CHAPTER TWO

In What Sense Can There Be Conflict Between the Levels of Selection?

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ABSTRACT This chapter proposes an analysis of the idea of conflict between levels of selection. An evolutionary conflict occurs when two parties have opposing evolutionary interests. I argue that, in multilevel contexts, the idea of opposing interests is difficult to articulate. The root of the problem, I show, is that often when applying the idea of conflict between levels, higher-level entities are composed of lower-level ones, rendering the evolutionary fate of the former inevitably tied to the evolutionary fate of the latter. Nonetheless, I propose different interpretations of the ideas of conflict between levels corresponding to scenarios involving different compositional relationships between lower and higher levels. The upshot is that the term "conflict between levels" can either be understood in a metaphorical sense or be redescribed as a case where the conflict occurs between parties that do not exhibit a relationship of composition. Finally, I apply my analysis in the context of the evolution of cancer, where cancerous cells have been described as in conflict with the organism.

Introduction

The idea of evolutionary conflict is often invoked in evolutionary biology literature, particularly in situations where a phenotype is regarded as suboptimal from the perspective of its bearer, either because it is a straightforward maladaptation or because it is an extravagant adaptation—that is, it is costly to produce (Queller and Strassmann 2018). For instance, a case of evolutionary conflict occurs when an ant is infected by the lancet liver fluke (*Dicrocoelium dendriticum*), a parasite that manipulates the ant's behavior, causing it to climb grass blades and clamp its mandibles onto the top of the blade. This behavior increases the chances of the ant being eaten by a herbivore (Moore and Moore 2002, 55–56), thereby allowing the parasite to continue its life cycle. This behavior is a straightforward maladaptation from the perspective of the ant due to a conflict between the ant and the parasite over the ant's behavior. Adaptations such as the exaggerated begging behaviors of juveniles in some species of birds or the antlers of a moose are “extravagant” because they would not exist in the absence of opposing interests: between offspring and parents in the case of begging juveniles and between males in the case of the moose.

In the contexts where adaptation and appearance of design are regarded either as what evolution ought to explain or as a working hypothesis—what Godfrey-Smith (2001) calls explanatory and methodological adaptationism, respectively—the existence of suboptimal phenotypes represents a puzzle that must be solved. Invoking the existence of a conflict between two parties is one available solution to this puzzle. Other candidate explanations include the existence of some underlying genetic constraints for the bearer of the phenotype and that the phenotype evolved as a result of a chancy process (i.e., drift).

One context in which the idea of evolutionary conflict has been used is the multilevel selection theory literature and related topics, such as the transition from unicellular to multicellular organisms and the evolution of cancer from a multilevel selection perspective. In these works, levels of organization at which a process of selection can occur, such as the genetic level and the individual level, or the cellular level and the organismal level, are regarded as two parties that can be in conflict, in a way that is similar to how the ant and the lancet liver fluke are in conflict.

Instances of work that have used the idea of a conflict between levels of selection, often in passing, are numerous (e.g., Maynard Smith 1988; Maynard Smith and Szathmáry 1995; Tsuji 1995; Michod and Roze 2001; Taylor et al. 2002; Joseph and Kirkpatrick 2004; Okasha 2006, 2021; Folse and Roughgarden 2010; Rainey and Kerr 2010, 2011; Alizon et al. 2011; Wade 2016; Ratcliff et al. 2017). For instance, Charlesworth (2000), discussing Haldane’s 1932 *The Causes of Evolution,* writes, “In addition to conflicts between different levels of selection, there is also the possibility of conflict between entities at the same level of organization, but which are subject to different rules of inheritance” (p. 493). In discussing the problem for the evolution of altruism, Wilson and Sober (1994) succinctly summarize their argument as follows: “Altruism involves a conflict between levels of selection. Groups of altruists beat groups of non-altruists, but non-altruists also beat altruists within groups” (p. 599).

While the case for evolutionary conflict between prey and predators, sexual conflicts, or hosts and pathogens—all of which occur between parties that are at a single level of organization (hereafter, “classical evolutionary conflicts”)—is straightforward to conceptualize, situations where a conflict involves multiple levels are more perplexing. In this chapter, I offer an analysis of this type of situation and, more specifically, examine the sense in which there can be conflict between the levels of selection. I argue that if this phrase is understood as referring to a genuine evolutionary conflict in the same way that classical evolutionary conflicts (as defined above) are understood, it is a mistake to claim that a conflict between levels of selection can exist. However, I argue that the notion of conflict involved in the multilevel selection literature can be understood in a metaphorical sense as it involves counterfactual scenarios; that is, there *would* be a conflict under different conditions. This way of conceiving conflict between levels of selection yields a different type of explanation from that of classical evolutionary conflicts. However, I argue that it can, once clearly separated from the classical notion, provide insight into the evolutionary mechanisms that have been at play to allow for the emergence and maintenance of higher-level entities that result from evolutionary transitions in individuality, such as multicellular organisms and superorganisms.

