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What are the ‘Levels’ in Levels of Selection?

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ABSTRACT

The levels of selection debate is generally taken to be a debate about how natural selection can occur at the various levels of biological organization. In this paper, we argue that questions about levels of selection should be analyzed separately from questions about levels of organization. In the deflationary proposal we defend, all that is necessary for multilevel selection is that there are cases in which particles are nested in collectives, and that both the collectives and the particles that compose them each separately undergo natural selection. We argue that adopting this deflationary account helps to disentangle the levels of selection and the levels of organization, and thereby contributes to advancing the levels of selection debate.

1 Introduction

From its beginning, the theory of evolution by natural selection has been chiefly an individualistic theory. In Darwin's ([1859]) *On the Origin of Species*, he described organisms varying one from one another, and that if the variations are heritable and differ in their fitness, they could drive adaptive evolution. He invoked higher levels of selection only in cases that appear difficult to explain otherwise by being detrimental to the organism but beneficial to other organisms, or to the group as a whole, such as the sterile insect casts in the social Hymenoptera (ants, bees, and wasps). In his ([1871]) *Descent of Man*, Darwin developed and extended the idea that natural selection can operate at higher levels, for example, "there can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection" (p. 166).

Interest in multilevel selection has waxed and waned in recent decades. In the 1960s, explanations were offered for traits that were "for the good of the species," but this kind of account received harsh criticism by Williams ([1966]) and others. The main problem with positing selection for higher-level benefits was that it seems vulnerable to subversion from within. Surrounded by individuals acting for the good of the species, an organism will be incentivized to act selfishly, to reap the benefits of its altruistic conspecifics without paying the costs of selflessness. But why stop at organisms? Taking the subversion-from-within argument to its apparent logical conclusion, selection was viewed by some to be fundamentally about competition among selfish genes: selection may appear to occur at the organismic or group or species level, but this is an illusion (Dawkins [1976]).

More recent times have seen a resurgence of interest in multilevel selection. This has been driven by the creation of better models (e.g., Wilson [1975], Heisler and Damuth [1987]) and a realization of the importance of cooperative behavior and higher levels of selection in certain episodes of evolution, such as the major transitions (Maynard-Smith and Szathmary [1995]; Michod, [1999]). It is common among philosophers and scientists working on evolutionary biology nowadays to acknowledge that selection can operate at multiple distinct levels, but they debate the nature and magnitude of the evolutionary effects of higher-level selection. Some identify higher-level selection as a major force (Wilson and Sober [1994]; Wilson and Wilson [2008]), while others see it as a minor contributor to evolution (see Eldakar and Wilson [2011] for an overview).

While there has been considerable debate about how to model selection at different levels, and about how powerful this selection is, there has been little scrutiny concerning the very idea that there are multiple *levels* upon which selection can act. Often, the idea of levels of selection is linked to the broader idea of levels of biological organization, but without giving an explicit characterization of the latter, leaving much room for different intuitions and interpretations. In this paper, we argue there are two distinct notions of hierarchical organization that have become entangled in the debates over levels of selection, but should in fact be kept separate. On the one hand, there are the “levels of the biological hierarchy” or “levels of organization,” consisting of, e.g., the level of molecules, cells, organisms, populations, and species, where entities at higher levels (e.g., cells) are typically composed of entities at lower levels (e.g., molecules). On the other hand, there is hierarchical organization based on fitness-affecting interactions, where there are particles and collectives (a group composed of particles), and both the particles and the collectives engage in fitness-affecting interactions. For example, in group selection both individual organisms (particles) and the groups that they form (collectives) engage in fitness-affecting interactions. This is a very specific notion of hierarchy, and the relationship between "levels" that come out of this definition and the levels understood in the previous sense is not straightforward. Many of the traditional "levels of organization" (e.g., the level of organs or tissues) are not levels in the fitness-affecting sense, or vice versa.

