 RESEARCH ARTICLE

Independence and the Levels of Selection

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The idea that selection can go in opposite directions or, more generally, be independent at different levels is well entrenched in both the biological and philosophical literatures. However, this idea is difficult to render precise. On the face of it, it seems unclear how two levels of selection could conflict with one another – and thus be independent if they ultimately refer to the same Darwinian substrate. In this paper, I present an analysis of this problem. I argue that it is impossible for selection at one level to be independent from selection at a different level if independence is to be understood in a strong (metaphysical) sense. However, I propose that independence can be understood in a weaker sense, so long as our conception of independence does not violate the metaphysical dependence of the higher levels on the lower ones. From there, I argue that none of the notions of particle-level or collective-level selection used in the classical formal approaches to multilevel selection capture this weaker form of independence. Finally, I propose a different approach that is compatible with both metaphysical dependence and the weaker form of independence outlined in this paper.

Keywords

levels of selection • natural selection • Price equation • contextual analysis • supervenience

1 Introduction

It is not uncommon in the biological and philosophical literature related to units and levels of selection[1] to read that two levels of selection can be in conflict.[2] For instance, when discussing the conditions for the evolution of altruism, Wilson and Sober (1994, 599) succinctly summarize this point as follows:

1. I include here the literature on major transitions or evolutionary transitions in individuality.
2. The term "conflict between levels of selection" or closely related ones can be found, for example, in Okasha (2006), Wade (2016), Michod and Roze (2001), Joseph and Kirkpatrick (2004), Ratcliff et al. (2017), Folse and Roughgarden (2010), Maynard Smith and Szathmary (1995), Rainey and Kerr (2010, 2011), or Alizon, Luciani, and Regoes (2011).

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> Altruism involves a conflict between levels of selection. Groups of altruists beat groups of nonaltruists, but nonaltruists also beat altruists within groups.

In multilevel selection, that two levels are in conflict is only one possibility. In many cases, one should expect that selection at two levels goes in the same direction. At any rate, whether selection processes at different levels go in the same or opposite directions, this assumes that they *can be independent* from one another.[3] Indeed, there would be no meaningful way to consider that different levels of selection are independent if there is no way to change the value of selection at one level without this leading to a change in the value at another level.

Thus, one can delineate the following requirement for multilevel selection:

> **Independence Requirement (for multilevel selection)**: Selection at one level can occur independently of selection at another level. That is, whether selection goes in one direction has nothing to do with the direction of selection at another level.

Despite the seemingly straightforward nature of the Independence Requirement, what independence amounts to in the context of multilevel selection is difficult to make sense of. This is so particularly because in a two-level setting, properties of the higher level mereologically supervene on those of the lower one. In consequence, how should we understand the Independence Requirement? Should we consider that "independence" means metaphysical independence? In other words, can different levels of selection be metaphysically independent while the entities they refer to hold relationships of mereological supervenience? Or should we understand independence in a weaker sense? In this paper, I aim to answer these questions. I provide an argument against the strong reading of the Independence Requirement (section 2). Instead, I propose that independence should be understood in a weaker sense, which I outline. From there, I argue that none of the notions of collective or particle selection used in classical formal approaches to levels of selection – namely, the multilevel Price equation (section 3) and two variants of contextual analysis (section 4) – satisfy the Independence Requirement in its weaker form. To remedy this problem, I propose an alternative formal approach to levels of selection based on the Price equation that satisfies this requirement (section 5).

Prima facie, a skeptic regarding the claim that for multilevel selection to make sense, there should be the possibility of processes going in opposite directions, could make the following analogy with physics. Suppose a ball is rolling down a hill. The movement of the ball depends on the gravitation that goes in one direction, the normal force that pushes back against the ball and prevents it from passing through the surface, and finally on frictions that go in a different direction. The three forces are not independent; however, everyone is content in decomposing them. Why should we then have to stipulate that there should be the possibility of independence in the case of multilevel selection? I address this potential response early in this paper so that my motivations are clear. There are three reasons why independence should be possible in multilevel selection. First, the analogy with the ball is misleading. In the case of the forces acting on the ball, the system is at a single level. A more accurate analogy would be that, say, the frictions of the ball as a whole are independent from the sum of the frictions of the atoms that compose them. Stated as such, the requirement of independence becomes clearer. I doubt any physicist would claim that the former can be independent from the latter. Second, in the case of the ball, independence between different forces can exist. For instance, I can push the ball in the opposite direction to its movement, and the resulting force is effectively independent from the other

3. By "level" here, I will follow the deflationary account of Eronen and Ramsey (2022) and not commit to the claim that the levels of selection correspond neatly to the levels of organization. For a more comprehensive overview of the topics of levels of organization in biology, see Brooks (2021).

forces. However, as we shall see, mereological supervenience prevents the possibility of parts being independent from wholes in hierarchical systems. This renders the claim that selection processes go in opposite directions suspicious.

2 The Supervenience Assumption or the Impossibility of Strong Independence

To begin, I will make a number of assumptions to render the analysis as simple as possible without losing its primary insights. First, I will assume a population organized in two levels. I refer to the lower-level entities as "particles" and assume that they are organized in higher-level entities, which I term "collectives." The number of levels could straightforwardly be increased to more than two levels, but that would render the analysis unnecessarily cumbersome. Second, I will assume that a collective is made of no other substrate than its constituent particles and that all the collectives have the same finite size, that events of particle-level and collective-level reproduction occur simultaneously and in discrete generations, that particles reproduce perfectly, and that the environment of a particle (other than other particles) is homogeneous. Here again, these assumptions could be relaxed without changing the conclusions reached in this paper. Third, I will consider that the status of collectives in the population is unquestioned. In other words, collectives are genuine biological entities rather than entities resulting from an observer's conventional decisions.

Another simplifying assumption I will make is that any collective-level character I discuss is a "statistical" aggregate – that is, a simple function of a character at the particle level (see Okasha 2006, 48–49). For instance, in a population of particles with different heights organized in collectives, the collective-level character "mean particle height in the collective" is a statistical aggregate. Note, however, that if a collective character is *not* a statistical aggregate,[4] it *does not* follow that, in principle, one would be unable to explain this character in terms of particle-level characters. If this were so, it would violate the supervenience assumption that collective-level properties supervene (i.e., always depend) on particle-level properties. (More on this assumption below.) Nevertheless, what a collective character not being a statistical aggregate character implies is that recovering this character from the particle level would involve considering multiple particle-level characters and knowing the complex functional relationships that link those characters to the collective-level character. For instance, the density of particles in a collective is a non-statistical aggregate collective character in the sense that multiple particle-level properties would have to be invoked to recover the density of particles in a collective.

Assuming that the particles and the collective they constitute are made of the exact same physical substrate, rejecting the mereological supervenience assumption of higher properties on the lower ones (henceforth, "the supervenience assumption") would go against physicalism: the idea that everything there is in the world is physical and obeys the laws of physics (Stoljar 2017). It would require that some collective-level properties do not ultimately have a physical basis. However, since science is methodologically physicalist, a scientifically valid account of levels of selection ought to be compatible with physicalism and the supervenience assumption. In the context of levels of selection, rejecting the supervenience assumption implies that at least some collective-level characters could be metaphysically thoroughly independent from the characters of the particles constituting the collective.[5]

4. This type of character is sometimes called "emergent" (Okasha 2006; Lloyd 1988). However, I avoid this term here because it is overly vague.

5. "Character" should be understood broadly here as meaning any properties that can be measured from the point of view of a particle. This might include relational properties such as being in a particular location or environment.