From a purely philosophical stance, disambiguating the notion of evolutionary conflict between levels of selection is important. Mixing different notions of conflict between levels of selection can lead to misunderstandings and impede scientific progress. This type of misunderstanding has been identified as a problem for the more general idea of a "level of organization" (Brooks 2021). This chapter is intended to offer a conceptual clarification to facilitate discussion surrounding the idea of evolutionary conflict in multilevel settings, such as multilevel selection theory, evolutionary transitions in individuality, intragenomic conflict, and cancer, as seen through the lens of multilevel selection.

The chapter is divided into three sections. In the first section, I propose a definition of a classical evolutionary conflict and a simple "test" to detect whether, in a given setting, there is an evolutionary conflict between two types of entities. In the second section, I apply this definition to a multilevel setting. I show that it can be interpreted in at least two different ways. Under the first interpretation, different levels refer to different physical substrates, such as a cell and the *rest* of the body of an organism. Under the second interpretation, they refer to the same substrate, such as a cell and the *whole* body of an organism, including the focal cell. I argue that only the first interpretation aligns with the classical notion of evolutionary conflict and that under the second interpretation, conflict can only be understood in a metaphorical sense because no factual conflict occurs between the different levels. Finally, in the last section, I briefly illustrate how my analysis can be useful in the context of recent discussions of the role of multilevel selection in the evolution of cancer and the ways in which the metaphorical idea of conflict between levels of selection, once properly separated from the classical sense of evolutionary conflict, can nevertheless be useful.

Defining and Detecting Classical Evolutionary Conflict

In this section, I begin with a simple definition of an evolutionary conflict.

> *Classical Evolutionary Conflict.* A situation where two or more (biological) entities have opposing evolutionary interests with respect to a particular trait, where an evolutionary interest is measured in terms of fitness (long-term growth rate).

A few remarks are in order regarding this definition. First, the term "conflict" refers here to evolutionary "entities" at any level of organization and in any domain. This is so because I consider there to be no a priori reason why there could only be evolutionary conflicts at a particular level or in a particular domain. In a given particular setting, "entity" might, for instance, refer to a gene, an organism, a group, a cell, a chromosome, a cultural item, and so forth. Second, the idea that two entities have divergent interests over a particular trait implies that they actually interact, such as when the lancet liver fluke *manipulates* the ant's behavior.

Third, one might consider that the definition I provide refers to the idea of competition for resources rather than conflict. A famous case of competition for resources was described by Gause (1934): two species of *Paramecium, P. caudatum* and *P. aurelia,* compete for resources, and *P. aurelia* outcompetes *P. caudatum* because *P. aurelia* has an advantage in resource utilization. In response to this, it should be noted that situations of competition for resources represent instances of evolutionary conflict. In such cases, the trait over which there is a conflict is which entity any limiting resources should go to (see also Queller and Strassmann 2018). While considering resources as a trait is nonstandard, it is aligned with the view that phenotypes can extend beyond the physical boundaries of an organism (Dawkins 1982; Haig 2012). Finally, while I mainly focus here on the idea of conflict, part of what I argue can be straightforwardly applied to the ideas of evolutionary cooperation (or synergy) and independence, in which cases evolutionary interests are aligned and independent, respectively.

With these remarks in place, given the definition of classical evolutionary conflict provided in this chapter, I propose a "test" to detect the presence of such conflicts in a particular setting. As was mentioned earlier, if two or more entities have divergent evolutionary interests with respect to a particular trait, the value of this trait depends on some interactions between the entities, as each will "push" the trait value in a particular direction. Therefore, eliminating such putative interactions and comparing the resulting evolutionary success of the entities to a situation in which the entities have the opportunity to interact provides a means to assess whether any evolutionary conflict is occurring between them (see also McCoy et al., this volume, for examples of ways to quantify conflict between corals and microalgae using specific traits as proxies). More specifically, if at least one of the entities benefits from the elimination of interactions, this is evidence that the two entities are in evolutionary conflict with respect to that trait. If both do worse in the absence of interactions, they are in synergy with respect to that trait. Finally, if there is no change, there was neither conflict nor synergy over this trait. Depending on the entities studied, different ways to implement the test could be devised, each providing different degrees of evidence for evolutionary conflict.

