter case, the 'parental' entity grows developmentally rather than reproduces. Thus, multiplication includes both developmental growth and the more classical sense of reproduction

Non-aggregative character character of an entity that results from the interactions of its components. It has a value that is distinct from the sum total of its component particles when they are measured independently. Non-aggregative characters can be functional or non-functional. Some non-functional non-aggregative properties do not satisfy the condition of compositional stability. *See also* functional aggregative character & functional non-aggregative character

Particle In a two-level abstract hierarchy, a particle represents the lowest level. A group of particles might form a collective, which is a unit of selection or multiplication. Particles in the abstract hierarchy are considered both units of selection and multiplication. *See also* collective

Price equation Mathematical identity used in evolutionary theory to describe the mean change in character of a population of entities between two times. There exist several variants of the equation. In one classical version, the mean change is equal to a covariance between the relative growth and the character of an entity, which is interpreted as the change associated with natural selection, and the mean difference in character between parents and average offspring weighted by relative growth, which is interpreted as the change associated with all evolutionary processes other than natural selection

Realism In the context of levels of selection, realism is the view that whether selection occurs at one level of organization is a matter of fact, not a product of convention. *See also* conventionalism

Unit of multiplication Unit of selection which is able to multiply in a way that is not solely the result of the independent multiplication of its components. A unit of multiplication corresponds to what Maynard Smith (1987) or Griesemer (2000) call a 'unit of evolution'

Unit of selection The definition varies depending on whether one adopts a conventionalist or realist perspective on levels of selection. If the former, it refers to a type of entity in a population that has the capacity to exhibit Lewontin's three conditions. If the latter, it corresponds to a functional unit or a unit of multiplication that has the capacity to exhibit Lewontin's three conditions. Entities that *do* exhibit Lewontin's three conditions in this population are *actual* units of selection, while those that merely have the *capacity* to do so are *potential* units of selection. *See also* functional unit

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