The supervenience assumption is closely related to the causal exclusion principle, an idea that originally comes from philosophy of mind (see Kim 2005, chap. 1). It tells us that in a physical world, if a phenomenon is *fully* explained at the lower level, any mention of the higher level is redundant and, thus, superfluous. For example, if raising your hand is fully explained in terms of neurological impulse patterns, invoking mental causation is redundant, since we assume that the lower-level (neurological) explanation is complete.

On the face of it, there seems to be a tension between the supervenience assumption of collective-level characters on particle-level ones and the Independence Requirement. Since the collective level supervenes on the particle level, it is tempting to argue that collective-level *selection* supervenes on particle-level *selection*. Further, because supervenience is a relation of dependence, following this argument, one would have to conclude that the Independence Requirement can never be satisfied. This argument is what Okasha (2006, 105) calls the "'supervenience argument' against the possibility of genuine collective-level selection."

I am of those who believe that the supervenience argument is fatal to the Independence Requirement if it is understood in an ontological sense. However, Okasha (2006, 105–7, see also Okasha 2012) provides a response to this argument. He tells us that the supervenience argument only commits one to collective-level selection supervening on some particle-level *processes*, not necessarily particle-level *selection*. Said differently, because selection at a given level is defined as fitness differences between the units forming a level, collective-level selection only commits us to the claim that the fitness of the collectives depends on some character(s) of their particle constituents, not necessarily their fitness. Sober (2011) concurs with Okasha.

What should one make of Okasha's argument? To assess this argument, one must know whether collective fitness can be independent of particle fitness. In other words, can the fitness value of a collective be kept constant while the fitness of one of its constituent particles varies? If it can, the Independence Requirement is compatible with the supervenience assumption. However, if it cannot, the Independence Requirement and the supervenience assumption are incompatible. Okasha (2006, 234) claims that collective and particle fitness can be independent. For example, when discussing a model from Michod (1999), he argues that the fitness of organisms like us does not depend on our number of cells. However, as I show below, this argument is problematic.

First, let us note that the fitness of an entity[6] is classically defined as its *expected* growth rate in a particular environment (Sober 2001; Beatty and Finsen 1989; Pence and Ramsey 2013; Doulcier, Takacs, and Bourrat 2021; Takacs and Bourrat 2022; Autzen and Okasha 2022). This value is commensurate with its long-term reproductive output in this environment. This makes fitness at any level an *asymptotic* (i.e., long run) property of entities.

Second, since collectives are made of particles, under the assumption that a collective cannot grow indefinitely,[7] the long-term reproductive output of a collective cannot be decoupled or remain independent from that of its constituent particles (Bourrat 2015b, 2015a, 2021a; Bourrat et al. 2022). Arguing the contrary would lead to the reductio that in a setting of collectives of finite size constituted of particles, one type of particle (e.g., altruist) can be selected and invade (or nearly so) a population, while the collectives they constitute could go extinct (or nearly so). In a hierarchical setting, the altruist type invading the population of particles can only do so in the long run by producing a large number of collectives. This leads to the conclusion that

6. To be more precise, we should refer to the *inclusive* fitness of this entity. Inclusive fitness accounts for both the direct offspring of the focal entity and the offspring of entities with the same type under the casual influence of the focal entity (Hamilton 1963, 1964; Bourke 2011).

7. There might be exceptions to this assumption, such as when the entity considered to be a collective is a species. Indeed, there is no constraint on the number of members a species can be composed of.

selection at the particle level and the collective level cannot be independent in the strong sense and, consequently, that Okasha's argument is flawed. Were fitness not an asymptotic property or assuming that particle reproductive output within a collective is not constrained by collective size, Okasha's argument would have been valid.

This conclusion relates to a classic distinction drawn in the literature between two definitions of collective fitness: namely, either as the number of offspring particles produced – Fitness 1, which corresponds to Multilevel Selection 1 (MLS1) – or as the number of offspring collectives produced – Fitness 2, which corresponds to Multilevel Selection 2 (MLS2) (see Damuth and Heisler 1988; Okasha 2006; Bourrat 2023c). In MLS2, it is classically admitted that particle fitness is not necessarily tied to collective fitness. This is so because endorsers of the distinction argue that a type could produce a very large number of particles, all within a single collective. In contrast, another type could produce a much smaller number of particles but more than a single collective. Thus, fitness differences, which constitute selection, could favor one type at the collective level but favor the other type at the particle level.

However, as we have just seen above with the example of altruist particles and collectives, if collectives have an upper-limit size, the long-term number of collectives produced by a collective will depend on the long-term number of particles produced by its constituent particles. This implies either that (i) the distinction between Fitness 1 and Fitness 2 (and, consequently, MLS1 and MLS2) does not correspond, in situations where collectives have size constraints, to the well-accepted notion of fitness as a long-term measure of evolutionary success (this is briefly explored in Bourrat 2021a, chap. 5), or (ii) that the distinction is simply a matter of convention rather than objective fact, with each measure sometimes referring to different environments (Bourrat 2023c).[8] While the distinction is not used consistently in the literature, on the whole, I favor the second interpretation. For related criticisms of the MLS1/MLS2 distinction, see Gardner (2015) and Waters (2011).

In this section, I have argued that the Independence Requirement is not compatible with the supervenience of collective fitness on that of their constituent particles, if independence is understood in a metaphysical or ontological sense. I refer to this version of the requirement as the Strong Independence Requirement.

> **Strong Independence Requirement (for multilevel selection)**: Selection at one level can occur independently of selection at another level in an ontological sense.

However, that a strong interpretation of independence between levels of selection is not attainable does not imply that other interpretations of the notion of independence between levels of selection are not valid. All that is required for an adequate concept of level of selection is that it jointly satisfies the Independence Requirement and does not violate the supervenience assumption. I call this conjunction the "Weak Independence Requirement."

> **Weak Independence Requirement (for multilevel selection)**: Selection at one level can be said to occur independently of selection at another level without this violating the supervenience of higher-level fitness on lower-level fitness.

8. However, when this collective can grow indefinitely, the two fitnesses can be decoupled in an evolutionary sense and, thus, form a genuine rather than conventional distinction.

Several formal approaches to the levels of selection based more or less directly on the Price equation (Price 1970) have been proposed in the literature. For a review, see Okasha (2006). However, in the next two sections, I show, using a "test" I call the Test for Weak Independence, that none of the notions of particle or collective selection used in these approaches satisfy the Weak Independence Requirement. This is so because, following these approaches, changing the strength of selection at one level without simultaneously changing the strength of selection at another level would amount to violating the assumption of supervenience. In section 5, I propose a different partitioning of the Price equation that satisfies the Weak Independence Requirement.

3 The Multilevel Price Equation

To understand the multilevel Price equation, it is useful to start with its single-level version. The single-level Price equation is a mathematical identity derived by Price (1970, see also Okasha 2006; Luque 2017). It represents the population-level change for a character z ($\Delta\overline{z}$) between two times (typically generations), in terms of covariance and expected value. Formally, we have:

$$\Delta\overline{z} = \underbrace{\mathrm{Cov}(\omega_i, z_i)}_{\substack{\text{Selection}\\ \text{term}}} + \underbrace{\mathrm{E}(\omega_i \Delta z_i)}_{\substack{\text{Transmission-}\\ \text{bias term}}}, \tag{1}$$

where $\Delta\overline{z}$ is the change between two generations of the average particle character value ($\overline{z}$) in the population, z_i is the character value of a particle i of the population, and ω_i is the relative reproductive output of i between the two generations, which is defined as the absolute reproductive output of i (w_i) divided by the average reproductive output in the population ($\overline{w}$) so that $\omega_i = \frac{w_i}{\overline{w}}$. The complete derivation of equation (1) is given in Okasha (2006).