One very crude but effective way to implement the test, inspired from Gause's (1934) famous experiment of competitive exclusion in *Paramecium* (Foster and Bell 2012), is illustrated in Figure 2.1. Suppose *A* and *B* are both microscopic organisms of the same species and that they reproduce asexually with perfect inheritance in the same environment. Suppose you know nothing about their biology except that they both need a particular nutrient that is available in limited quantities to grow. Besides this nutrient, everything they need to grow is always present in an optimal concentration at all times. You also know that, given their planktonic (i.e., free-living) lifestyle, any interaction between them will be mediated by their liquid environment. Crucially, you do not know whether they can synthesize this nutrient or whether there is some variation for this trait. You want to know whether these two entities are in evolutionary conflict over gathering this nutrient in the environment. To do so, you measure the long-term growth rate of the two entities in situations where they coexist in their natural environment (see Figure 2.1a)

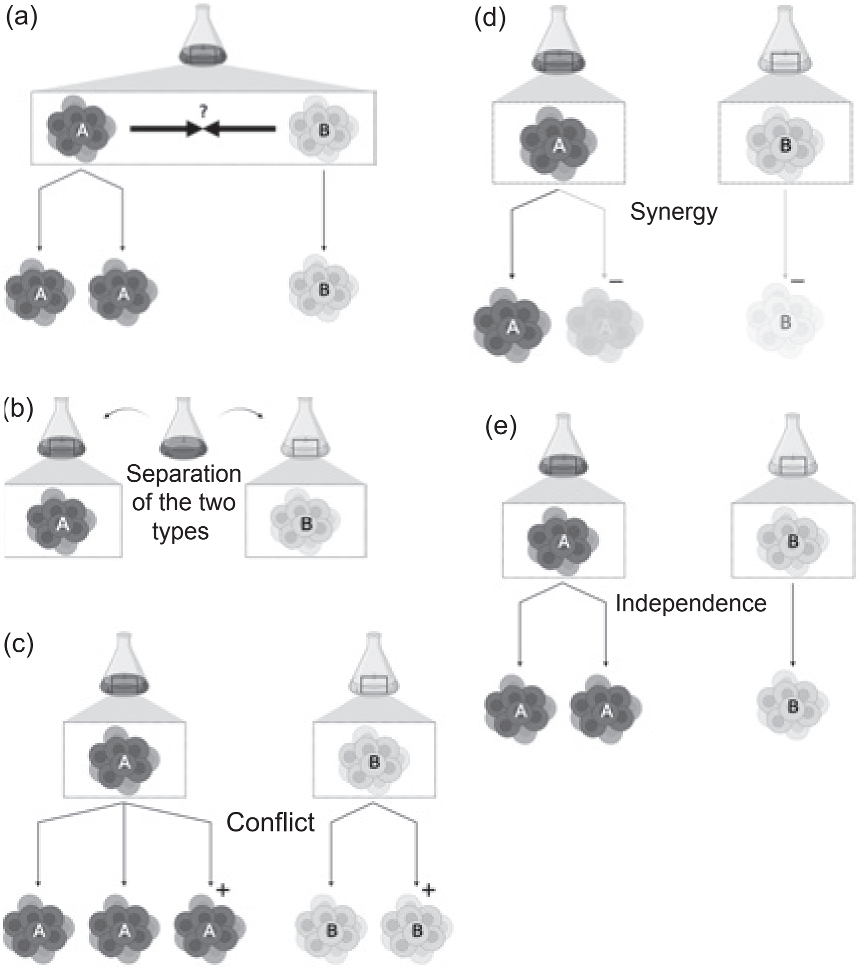

Figure 2.1. Possible implementation of a test for detecting an evolutionary conflict between two entities. (a) When two types of entities are in an environment where they have the opportunity to interact with respect to a trait, one way to assess whether there is an evolutionary conflict is to eliminate any opportunity for interactions between them by keeping them separate, as shown in (b). If the fitness (measured here as growth after some time) of at least one of the two entities is different when separated from the other entity, then there are interactions between the two entities. In particular, an evolutionary conflict occurs between two entities when at least one entity does better (in fitness terms) when separated from the other type, as in (c). Evolutionary cooperation or synergy occurs when both entities do worse in the absence of the other type, as in (d), or one does worse with no change for the other. Finally, if no change in fitness is observed as the result of the separation, as in (e), there is evolutionary independence of the two entities with respect to the trait.

and make the same measurement (in the same conditions) in situations where they are separated from one another (see Figure 2.1b). In this setting, if one or both of the two entities grows at a higher rate in the absence of the other, then there is strong evidence that an evolutionary conflict between the two entities occurs (see Figure 2.1c). This is because any interaction between two entities that prevents one or both from growing optimally is eliminated when the two types are separated. If both do worse, the two entities are cooperating or synergizing with respect to the trait (see Figure 2.1d). This is because any interaction between the two entities that allowed for the nutrient to be produced in a higher concentration by one entity is eliminated when they are separated. Finally, if there is no difference in growth rate, there is no conflict or synergy; in other words, there is evolutionary independence between the two entities with respect to the trait (see Figure 2.1e). The lack of changes between the two conditions indicates that there is no interaction between the two entities when they are in the presence of each other.[1]

Are Genuine Conflicts Between Levels of Selection Possible?