The first term on the right-hand side of equation (1) represents the covariance between the particles' character (z) and their relative reproductive output (ω), the latter of which tracks their fitness. If we assume there is a linear causal relationship between z and ω and no drift in the population, we can interpret this term as the change in character between two generations due to natural selection. This term is classically referred to as the "selection term." The second term on the right-hand side represents the average change in character z due to the transmission from parents to offspring being imperfect, or due to the change coming from factors other than natural selection. It is classically referred to as the "transmission-bias term." If particles reproduce perfectly, this term is nil.

Another useful formulation of equation (1), for my purposes, is in terms of linear regression. We know, by least squares theory, that the covariance between two variables Y and X is equal to the slope of the linear regression coefficient of Y on X times the variance of X (see Lynch and Walsh 1998, chap. 3). Transforming the covariance of equation (1) into a regression, we can rewrite it as:

$$\Delta\overline{z} = \underbrace{\underbrace{\beta_{\omega z}}_{\substack{\text{Strength of}\\ \text{selection}}} \mathrm{Var}(z_i)}_{\substack{\text{Selection}\\ \text{term}}} + \underbrace{\mathrm{E}(\omega_i \Delta z_i)}_{\substack{\text{Transmission-}\\ \text{bias term}}}, \tag{2}$$

where $\mathrm{Var}(z_i)$ is the variance of the particle character and $\beta_{\omega z}$, which is the slope of the linear regression of relative reproductive output on the character z. It represents the strength of selection for z.

With the single-level version of the Price equation defined, we can now move to its multilevel version. Recall that, in our setting, we assumed that the particles of the population are structured in collectives. We can define the character Z_k of the collective k as the average character value of the N particles constituting this collective, so that:

$$Z_k = \frac{1}{N}\sum_{j=1}^{N} z_{kj}.$$

Similarly, we define Ω_k, the relative reproductive output of k between two generations, as the average reproductive output of the particles constituting k, so that:

$$\Omega_k = \frac{1}{N}\sum_{j=1}^{N} \omega_{kj}.$$

Starting from equation (1), following the approach of Price (1972) and assuming that the particles reproduce perfectly (as I will assume throughout), one can rewrite the average change in character z between two generations (Δz), which is equal to (ΔZ), as follows:

$$\Delta\overline{Z} = \underbrace{\mathrm{Cov}(\Omega_k, Z_k)}_{\substack{\text{between-collective}\\ \text{selection}}} + \overbrace{\mathrm{E}(\Omega_k\,\mathrm{Cov_k}(\omega_{kj}, z_{kj}))}^{\substack{\text{within-collective}\\ \text{selection}}}, \tag{3}$$

where $\mathrm{Cov_k}(\omega_{kj}, z_{kj})$ represents the covariance between particle character and relative particle reproductive output within collective k, as opposed to the whole population.[9]

The first term on the right-hand side of equation (3) is classically referred to as the "between collective" (or "between group") selection term, while the second term on the right-hand side is referred to as the "within collective" (or "within group") selection term. Within-collective selection is typically understood as particle-level selection and between-collective selection as collective-level selection.

As with equation (1), we can rewrite the covariance terms of equation (3) in a regression form. Once this is done, equation (3) becomes:

$$\Delta\overline{Z} = \underbrace{\beta_{\Omega Z}\,\mathrm{Var}(Z_k)}_{\substack{\text{between-collective}\\ \text{selection}}} + \overbrace{\mathrm{E}(\Omega_k\beta_{k\omega z}\,\mathrm{Var_k}(z_{kj}))}^{\substack{\text{within-collective}\\ \text{selection}}}, \tag{4}$$

where $\mathrm{Var_k}(z_{kj})$ is the variance of the particle-level character within collective k.

The two terms on the right-hand side of equation (4) have the same interpretation as those of equation (3). However, in the first term on the right-hand side, $\beta_{\Omega Z}$ represents the slope of the regression of relative collective reproductive output on collective-level character, which can be regarded as the strength of selection at the collective level. In contrast, in the second term on the right-hand side, $\beta_{k\omega z}$ represents the coefficient of the linear regression of relative particle reproductive output on particle-level character *within collective* k, which can be interpreted as the strength of selection within collective k.

9. For a full derivation, see Frank (1998).

Having presented the multilevel Price equation, we can now ask whether it satisfies the Weak Independence Requirement. To satisfy this requirement would amount to 1) showing that it is generally possible to change the strength of selection at the particle level ($\beta_{k\omega z}$) 2) without this necessarily leading to a change in the strength of selection at any other level ($\beta_{\Omega Z}$), and 3) without violating the supervenience assumption. This represents the "Test of Weak Independence."[10] Before applying the Test of Weak Independence to the multilevel Price equation, we must know what sort of change is required for the entities of a population (say, the particles) to change the strength of selection in a single-level setting.

There are at least two ways this can be accomplished. The first is by intervening on the character value of a particle, while keeping the same number of offspring for this particle. Second, the number of offspring could be intervened upon while the the character of the particle is kept constant, while its number of offspring is changed. In both cases, the term $\beta_{\omega z}$ in equation 2 would change.

To see this at an intuitive level, we could imagine a population of moths with variation in wing shade.[11] Assume that, everything else being equal, darker-winged moths have more offspring than lighter-winged moths. We could suppose that this outcome results from the fact that, in their particular environment, dark-winged moths are more successful at hiding from predators. Suppose that moths with a shade score of 0 are completely white and those with a score of 3 are dark. In between, moths have different shades of grey with a higher score meaning a darker shade. To keep things simple, suppose that the shade score exactly matches the number of offspring produced by an individual – that is, a white moth has no offspring, while a dark moth has 3.

In this setting, we can ask what would amount to changing the strength of selection for one of the moths without this affecting anything else. Following the first way, this could be achieved by reducing or increasing the character value of this individual, without this affecting the number of offspring it produces. Despite this individual having a lighter (darker) shade, it would have no more (less) chance to encounter a predator. Following the second way, this would be achieved by increasing (decreasing) the number of a moth's offspring without changing its character value. For each approach to multilevel selection, I will illustrate both ways to alter the selection strength.

According to this reasoning, applying the Test of Weak Independence to the multilevel Price equation (following its standard interpretation) amounts to changing the character (reproductive output) value z (ω) of one particle in the population by intervention (and, consequently, the character (reproductive output) of the collective it belongs to), without changing its relative reproductive output ω (character value z). When such an intervention is carried out on particle j of collective k, the strength of particle-level selection (i.e., $\beta_{k\omega z}$) changes as expected. However, it also leads to a change in the strength of collective-level selection (i.e., $\beta_{\omega Z}$). Thus, the multilevel Price equation does not satisfy the Weak Independence Requirement, since it does

10. The idea of this test is inspired by the minimal test for causation within the interventionist account (Woodward 2003). However, the Test of Weak Independence does not correspond neatly to testing whether selection at the particle level also *causes* selection at the collective level. This is so because, following the supervenience assumption and the coupling of reproductive output between the two levels (recall section 2), any ideal intervention performed at the particle level will necessarily translate into a change at the collective level. Yet, an ideal intervention assumes no other change in any other variable at the time of change.

11. This thought experiment is inspired by the famous work of Kettlewell on the peppered moth (see Kettlewell 1955; see also Ridley 1996, 108–44 for a review).

Table 1: Values for particle-level and collective-level characters and their respective relative reproductive outputs in a simple hierarchical setting.

Coll. index	z_{kj}	w_{kj}	ω_{kj}	Z_k	W_k	Ω_k
1	1	1	0.5	1.5	1.5	0.75
	2	2	1			
2	2	2	1	2.5	2.5	1.25
	3	3	1.5			

(a) In normal conditions

Coll. index	z_{kj}	w_{kj}	ω_{kj}	Z_k	W_k	Ω_k
1	1	1	0.5	1.5	1.5	0.75
	2	2	1			
2	**1**	2	1	2	2.5	1.25
	3	3	1.5			

(b) Once an intervention on the character value z of a particle (bolded) has been carried out

Coll. index	z_{kj}	w_{kj}	ω_{kj}	Z_k	W_k	Ω_k
1	1	1	0.444	1.5	1.5	0.75
	2	2	0.888			
2	2	**3**	1.333	2.5	3	1.25
	3	3	1.333			

(c) Once an intervention on the reproductive output value ω of a particle (bolded) has been carried out

not pass the Test of Weak Independence. Therefore, the conclusion is that it does not represent a sound model of multilevel selection.[12]

To illustrate why my implementation of the Test of Weak Independence is not satisfied by the multilevel Price equation, suppose the simplest possible case of an idealized population made of two collectives, each composed of two particles with the value for particle and collective characters and reproductive outputs between two generations presented in table 1a. Now, suppose that within-collective selection is reduced in Collective 2 by changing the value of the character of the particle with character value 2 to 1, as represented in table 1b. The reproductive output is kept the same, as in (a). Following the supervenience assumption of the collective character on the particle character, this intervention on the particle's character in Collective 2 also changes the value of the average character value of Collective 2 from 2.5 to 2, as shown in (b).

Using the values of table 1, we can compute the strength of selection within collectives and between collectives under normal conditions and when the intervention on the particle of Collective 2 is carried out. Once this is done, we can see in table 2 that the strength of selection within Collective 2 ($\beta_{2\omega z}$) changes from 0.5 to 0.25. Following the classical interpretation, this means that particle-level selection decreases, as expected. However, we can see that there is also a change in the strength of selection at the collective level ($\beta_{\Omega Z}$) from 0.5 to 1. Thus, the Test of Weak Independence is not satisfied; consequently, the multilevel Price equation is not compatible with the Weak Independence Requirement.

Using the same reasoning, but this time increasing the reproductive output's value of the particle with the character value 2 by one unit in Collective 2, from 2 (in (a)) to 3 (in (c)), we reach the same conclusion. As we can see in table 2, the strengths of particle-level and collective-level selection are altered from 0.5 at all levels in normal conditions to 0.444 at the particle level in Collective 1, 0 at the particle level in Collective 2, and 1.5 at the collective level.

12. A similar conclusion has already been reached by a number of authors for different reasons (see Okasha 2006). However, to my knowledge, the reason provided here is new.

Table 2: Comparison of the strengths of selection within and between collectives in a population of collectives each made of two particles.

Level		Strength: Normal conditions	After interv. on z	After interv. on w
Particle ($\beta_{k\omega z}$)	**Coll. 1**	0.5	0.5	0.444
	Coll. 2	0.5	0.25	0
Collective ($\beta_{\Omega Z}$)		0.5	1	1.5

How should we explain those results? In the case of the intervention on particle character, this result can be explained by the fact that intervening on a particle's character value also affects the mean value of its collective character. This, in turn, affects the mean collective character value at the population level. In the case of the intervention on reproductive output, because what matters for the selection is the relative "reproductive output," any single change in the reproductive output of one individual will change the mean absolute reproductive output of the whole population and consequently the relative reproductive output of all the individuals of the population, the latter of which supervene on the reproductive output of the particles that compose it. Thus, because a "level" in the distinction between within-collective and between-collective selection following the multilevel Price equation invokes a relationship of supervenience, the Independence Requirement, even in its weak form, is unattainable. For the two coefficients to be independent, one would have to violate the supervenience assumption.

One possible objection to my way of implementing the Test of Weak Independence would be to say that although intervening *on a single particle* does not satisfy the Weak Independence Requirement, intervening *on more than one particle* in the population sometimes could preserve the strength of between-collective selection and thus satisfy the criterion (see Clarke 2016, for a specific example of this that he calls "structural collapse to the mean"). In other words, a particular strength of collective-level selection is "multiply realizable" by distinct particle-level properties. However, a different realizer of collective-level selection can only appear when changes in particle-level properties compensate each other, so that it yields no change in the mean. This is a very specific requirement that does not generalize. In general, a change in the strength of particle-level selection will lead to a change in the strength of collective-level selection. Therefore, even under this implementation of the test, it would be a very partial win for a proponent of the claim that the multilevel Price equation satisfies the Weak Independence Requirement. Further, it is reasonable to demand that independence between levels of selection is satisfied when the smallest possible change(s) at the particle level are performed. In our setting, this corresponds to altering the value for a property of a *single* particle. Under that type of change, the Weak Independence Requirement cannot be satisfied as it not possible to intervene on a single particle property that changes the strength of selection at the particle level without this also altering the strength of selection at the collective level.

4 Contextual Analysis and the Neighbor Approach

In the previous section, I showed that the Weak Independence Requirement is not satisfied by the multilevel Price equation because it fails the Test of Weak Independence as I implemented it. In this section, I show that the same is true of contextual analysis and another approach close to contextual analysis, which Okasha calls the "neighbor approach" (Okasha 2006, 198–202).[13] Both contextual analysis and the neighbor approach are rival interpretations of multilevel selection to the multilevel Price equation.

Contextual analysis originated in the social sciences (see Boyd and Iversen 1979) where it has a broad range of applications. It was initially proposed by Heisler and Damuth (1987; see also Goodnight, Schwartz, and Stevens 1992) in the context of multilevel selection and has since been used in a number of studies in this literature (e.g., Goodnight and Stevens 1997; Tsuji 1995; Stevens, Goodnight, and Kalisz 1995; Aspi et al. 2003). The motivation to develop an alternative to the multilevel Price equation stemmed from its lack of constraints on what can constitute collective-level selection. Indeed, it has been noted numerous times in the literature that the multilevel Price equation cannot distinguish between a process of selection occurring at the collective level from situations where there is only selection at the particle level but where the "effects" translate at the collective level. These situations are called "cross-level by-products" by Okasha (2006). Contextual analysis has been proposed as a solution to this problem.

To illustrate the idea of a cross-level by-product and why the multilevel Price equation fails to detect them, take a classic example found in Sober (1984, 258–60).[14] Suppose a population is made of collectives with individuals of different heights, but with no height variation within each collective. Crucially, the height of a collective does not depend on the height of any other individual in the collective or the population. Assume that an individual's fitness depends on its height. In this situation, because there are no interactions between individuals within a collective, there cannot be any selection at the collective level – assuming that a minimal requirement for collectives to be genuine biological entities is some interaction between the particles that compose them (more on this point below and in section 5). All the selection occurs at the individual level. Yet, the multilevel Price equation detects that all the selection occurs at the collective level. This is so because the first term on the right-hand side of equation (3) is non-nil, whereas the second term is nil. However, this is an absurd conclusion since we stipulated that an individual's fitness depends solely on its character value.[15] The relationship between collective character and collective fitness is purely due to differences made at the particle level, which is the definition of a cross-level by-product.