In the previous section, I proposed a definition of evolutionary conflict and described an associated test for determining whether there is conflict between two or more types of entities. In this section, I apply this definition to a situation where the entities refer to different levels of selection. This yields the following definition:

> *Evolutionary Conflict (levels of selection).* A situation where two or more (biological) entities at different levels of selection have divergent evolutionary interests with respect to a particular phenotype, where an evolutionary interest is measured in terms of fitness (long-term growth rate).

This definition can be understood in at least two different ways. In the first sense, the higher-level and lower-level entities (henceforth, "collectives" and "particles") are physically distinct entities (see Figure 2.2a),

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[1] To be clear, the test presented here is intended to illustrate the point rather than present a surefire test. Nonetheless, given any setting, a test of this form could in principle be designed.

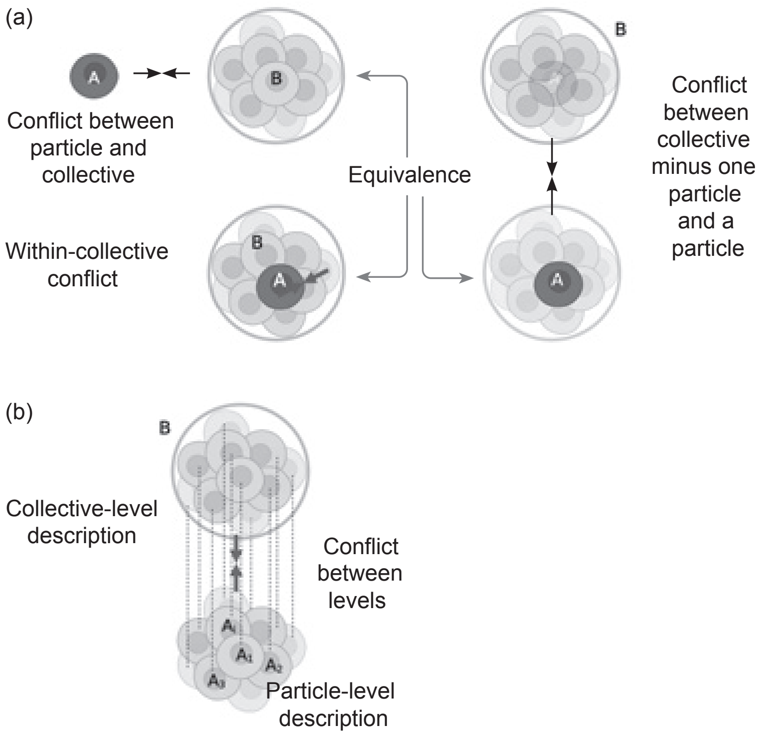

Figure 2.2. Two senses under which an evolutionary conflict between higher-level and lower-level entities can be understood. In both cases, A and B refer to the lower-level and higher-level entity, respectively. (a) Three instances in which A and B are physically distinct entities. This type of situation does not pose any conceptual problem, as it is on par with classical evolutionary conflict. (b) A and B are made of the same physical substrate so that B constitutively depends on multiple A. This poses a conceptual problem because any change in the long-term fitness of A will also lead to a change in fitness in the same direction of B.

such as a cell and an organism minus this cell. In the second sense, the collectives and particles are made of the same physical substrate (i.e., particles constitute a collective; see Figure 2.2b), such as an organism and the cells that compose this organism. A conflict between levels could also apply to more ambiguous cases where particles partially constitute a collective, such as when an organism is considered to be composed of more than its cells and includes, for example, an extracellular matrix. I will only discuss clear-cut cases here.