Contextual analysis is based on the same type of multiple linear regression developed by Lande (1979; see also Lande and Arnold 1983) for correlated characters. In contextual analysis, relative reproductive output (ω) – or some other quantity related to growth – is the dependent variable of the regression. In a two-level scenario, there are two independent variables: the particle character (z) and a contextual character. The contextual character refers to some collective-level property but is defined from the particle-level perspective. Typically, but not necessarily (more on this in a moment), this character is chosen as the average particle character value in a collective (Z). The particle character and the contextual character represent the "effect" of the

13. It should be noted that the neighbor approach is, arguably, a version of contextual analysis; see Goodnight (2020, 199–200). However, Okasha's distinction yields two approaches with interesting differences concerning the interpretation of particle and collective selection.

14. Another classic example is that of Williams (1966, 16–17), where he argues that a fleet herd of deer being fit is simply the result of each individual deer of the herd being fleet.

15. In a less extreme version of this example, we could assume that there is some variation within each collective. In this case, the multilevel Price equation would detect some selection at both the particle and collective level when, again, all the selection occurs at the particle level *ex hypothesi*.

particle character and collective character, respectively, on the relative reproductive output of the particle.[16]

The formalism underlying contextual analysis can be derived in a few simple steps. We define the fitness of a particle j in Collective k, following the above multiple linear regression, as:

$$\omega_{kj} = \beta_{\omega z|Z} z_{kj} + \beta_{\omega Z|z} Z_k + e_{kj}, \tag{5}$$

where $\beta_{\omega z|Z}$ is the partial regression coefficient of relative particle reproductive output on particle character, keeping the collective character constant, $\beta_{\omega Z|z}$ is the partial regression coefficient of relative particle reproductive output on collective character, keeping the particle character constant, and e_{kj} is the residual. Equation (5) can then be plugged into equation (1). Assuming perfect particle reproduction, so that $\mathrm{E}(\omega_i \Delta z_i) = 0$, and recalling that, by standard least squares theory, there is no correlation between e and z, so that $\mathrm{Cov}(e_{kj}, z_{kj}) = 0$, we obtain:[17]

$$\Delta\bar{z} = \underbrace{\beta_{\omega z|Z}\,\mathrm{Var}(z_{kj})}_{\substack{\text{Particle-level}\\ \text{selection}}} + \underbrace{\beta_{\omega Z|z}\,\mathrm{Cov}(Z_k, z_{kj})}_{\substack{\text{Collective-level}\\ \text{selection}}}. \tag{6}$$
[18]

Classically, the first term on the right-hand side of equation (6) is interpreted as particle-level selection. The second term is interpreted as collective-level selection. Following this interpretation, the two βs refer to the selection strength at each level.

We are now in a position to see why contextual analysis, contrary to the multilevel Price equation, yields the correct answer in situations of cross-level by-products. When there is no interaction between particles within a collective, ω is explained fully by the independent variable z so that the slope of the partial regression coefficient $\beta_{\omega Z|z}$ is nil. Since it is nil, the interpretation is that there is no selection at the collective level – which is the correct conclusion.

That contextual analysis yields the correct answer in situations of cross-level by-products forms an improvement over the multilevel Price equation. However, we can now ask whether it satisfies the Weak Independence Requirement. As with the multilevel Price equation, the answer is that it does not. To illustrate this, we can apply the Test of Weak Independence devised in the previous section to the same population of collectives made of two particles, after having changed the setting slightly. Suppose that the reproductive output of a particle j is determined perfectly (i.e., the residuals are nil) with equal magnitudes and directions by two independent variables – namely, its character and the character of its collective k (defined as the average character of the particles in this collective) – so that we have $w_{kj} = z_{kj} + Z_k$ (thus, $\beta_{wz|Z} = 1$ and $\beta_{wZ|z} = 1$). According to the classical interpretation of contextual analysis, there is selection at both the particle and collective levels in the same direction and with the same strength. If we apply this model to our example, we get the relative reproductive output values presented in table 3a and the strength of selection at the two levels presented in the second column of table 4: namely, $\beta_{\omega z|Z} = 0.25$ and $\beta_{\omega Z|z} = 0.25$.

16. For the interested reader, following Okasha's treatment of contextual analysis, a number of philosophers have discussed different problems surrounding contextual analysis in the context of multilevel selection. Some of these analyses can be found in Glymour (2008), Jeler (2014), Earnshaw (2015), Bourrat (2016), and McLoone (2015).

17. For details, see Okasha (2006, chap. 3).

18. Contrary to the multilevel Price equation, the collective-level character in contextual analysis need not be a statistical aggregate, which I assume throughout. If the contextual character is the average collective character (i.e., a statistical aggregate), we have $\mathrm{Cov}(Z_k, z_{kj}) = \mathrm{Var}(Z_k)$. Note also that we assumed there is no interaction between z and Z. In more complex cases, an interaction term could be added to equation (6).

Table 3: Values for particle-level character, contextual character, neighborhood character, absolute and relative particle reproductive output in a simple hierarchical setting.

Coll. index	z_{kj}	Z_k	X_k	w_{kj}	ω_{kj}
1	1	1.5	2	2.5	0.625
	2	1.5	1	3.5	0.875
2	2	2.5	3	4.5	1,125
	3	2.5	2	5.5	1.375

(a) In normal conditions

Coll. index	z_{kj}	Z_k	X_k	w_{kj}	ω_{kj}
1	1	1.5	2	2.5	0.625
	2	1.5	1	3.5	0.875
2	**1**	2	3	4.5	1,125
	3	2	1	5.5	1.375

(b) Once an intervention on the character value z of a particle (bolded) has been carried out

Coll. index	z_{kj}	Z_k	X_k	w_{kj}	ω_{kj}
1	1	1.5	2	2.5	0.588
	2	1.5	1	3.5	0.824
2	2	2.5	3	**5.5**	1,294
	3	2.5	2	5.5	1.294

(c) Once an intervention on the reproductive output value ω of a particle (bolded) has been carried out

Now, let us alter the strength of selection at the particle level by intervening on the character value of the particle in Collective 2 with the value 2 in table 3a and setting it to 1 (as shown in (b)), as we did earlier. As previously, for contextual analysis to pass the Test of Weak Independence, we should observe no change in the strength of selection at the collective level. However, this is not what we observe. As can be seen in table 4, if the change described is made, the strength of particle-level selection, $\beta_{\omega z|Z}$, decreases from 0.25 to 0.15, as expected. However, the strength of collective-level selection, $\beta_{\omega z|Z}$, increases from 0.25 to 0.85.[19] A similar conclusion is reached if we now increase the reproductive output of the particle in collective 2 with the value 4.5 in (a) to 5.5 in (c), instead of its character. As can be seen in the third column of table 4, in this case too, not only does the strength of selection at the particle level decrease from 0.25 to 0.118, but the strength of selection at the collective level increases from 0.25 to 0.471.[20] This demonstrates that contextual analysis does not satisfy the Weak Independence Requirement. As with the multilevel Price equation, this result can be generalized to more complex situations.

Perhaps the result obtained from contextual analysis comes from the fact that the linear regression model presented in equation (5) is not adequate. Indeed, there is something odd in this model, as noted by Okasha (2006, 198–201). The oddity comes from the fact that if it makes sense for a particle to interact with the other particles of a collective (its neighbors), it does not make sense to say that it interacts with its neighbors plus itself. Yet, the collective character in the contextual model takes into account the focal particles, which cannot be interpreted biologically. This leads Okasha, relying on the analysis proposed by Nunney (1985), to propose an alternative linear model to contextual analysis that he calls the "neighbor approach." In this

19. Ultimately, this is due to the fact that there is some collinearity between the variables z and Z (i.e., the two variables are correlated). For more on the problem of collinearity between variables in regression analysis, see Chatterjee and Hadi (2015, chap. 9).

20. The reason here why altering the fitness of a particle also affects the strength of selection at the collective level is that it changes the relative fitness of all the particles in the population.

Table 4: Comparison between the values for the strengths of selection at the particle and collective levels under contextual analysis in normal conditions and when an intervention on the character z of a particle has been carried out.

Level	**Strength**		
	Normal conditions	**After interv. on z**	**After interv. on w**
Particle ($\beta_{\omega z\|Z}$)	0.25	0.15	0.118
Collective ($\beta_{\omega Z\|z}$)	0.25	0.85	0.471

model, the relative reproductive output of a particle is explained by the character of the particle and its collective minus the focal particle (its neighborhood), which is more adequate from a biological standpoint.[21]

More formally, the neighbor linear regression model can be written as:

$$\omega_{kj} = \beta_{\omega z|X} z_{kj} + \beta_{\omega X|z} X_k + e_{kj}, \tag{7}$$

where X_k is the neighbor character (collective character minus character of the focal particle), $\beta_{\omega z|X}$ is the partial regression coefficient of relative particle reproductive output on particle character (keeping the neighborhood character constant), and $\beta_{\omega X|z}$ is the partial regression coefficient of relative particle reproductive output on neighborhood character (keeping the particle character constant).[22]

Following the same steps as with equation (5), we can plug this equation into equation (1). After a few rearrangements and simplifications, this yields:

$$\Delta\bar{z} = \underbrace{\beta_{\omega z|X} \operatorname{Var}(z_{kj})}_{\substack{\text{Particle-level}\\ \text{selection}}} + \underbrace{\beta_{\omega X|z} \operatorname{Cov}(X_k, z_{kj})}_{\substack{\text{Collective-level}\\ \text{selection}}}. \tag{8}$$

Despite the neighbor partitioning representing an arguably more adequate approach to the question of levels of selection than contextual analysis, it does not yield weak independence. This can be illustrated using again the example of the two collectives composed of two particles, as represented in table 3. An intervention on the particle in Collective 2 with character value 2 – setting its value to 1 – yields the change in the neighborhood X reported in table 3b.[23] As can be seen in the second column of table 5, this intervention leads to a change in the strength of selection at the particle level, from 0.375 to 0.575, and a change in the strength of selection at the collective level, from 0.125 to 0.425. Following the same step, but increasing this time the reproductive output of the particle in Collective 2 with a value of 4.5 in (a) to 5.5 in (c), we can see in the third column of table 5 that both the strength of selection at the particle and collective level change from 0.375 to 0.353 and from 0.125 to 0.235, respectively.

The failure to satisfy the Test of Weak Independence for both contextual analysis and the neighbor approach when an intervention is made on a particle's character or reproductive output, can be explained, as with the multilevel Price equation, by the fact that this intervention

21. As mentioned in footnote 13, the neighbor approach can be considered part of contextual analysis understood broadly, since a contextual character does not have to be the average particle character in a collective. Note also that this approach has been criticized by Godfrey-Smith (2008) for reasons I will not discuss here.

22. As Okasha (2006) notes, there is a straightforward relationship between $\beta_{\omega z|Z}$ and $\beta_{\omega z|X}$, in addition to $\beta_{\omega Z|z}$ and $\beta_{\omega X|z}$. See also Bourrat (2016, appendix).

23. Since the collectives are composed of only two particles, the neighborhood of a particle is simply the other particle of the collective.

Table 5: Comparison between the values for the strengths of selection at the particle and collective levels under the neighbor partitioning in normal conditions and when an intervention on the character z of a particle is carried out.

Level	**Strength**		
	Normal conditions	**After interv. on z**	**After interv. on w**
Particle ($\beta_{\omega z}$)	0.375	0.575	0.353
Collective ($\beta_{\omega X}$)	0.125	0.425	0.235

necessarily, following the supervenience assumption, leads to a change in properties at the population level that supervene on the particle's property. This is true even with the neighbor approach where a change in the character of the particle is associated with no change in the neighborhood of this particle. Yet, and this is crucial, it is associated with a change in the neighborhood *of other particles* in the collective. For that reason, it does not permit us to circumvent the supervenience assumption. The same is true when intervening on the fitness of a particle, which changes the relative fitness of all the particles in the populations. Thus, a change in the strength of selection at the particle level will be associated with a change in the strength of selection at the collective level.[24]

5 The Non-Aggregative Approach: A New Hope

In the previous two sections, I showed that none of the notions of collective or particle selection used in the classical approaches to levels of selection satisfy the Weak Independence Requirement. In this section, I propose another approach that starts from the idea that to count as a level of selection, a character defined at a given level should be one that interacts directly with its environment. This corresponds to the definition of a unit of selection as an "interactor" proposed by Hull (1980). However, it is difficult to characterize what "interacting directly with the environment" means. Whether a collective interacts directly with its environment *cannot* correspond to a situation where a collective character can interact with its environment independently – in a metaphysical sense – from its particles. Remember that this is so because, following the supervenience assumption, this type of strong independence is not physically possible.

Nonetheless, whether a collective interacts directly with its environment can be given a weaker meaning – namely, whether there is anything left of the collective-level character once the character of its constituent particles is measured independently of the collective context. Any portion of the collective character remaining once this subtraction has been performed can be understood as the part of the collective-level character particles due "solely" to the interactions between the particles *as if* there was no particle effect. The term "as if" is crucial here. It indicates that this way of characterizing a level of selection does not correspond to a notion of actual interaction occurring between the collective character and its environment, which is physically impossible because there is a relation of supervenience between the two levels. Rather, it tells

24. Here again, I refer to *expected* changes. Some interventions might lead to no change when a change in a particle property's value is compensated by another change in the value of another particle's property. However, as discussed in the previous section, this type of case does not threaten the point that generally it is not possible to change the strength of selection at the particle level without this changing the strength of selection at the collective level under either contextual analysis or the neighbour approach.

us what the collective character *would* be, assuming we can obtain a measure of the character of its particle independently.

The phrase "independently of the collective context" is also important. One might wonder how measuring the character of a particle independently of its collective context should be operationalized. This is a difficult question, which I will not address here; I have done so elsewhere (see Bourrat 2021b, 2021a, 2022, 2023b). Suffice it to say that in any situation of particles organized into collectives, it would be possible to consider a counterfactual situation, which often could be approximated experimentally or by relying on data from comparative biology, where a particle is "plucked out" of its collective and its character (or reproductive output) is then measured in an isolated situation. For instance, we could imagine a primordial multicellular organism from which we remove a cell. We then measure the value of one of its characters (e.g., resistance to UV radiation). We do the same for each cell of the multicellular organism. From there, we average the values obtained in isolation. The averaged value represents the cross-level by-product of the collective-level character. If this value is different from the value measured in situ (i.e., a measure of the character of the multicellular organism in normal condition), the deviation corresponds to the part of the collective character we can attribute "independently" to the collective itself.

Following Wimsatt's (1986, 2007) distinction between aggregative and non-aggregative properties, this deviation measures the degree to which a collective character is a non-aggregative property of its constituent particles' characters. The part of the collective character that is merely the outcome of the aggregation of its particles – and, consequently, where any interaction between two or more particles is severed – represents the aggregative part of the collective. Wimsatt's idea is related to the idea of a near-decomposable system as opposed to the decomposable one initially proposed by Simon (1962). In a decomposable system, where the system would correspond to a collective here, the interactions within the subsystems (here the particles) that compose it are much more important than those between them. As a result, the latter are negligible. In terms of aggregativity/non-aggregativity, a decomposable system is one in which the properties of the subsystem are aggregative. In a near-decomposable system, however, some non-aggregativity is exhibited between the subsystems. While the decomposable/near-decomposable system distinction is a useful one, as pointed out by Wimsatt (1972), it neglects the fact that in evolving systems, the subsystems evolve together, which might render them ultimately non-decomposable.