Discussing an evolutionary conflict between two or more levels (of selection) in the first sense is straightforward. One just needs to be aware

(1) that the entities at the "higher" and "lower" levels refer to levels of description (i.e., they are just ways to describe biological objects), and (2) that one could provide an equivalent description using a single level. This type of case is more accurately characterized as a case of conflict between entities *described* at different levels, rather than conflict between levels, where the conflict would be a phenomenon in the world rather than in the mind of the observer. In simple cases, a "collective" (*B*) can be equivalently redescribed in terms of "particles" (*A*) (see Figure 2.2a). For instance, assuming that a simple multicellular organism is only composed of cells and no other substrate, it can be redescribed in terms of cells. A multicellular organism (*B*) is a collection of cells (*A*) that have adhesive powers. This way of switching back and forth between the particle and collective levels of description is particularly interesting in the context of the first stages of an evolutionary transition in individuality (Godfrey-Smith and Kerr 2013; Bourrat 2023a). However, switching back to a particle-level description and retaining the full information of the system becomes more challenging in situations where the complexity of the collective increases. When this occurs, the only pragmatic description becomes a collective-level one (Bourrat 2023a). At any rate, whether an adequate lower-level description is available or not, one can always, *in principle,* apply the test presented in Figure 2.1c to cases where the two entities do not physically overlap, for *A* and *B* could potentially be separated. Note that whether this can be done in practice has no bearing on the conceptual distinction. Thus, these cases are very much like classical cases of evolutionary conflict at a single level.

I mentioned in the previous paragraph that the early phases of an evolutionary transition in individuality, such as cells exhibiting both a unicellular and colony mode of living, represent situations where this sense of evolutionary conflict between "levels" can be applied. As we shall see in "Subversion from Within and Conflicts Between the Levels of Selection," the evolution of cancerous cells within an organism can also be examined from this perspective.

Referring to evolutionary conflict in the second sense (i.e., where particles constitute a collective) is more problematic. As in the first sense, "higher" and "lower" levels also refer to levels of description, but because collectives are constituted by particles so that both descriptions refer to the same substrate (see Figure 2.2b), levels are not merely different ways to describe different objects—they are also compositional, so that the different description applies to one object (*B*) and a part of it (*A*). This distinction from the previous sense of conflict is important if one is committed to the standard scientific assumption that in a situation where there is a strict compositional relationship between different levels, the higher levels mereologically supervene—that is, constitutively depend—on the lower levels.

One implication of this assumption is the existence of the following constraint (more fully explored in Bourrat 2024): If one were to change some property of a single particle (*A*) that is part of a collective (*B*), there would necessarily also be a change in some property of *B*. If the particle-level property that is changed has an effect on the fitness of the particle, so that its long-term growth is affected, by virtue of being part of a collective, this implies that the long-term growth rate of the collective will also be altered in the same direction.[2] Concretely, altering the long-term reproductive success of a particle, when particles form collectives and collectives cannot grow indefinitely, necessarily translates into a higher number of collectives being produced in the long run (Bourrat 2021; Bourrat et al. 2022).

If the supervenience assumption were to be violated, nothing could prevent causal chains at the collective level from being created *ex nihilo*. That is, particles would not have to play any role in the existence of collective-level processes, the latter of which would be *strongly* emergent. However, the scientific consensus is that emergent phenomena are always *weak* so that any process at the collective level could always, in principle, be accounted for by processes at the particle level (see Bedau 1997 for more on the distinction between strong and weak emergence).

The constraint that a change in a particle's property affecting fitness would necessarily affect the fitness of the collective this particle belongs to in the same direction—and further, that in the long run, the particle and the collective would have the same evolutionary fate—poses a problem for the claim that an evolutionary conflict can exist between different levels of selection.[3] This is so because an evolutionary conflict presupposes not only that the fitnesses of the parties involved are distinguishable but also that they go in opposite directions. Both conditions

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[2] This constraint is related to Kim's exclusion principle (Kim 1988); for a brief discussion, see Okasha (2006), 106–107.

[3] There are exceptions to this when a collective can grow indefinitely or have an infinite size, but both assumptions are idealizations and therefore do not undermine this reasoning (see Bourrat 2021 for details).

are precluded from the existence of a constitutive relationship between the particles and the collective. Therefore, the idea of conflict between levels cannot be understood literally in such a setting.

This problem can be appreciated more concretely by implementing the test presented in Figure 2.1c in the situation where a collective is strictly composed of particles. In attempting to perform the test, one would be confronted with the practical problem of being unable to physically separate *A* from *B* without changing the nature of *B*. It is not possible to separate a cell from its collective without changing the nature of the collective. From there, any increase in long-term reproductive output of the collective, once the particle has been removed, does not correspond to a comparison of the fitness of *B* in the presence and absence of *A* that could reveal an evolutionary conflict in the same way that there is a conflict between an ant and a lancet liver fluke. Instead, this corresponds to a comparison of the fitness of *B* and the fitness of another type of collective that does not contain *A*. Similarly, from the perspective of the particle, the comparison would be a comparison between a particle in the presence of a collective minus a particle and the absence of it (leading us back to the setting presented in Figure 2.2a), not the presence or absence of a whole collective.