Following this interpretation, we can formally decompose the character z of particle j in collective k as follows:

$$z_{kj} = \alpha_{kj} + \gamma_{kj} \, , \tag{9}$$

where α_{kj} is the character of particle j belonging to collective k when it is measured in isolation (i.e., in the absence of other particles), and γ_k represents the non-aggregative component, which is simply the difference between the character of particle j measured in the context of the collective k (z_{kj}) and its value when measured in isolation (α_{kj}).

Similarly, we can decompose the relative reproductive output ω of particle j in collective k as follows:

$$\omega_{kj} = \omega_{\alpha kj} + \omega_{\gamma_{kj}} \, , \tag{10}$$

where $\omega_{\alpha kj}$ is the reproductive output of particle j belonging to collective k when it is measured in isolation, and $\omega_{\gamma_{kj}}$ represents the non-aggregative component.

From there, we can plug equation (9) or equation (10) into the covariance term of equation (1), assuming the particles reproduce perfectly (so that $\mathrm{E}(\omega_{kj}\Delta z_{kj}) = 0$). Following the distributive property of covariance, starting with equation (9), we obtain:

$$\Delta\bar{z} = \Delta\overline{Z} = \underbrace{\mathrm{Cov}(\omega_{kj}, \alpha_{kj})}_{\substack{\text{Particle-level}\\ \text{selection}}} + \underbrace{\mathrm{Cov}(\omega_{kj}, \gamma_{kj})}_{\substack{\text{Collective-level}\\ \text{selection}}}. \tag{11}$$

The first term on the right-hand side of equation (11) can be interpreted as the change in mean character due to particle-level selection (following the reasoning developed above), defined as the covariance between the aggregative component of the particle character and relative particle reproductive output. The second term on the right-hand side can be interpreted as the change in mean character due to collective-level selection, defined as the covariance between the functional non-aggregative component of particle character in its collective and relative particle reproductive output.

As previously, from least squares theory, we can rewrite equation (11) as:

$$\Delta\overline{Z} = \beta_{\omega\alpha}\,\mathrm{Var}(\alpha_{kj}) + \beta_{\omega\gamma}\,\mathrm{Var}(\gamma_{kj}),$$

where $\beta_{\omega\alpha}$ and $\beta_{\omega\gamma}$ are the regression coefficients of relative particle reproductive output on the aggregative and non-aggregative components of the particle character, respectively. They can be interpreted as the strength of selection at the particle and collective levels, respectively, under the aggregative/non-aggregative interpretation of multilevel selection.

Performing the same procedures but using equation (10), we get:

$$\Delta\bar{z} = \Delta\overline{Z} = \underbrace{\mathrm{Cov}(\omega_{\alpha kj}, z_{kj})}_{\substack{\text{Particle-level}\\ \text{selection}}} + \underbrace{\mathrm{Cov}(\omega_{\gamma_{kj}}, z_{kj})}_{\substack{\text{Collective-level}\\ \text{selection}}}. \tag{12}$$

The first and second term of equation (12) can also be interpreted as the change in mean character due to particle-level and collective-level selection, respectively defined as the covariance between the particle character and the aggregative component of particle relative reproductive output and the covariance between the particle character and the non-aggregative component of particle relative reproductive output.

Once transformed into variance, by least-square theory, equation (12) becomes:

$$\Delta\overline{Z} = \beta_{\omega_\alpha z}\,\mathrm{Var}(z_{kj}) + \beta_{\omega_\gamma z}\,\mathrm{Var}(z_{kj}),$$

where $\beta_{\omega_\alpha z}$ and $\beta_{\omega_\gamma z}$ are the regression coefficients of the aggregative and non-aggregative components of relative particle reproductive output on particle character, respectively. They too, following a different interpretation, can be understood as the strength of selection at the particle and collective levels, respectively, under the aggregative/non-aggregative interpretation of multilevel selection.[25]

25. A number of variants of the Price equation based on the aggregative/non-aggregative distinction can be derived. I selected here only the simplest form. For alternative forms, see Bourrat (2021b). Shelton and Michod (2014, 2020) provide an equation close to equation (12), where they consider ω to be decomposed into two components, with one corresponding to relative reproductive output in isolation and the other the deviation in relative reproductive output when compared to the reproductive output of the particle when living in the collective. Close versions of this equation can also be found in the literature on indirect genetic effects (for an overview, see Walsh and Lynch 2018, chap. 22). A straightforward extension of the equations proposed here would be to use both aggregative and non-aggregative components for particle character and relative reproductive outputs in a single equation.

Table 6: Values for particle character, aggregative and non-aggregative components, and relative particle reproductive output in a simple hierarchical setting.

Coll. index	α_{kj}	γ_{kj}	z_{kj}	w_{kj}	ω_{kj}
1	0.5	0.5	1	1	0.5
	1.5	0.5	2	2	1
2	1	1	2	2	1
	2	1	3	3	1.5

(a) In normal conditions

Coll. index	α_{kj}	γ_{kj}	z_{kj}	w_{kj}	ω_{kj}
1	0.5	0.5	1	1	0.5
	1.5	0.5	2	2	1
2	**0**	1	1	2	1
	2	1	3	3	1.5

(b) Once an intervention on the aggregative component of character value α of a particle (bolded) has been carried out

With this in place, we can now ask whether the aggregative/non-aggregative partitionings satisfy the Weak Independence Requirement. The answer is that it depends. When using the particle character decomposition, the requirement is satisfied. However, when using the reproductive output decomposition, it is not. We can see this by using, again, the example of the two collectives comprising two particles. Starting with the character z decomposition, we must know the character value of the particles of each collective when measured in isolation. Suppose that the values obtained for α are those provided in the first column of table 6. We can then deduce the value of γ, reported in the second column of the same table. Let us now, as previously, change the value of character of the particle in Collective 2 with the value of 2 in (a) and set its value to 1 in (b). To do so, the value of the aggregative component (which is associated with particle-level selection) is intervened upon and changed from 1 in (a) to 0 in (b). Once this intervention is carried out, we can see from table 8 that it only leads to a change in the strength of selection at the particle level, not the collective level. Indeed, $\beta_{\omega\alpha}$ changes from 0.6 to 0.3, while $\beta_{\omega\gamma}$ remains 1. Thus, the Test of Weak Independence is passed, demonstrating that the Weak Independence Requirement is fulfilled.[26]

Moving now to the reproductive output decomposition, we can see in table 7 that if, by intervention, we increase the value of the aggregative component of the reproductive output of the particle in Collective 2 with value 2 (in (a)) by one unit (in (b)), this leads to a change in both the strength of selection at the particle level and at the collective level, from 0.375 to 0.556 and from 0.125 to 0.111, respectively, as shown in table 9. Thus, following this decomposition, the Test of Weak Independence is not met.

How should we explain the difference between the two partitionings based on the aggregativity/non-aggregativity distinction? In the case of the character z decomposition, when the aggregative component is changed by intervention, the only other change it leads to is a change in the value of the character, from 2. The collective component (γ) does not change. However, when the aggregative component of the reproductive output (ω_α) is intervened upon, it changes not only the value of reproductive output but also all the values of the relative reproductive output of all the particles in the population, as can be seen in table 7, when comparing (a) and (b), and as was the case with the other partitionings presented earlier.

The conflicting results obtained from the two aggregative/non-aggregative paritionings provide some fuel for the view that a trait-based rather than a fitness (reproductive output)-based approach to multilevel selection is more amenable to providing an adequate understanding of

26. This result can be generalized to more complex cases.

Table 7: Values for particle character, reproductive output, aggregative and non-aggregative components of reproductive output, relative particle reproductive output, and aggregative and non-aggregative components of relative reproductive output in a simple hierarchical setting.

Coll. index	z_{kj}	w_{kj}	$w_{\alpha kj}$	$w_{\gamma kj}$	ω_{kj}	$\omega_{\alpha kj}$	$\omega_{\gamma kj}$
1	1	1	0.5	0.5	0.5	0.25	0.25
	2	2	1.5	0.5	1	0.75	0.25
2	2	2	1	1	1	0.5	0.5
	3	3	2	1	1.5	1	0.5

(a) In normal conditions

Coll. index	z_{kj}	w_{kj}	$w_{\alpha kj}$	$w_{\gamma kj}$	ω_{kj}	$\omega_{\alpha kj}$	$\omega_{\gamma kj}$
1	1	1	0.5	0.5	0.444	0.222	0.222
	2	2	1.5	0.5	0.889	0.667	0.222
2	2	2	1	1	0.889	0.444	0.444
	3	4	**3**	1	1.778	1.333	0.444

(b) Once an intervention on the aggregative component of reproductive output value ω_α of a particle (bolded) has been carried out

the notion of independence between levels of selection. This is a point my collaborators and I have already made in several other places (Takacs, Doulcier, and Bourrat 2023; Bourrat 2021a; Bourrat et al. 2022); moreover, I am not alone in that respect. For instance, Bijma (2014, 66–67) argues that reasoning about evolution in a fitness-centered way can be problematic, particularly in the context of social evolution, due to indirect genetic effects, which are strongly related to the multilevel selection literature (e.g., Bijma and Wade 2008; Wade 2016). Bijma provides several reasons for this point, but the most relevant here is that a classical way to conceive of evolution causally, especially in the quantitative genetics literature, is that genes affect phenotypes, which in turn affect fitness. In the context of a phenotypic model (i.e., where genetics is not specified), to assess what causes differences in selection at different levels, it is more adequate to intervene on the more causally upstream cause of evolution: that is, on the characters themselves rather than their fitness consequences (reproductive output).

Before concluding, there is a subtle point that needs addressing with respect to the result that the aggregative/non-aggregative partitioning of z satisfies the Test of Weak Independence. I have assumed that α and γ are independent, so that an intervention on α does not lead to a change in γ. However, it is possible that in some cases, there is no empirical way to intervene on the character so as to only affect the aggregative component. This might be regarded as a problem for the claim that particle-level and collective-level selection can be independent. To this point, I respond that all that is required for the Test of Weak Independence to be passed is that the independence is *in principle* possible, where what is possible is only constrained by logic. For instance, assuming as we did throughout that the collective-level character is defined in terms of a particle-level character, because it is a statistical aggregate, it would be logically incoherent to intervene on a particle without this also changing the value of the collective-level character. In the case of α, there is nothing logically incoherent in changing its value without

Table 8: Comparison between the values for the strengths of selection at the particle and collective levels under the aggregative/non-aggregative partitioning in normal conditions and when an intervention on the aggregative component (α) of character z is carried out on a particle.

Level	Strength	
	Normal conditions	After interv. on α
Particle ($\beta_{\omega\alpha}$)	0.6	0.3
Collective ($\beta_{\omega\gamma}$)	1	1

Table 9: Comparison between the values for the strengths of selection at the particle and collective levels under the aggregative/non-aggregative partitioning in normal conditions and when an intervention on the aggregative component of the reproductive output w_α is carried out on a particle.

Level	Strength	
	Normal conditions	After interv. on $\mathbf{w}_\alpha$
Particle ($\beta_{\omega_\alpha z}$)	0.375	0.556
Collective ($\beta_{\omega_\gamma z}$)	0.125	0.111

changing the value of γ. It would, however, be incoherent to intervene α without changing z if γ is kept constant, or without changing γ if z is kept constant.

Although the above example demonstrates that Weak Independence is *in principle* possible following the aggregative/non-aggregative partitioning of z, does this theoretical possibility nonetheless translate into some biological situation? This is a more difficult question to answer since one would have to conduct some experiments to answer it. However, *prima facie*, I believe that it does. There are plenty of biological situations where changing the aggregative character of a particle would, in all likelihood, have no impact on its non-aggregative component.[27] Consider the following example. Aggregation is a significant phenomenon in woodlice, which are terrestrial crustaceans. This behavior has been associated with a number of changes in character that can be defined both at the individual and aggregate levels (and, thus, are statistical aggregates), such as "rate of oxygen consumption" or "resistance to desiccation." When in groups, woodlice consume less oxygen and exhibit better resistance to desiccation (for a review, see Broly, Deneubourg, and Devigne 2013). In this example, we could imagine that changing the value of an individual's aggregative component for resistance to desiccation or oxygen consumption does not affect the overall gain in resistance to desiccation or reduction in oxygen consumption solely due to the interaction between the individuals of the aggregation (i.e., the non-aggregative component). This could be explained by the fact that the mechanisms of resistance to desiccation and oxygen consumption are different when an individual is in isolation compared to in a collective. Of course, such a hypothesis would have to be tested experimentally.

27. This assumes a certain value range for the change and the definition of an environment where the particle can be considered as being independent from the collective context.

6 Conclusion

In this paper, I have provided an analysis of the notion of independence between levels of selection. First, I showed that if independence is understood in a strong metaphysical sense, two levels of selection cannot be independent. However, I argued that one need not commit to this strong reading. Instead, one could consider independence more weakly – as the possibility for the strength of selection at a given level to be different – without this changing the strength of selection at another level, given some reasonable interpretation of the notion of strength of selection. Nonetheless, I showed that the classical formal approaches to multilevel selection – namely, the multilevel Price equation, contextual analysis, and the neighbor approach – all fail to refer to a weaker notion of independence. This is so precisely because they are built on the idea that levels refer to relationships of supervenience. Consequently, changing the strength of selection at one level leads to a change in the strength of selection at another level. From there, I proposed two partitionings using a different approach where different levels of selection are not defined from a relationship of supervenience but rather from the aggregative and non-aggregative components of a particle's properties. In one partitioning, the focal contribution is toward a character; in the other, the contribution is toward reproductive output. I showed that two levels can be regarded as independent within this approach when considering the partitioning focusing on collective character.

This analysis speaks to the debate that occurs in social evolution between kin selectionists, who argue that any evolutionary phenomenon can ultimately be explained from the point of view of the particles that compose a collective (e.g., Dugatkin and Reeves 1994; West, Griffin, and Gardner 2007; Kerr and Godfrey-Smith 2002), and others, who disagree with this argument (Bijma and Wade 2008; Nowak, Tarnita, and Wilson 2010; Lloyd, Lewontin, and Feldman 2008; Lloyd et al. 2005; Wade et al. 2010; Sarkar 2008). In distinguishing the strong from the weak sense of independence between levels of selection, one can see that the two camps need not oppose each other. It is possible metaphysically to reduce everything down to the lower level. However, in doing so, one may miss a crucial explanatory aspect of the dynamics occurring between particles within a collective, a point I treat in more depth in Bourrat (2023a), but which the distinction between aggregative and non-aggregative collective character makes striking.

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