How should we thus interpret the idea of conflict between levels in situations where particles and collectives refer to the same physical substrate? I propose that conflict between levels in such situations actually corresponds to cases where fitness at each level is estimated over different timescales and for which the environment over these different timescales cannot be considered to be the same on average (Bourrat 2015a, 2015b, 2021, 2023a, 2023b; Black et al. 2020; Bourrat et al. 2022). Particle-level fitness is often estimated over a much shorter timescale than collective-level fitness. For instance, the fitness of a cell is often estimated over a timescale that does not exceed the lifespan of the organism it is part of. In contrast, the fitness of an organism is estimated over at least one organism's generation. Now, if a long-term projection is made with these estimates over different timescales, they might not match, and there might appear to be conflict between levels. However, a measure made over the same timescale at both levels would reveal no such conflict.

To see this point, take the example proposed by Wilson and Sober in the Introduction to this volume. Assume a population of altruistic and selfish individuals organized in groups with a phase during which the group reproduces in a mixing pool following the trait group model (Wilson 1975), one of the simplest models used in the multilevel selection literature to demonstrate the power of group-level selection. Measuring the fitness of both types within a group will show that selfish individuals do better. However, when measured at the level of the group, groups composed of more altruistic individuals do better (produce more offspring) than those composed predominantly of selfish individuals. According to Wilson and Sober, this would demonstrate a conflict between the individual and group levels, as quoted in the Introduction. However, a more accurate description is that estimating the success of an individual within a group does not correspond to its fitness in the long run, as it does not take into account events that are typically described at the group level (e.g., a dissolution of the group, formation of new groups). However, such events can also be accounted for from the perspective of an individual. When this is done, taking the long-term growth rate of an altruistic individual considering events beyond that of the immediate group of this individual leads to no discrepancy or conflict between the two levels.

It follows from this reasoning that discussing conflict between lower and higher levels of selection in situations where the higher levels are composed of lower ones can only be understood in a specific counterfactual sense. In the trait group model, there *would be* a conflict between the lower and the higher level if being selfish (and successful) within a group did not entail being unsuccessful in the long run, as both selfish groups and selfish individuals are unsuccessful when altruism prevails. Accordingly, one might embrace the notion of "counterfactual conflict." I find this problematic due to the oxymoron it creates. An evolutionary conflict either does or does not occur; in the case of the trait group model, no such conflict exists or could even exist without violating the supervenience assumption. Instead, I prefer to refer to such conflicts as metaphorical conflicts or "conflicts."

Thus far, I have argued that when entities at different levels are made of different physical substrates, a genuine evolutionary conflict can only occur between them. However, in such cases, applying a unique level of description would show that such conflicts are not strictly conflicts *between* levels of selection but rather conflict occurring *in multilevel settings*. Second, when the entities are made of the same physical substrate, I argued that due to the constraint that a higher level is constituted from entities of the lower level, separating the evolutionary fate of the higher-level and lower-level entities is not possible (measured by long-term fitness). As a result, the term conflict can only be understood in a metaphorical sense because it relies on counterfactual scenarios.

Subversion from Within and Conflicts Between the Levels of Selection

One context where the foregoing analysis can be useful is cancer, which is often viewed as a case exemplifying multilevel selection, where the levels of the organism and that of the cancerous cells are said to be in conflict (Lean and Plutynski 2016; Shpak and Lu 2016; Okasha 2021). Cancerous cells proliferate in a way that is detrimental to this organism. However, this idea has been contested by Gardner (2015) and Shpak and Lu (2016), who both note that one issue with the idea of conflict between levels of selection in situations of cancer is that cancer cells typically die with the organisms bearing them; in other words, they are an evolutionary dead end. Okasha (2021) calls this the evolutionary dead-end argument (EDA), and I follow suit.

I partly agree with the proponents of the EDA but disagree with some of their claims. First, cancerous cells might be regarded as physically distinct from the rest of the organism. In such cases, one can regard the cancerous cells and the rest of the organisms as being in evolutionary conflict, if the former is interpreted as *A* and latter as *B*, as in Figure 2.2a. When the cancer is transmissible, such as in cases of transmissible cancers in Tasmanian devils and dogs or in rare cases of transmission during pregnancy in mammals, both Shpak and Lu and Gardner agree that a conflict exists. However, they argue that this is not a conflict between *levels of selection* but rather a conflict between two *individuals* (albeit one being parasitic on the other). This argument concurs with my analysis; when the higher-level and lower-level entities can be separated, it is a stretch to say that a conflict between levels exists. It is more accurate to refer to conflict between two types of entities, where each is described at a different level of description.

If the cancer is not transmissible, Gardner (2015) argues that cancerous cells have no reproductive value (a measure of fitness related long-term growth rate). This is so because the cancerous cells die with the organism that bears those cells. Thus, when using the notion of "reproductive value," if he requires that it only applies to situations where evolution is indefinite, he is correct that cancerous cells have no reproductive value. However, as pointed out by Okasha (2021), the same argument could be applied for nearly any entity at any level of organization. This is so because, as famously argued by John Maynard Keynes, "in the long run, we are all dead." When estimating the long-term fitness of an organism in a population, it is often assumed that the species to which this organism belongs does not go extinct. However, we know that species extinction is, in the long run, very likely to occur. Using the same tool but applying it at a different scale, we could end up concluding that the long-term fitness of any organism is nil. Thus, if by "indefinite," Gardner means truly indefinite, it is overly restrictive.

There is nothing preventing us from studying within-organism evolutionary dynamics and applying the notion of long-term reproductive success in this context. However, "long term" here refers to a projection in which no deleterious effects of cancer on the well-functioning of the organism are included, rather than "long term" in the absolute sense. The assumption that there is no deleterious effect on the organism is at the basis of the somatic evolution model of cancer, which applies evolutionary principles to study cancer evolution within an organism (e.g., Vogelstein and Kinzler 1993; Burt and Trivers 2006; Lean and Plutynski 2016; Fortunato et al. 2017; Okasha 2021). During the lifetime of an organism, cell lineages exhibit variation, differences in reproductive output, and heritability, three properties that constitute the core of the Darwinian scheme (Lewontin 1985; Godfrey-Smith 2009). Further, because cells within an organism have an asexual mode of reproduction with near-perfect transmission, one can expect that adaptations will occur if mechanisms preventing the suppression of variation are ineffective, as is thought to be the case in cancer (Burt and Trivers 2006; Aktipis et al. 2015; Shpak and Lu 2016). Seen through this lens, the diversity of cancers points to a number of hallmark adaptations within organisms (Gerlinger et al. 2014; Lean and Plutynski 2016; Shpak and Lu 2016; Fortunato et al. 2017). However, it should be noted here that such within-organism conflict (in line with what I argued earlier) could easily be described as conflict arising between different types of cells—that is, as conflict at a single level—which seems to be the interpretation provided by Burt and Trivers (2006, chap. 11) or Frank (2007), among others.

Another more charitable interpretation of Gardner's position is that the context in which he made his remark was one in which he was assuming (along with other protagonists in this literature) that organisms reproduce. Because legitimate fitness comparisons require that they are measured over the same set of events (Bourrat et al. 2022), the reproductive value of cancerous cells over such a timescale is indeed nil. Thus, if cancer is seen in a context where cancerous cells are regarded as an integral part of the higher-level entity—that is, as part of the organism—their fitness should be regarded as nil.

However, this argument does not apply to all forms of cancer. To see this, take the case of inherited cancers: cancers passed on through the germline, such as breast and ovarian cancer due to mutations in the *BRCA1* and *BRCA2* genes. Like their somatic counterpart, these cancers lead to cell proliferation. Despite having reduced fitness, individuals carrying these mutations might still have the opportunity to reproduce. Similarly, consider a case of cancer in an organism for which there is no germ-soma separation (e.g., plants), where a mutation can be passed on to the next generation of plants. In such cases, the EDA, which rests on the existence of a germ/soma separation and the cancer arising in the soma, would not work.

Notably, according to Shpak and Lu, inherited cancers or cases of cancer in organisms without germ-soma separation could nonetheless represent true cases of multilevel selection with a conflict between levels, for they appear to embrace the idea that fitness at the lower level is high while fitness at the higher level is low, using the multilevel Price equation (Price 1972; Okasha 2006; Bourrat 2021; see also Patten, this volume), a popular equation in evolutionary theory for apportioning the effect of selection at multiple levels of organization and where "higher" and "lower" level selection are operationalized into "between" and "within" collective selection. Following my analysis, however, caching out the distinction between higher and lower levels of selection in terms of between-collective and within-collective selection suggests a counterfactual notion of conflict that is not on par with the traditional notion of an actual evolutionary conflict between two entities (see Shelton and Michod 2014 for more details about the distinction between these two ways to understand individual-level selection). When using the between/within distinction and arguing that the fitness (which could include inclusive fitness effects) of a cancerous cell is high while reducing the fitness of the organism of which it is part, one does not answer the question of whether an actual evolutionary conflict between two entities *A* and *B* (as described earlier) exists. Instead, one provides an answer to the question of whether the fitness of a cancerous cell *would be* in conflict with that of the organism bearing it if, when measuring cell fitness, the constraints on the growth and survival of the organism bearing this cell were eliminated.

If no genuine conflict exists between levels of selection, one might ask what role(s) using this phrase plays in multilevel selection theory. Before answering this question, it should be noted that one main criticism of the idea that group selection can occur is that a selfish mutant that would not contribute to the production of collective-level benefits could invade the group and ultimately lead to a situation where there is no group benefit to be shared (see Okasha 2006, chap. 6 for an overview of this controversy). Therefore, whether the invasion of selfish mutants is possible, given a particular setting, is an important aspect of multilevel selection theory (Maynard Smith 1964). However, this idea is quite independent from the idea of conflict between levels, where levels are compositional. Nonetheless, the two ideas have not been neatly separated in discussions about levels of selection.

In a hierarchical system, asking about the emergence or maintenance of a higher level of organization has fundamentally to do with whether the invasion of "selfish" entities that would benefit in the short term from disrupting this level is possible. This can be viewed as a "conflict" (i.e., in a metaphorical sense). There *would be* conflict between the levels if these were independent. However, given the many ambiguities surrounding the notion of levels of selection, I prefer referring to this type of situation as a "paradox," as in the expression "the paradox of the organism" (Dawkins 1990; Patten et al. 2023). The existence of higher-level individuals such as organisms appears paradoxical when some factors are neglected or when those factors play out differently in different contexts. However, this paradoxical nature disappears once these factors are fully accounted for.

My proposal is in part compatible with that of Okasha (2021). Following his previous analysis of the levels-of-selection question (see Okasha 2006), he proposes to distinguish a synchronic (i.e., at a time) and a diachronic (i.e., over time) approach to this question. The diachronic approach permits one to ask questions about the origin or emergence of new levels of organization while the synchronic approach permits one to answer questions about whether selection acts at multiple levels at the same time—and, if so, whether they are in conflict. Okasha, following Buss (1987), makes the case that when seen from a diachronic perspective, organismal level adaptations might have been developed against cancer. While I concur with his analysis, I disagree that this shows a conflict between levels other than in a metaphorical sense. There might have been conflict between different lineages of unicellular organisms and the possibility of building higher-level individuals required mechanisms that allowed for the maintenance of these. However, conflict was not occurring *between* compositional levels. It instead occurred between entities at a *single* level and, for the most part, has been solved in modern multicellular organisms through the emergence of anti-cancer adaptations (which sometimes fail). It is correct that a diachronic perspective permits us to explain the existence of such adaptations, but one can make this point without reference to the notion of conflict between levels of selection. In contrast, talking about a "paradox" appears to be more appropriate, as this implies it can be solved and disappear, whereas a "conflict" is grounded in facts.

At that point, some might want to claim that the difference between a paradox or a metaphorical conflict (as I defined them) is merely terminological, that whether one terms the same phenomenon a "conflict" or a "paradox," the same phenomenon has little importance, so long as one is clear about what they mean. However, the problem here precisely lies in the fact that the ideas surrounding multilevel selection have been applied in a wide variety of contexts and to refer to so many phenomena that some terminological hygiene can only be beneficial.

Conclusion

In this chapter, I provide an analysis of the idea of conflict between levels of selection. The upshot is that the idea of conflict between levels of selection is rather ambiguous and can be understood in different ways. When levels are not compositional but merely ways of describing different types of entities, the notion of conflict makes sense. However, discussing conflicts between levels as if more than one process of selection is happening, each occurring at one level of organization, is suboptimal because in many cases one could redescribe the whole setting using a single level of description. Strictly speaking, when levels of selection refer to compositional levels where higher levels are constituted of entities at lower levels, an evolutionary conflict between them cannot exist because long-term evolutionary interests at the different levels are the same. One way to make sense of the idea of conflict in such situations is to refer to counterfactual scenarios in which describing the evolutionary dynamics at the lower level does not impact the evolutionary dynamics at the higher level because the two levels refer implicitly to different scenarios. However, in such cases, any "conflict" is of a metaphorical nature. Finally, I argue that in situations where such "conflict" would occur, such as when an organism develops cancer, it is more appropriate to refer to a paradox standing to be dissolved: Why, despite the short-term benefit of proliferating in the case of cancer or of remaining a free-living particle in the case of evolutionary transitions in individuality, do we observe the maintenance and emergence of collective-level individuality? Once the ecological and evolutionary mechanisms are understood and the paradox is dissolved, so are the conflicts between levels.

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