In the next section, we discuss the role of levels in the debate, and show that levels of selection are typically assumed to neatly map onto levels of biological organization. In section 3, we discuss extant definitions of the 'levels', focusing on Okasha ([2006]), who has provided the most extensive discussion of this issue to date. In section 4, we present our approach—in which the 'levels' in the levels of selection debate are partitioned into two distinct concepts—and show how this helps to clarify the nature of levels of selection. The implications of this for the multilevel selection debate are discussed in section 5.

2 The role of "levels" in debates over the nature and scope of selection

When levels of selection are discussed, it is common practice to describe these levels by referring to "levels of biological organization" or "levels of the biological hierarchy." We will illustrate this by presenting quotes from some key articles. In his classic article "The Units of Selection," Lewontin argued as follows:

> The principle of natural selection as the motive force for evolution was framed by Darwin in terms of a "struggle for existence" on the part of organisms living in a finite and risky environment. The logical skeleton of his argument, however,

> turns out to be a powerful predictive system for changes at *all levels of biological organization*. (Lewontin [1970], p. 4000; emphasis added.)

Lewontin then goes on to discuss selection at, for example, the level of molecules, cells, gametes, organisms, populations, and species.

David Sloan Wilson, one of the main proponents of multilevel selection theory, is similarly explicit about the connection between levels of selection and the hierarchy of levels: "One of the beauties of multilevel selection theory is that the same conceptual framework is applied to *all levels of the biological hierarchy*" ([1997], p. 123, emphasis added). And in a joint article with Edward O. Wilson:

> There's no question that natural selection acts on individual organisms: Those with favorable traits are more likely to pass along their genes to the next generation. But perhaps similar processes could operate at *other levels of the biological hierarchy*…We can extend the hierarchy downward to study selection between genes within a single organism, or upward to study selection between even higher-level entities. (Wilson and Wilson [2008], p. 380, emphasis added.)

Philosophers of biology also rely on the notion of levels of biological organization when discussing levels of selection. Wimsatt ([1980]) aims at formulating clear and unambiguous criteria for units of selection that are applicable "at any level of organization" (p. 124), and his definition for a unit of selection explicitly refers to levels of organization (p. 144; see also Lloyd [1989], pp. 397-398). Waters summarizes the levels of selection debates in the following way: "Genic selectionists and their foes agree that evolutionary adaptation is the result of selective forces, but they disagree about the *level* at which these forces act. The traditional view is that selection acts at *the level of individual organisms*" ([1991], 554, emphasis added).

Thus, a biological world structured into multiple hierarchical levels of organization often serves as a background assumption in the levels of selection debate. As these quotes suggest, the concept of levels is invoked to show how the scope of natural selection can be extended beyond organisms, and to describe the potential targets on which natural selection can operate (Griesemer, [2005]).[1] As pointed out by Griesemer ([2005]), the assumption of levels of organization also seems to be treated as conceptually prior to the question of whether selection occurs at a given level of selection: the multi-level biological hierarchy is taken as the starting point, and the question then is at which of these levels natural selection occurs. In the debate on evolutionary transitions (Maynard Smith and Szathamary [1995], Michod, [1999]; [2005]), the traditional levels of organization also serve as the starting point, but they have the role not as assumption, but *explanandum*: The models of evolutionary transitions aim to provide an explanation for the levels of

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[1] This is closely related to the question of evolutionary individuality, which is a huge topic that we cannot adequately cover here (see Wilson and Barker ([2019] for more). In general, there are important connections between the debate on individuality and the debate on levels of selection that should be further explored (see, for example, Clarke ([2016]), or Michod ([2007])). We mention some of these connections later in the article.

organization that we observe in nature (cf. Griesemer, 2000; we return to this in section 4.3).[2]

As we will argue in more detail in section 5, treating the traditional levels of organization as a basic assumption or a starting point for multilevel selection may result in too simplified a picture of the organization of nature, and may lead to overgeneralizations regarding multilevel selection. Moreover, these levels of organization are nearly always introduced by simply giving a list of typical levels, which leaves it unclear why exactly these levels are the right candidates for levels of selection. An important exception can be found in the work of Okasha ([2006]), to which we will now turn.

3 Proposed Definitions of Levels of Biological Organization

The precise way in which "levels" in the context of multilevel selection should be understood is often left implicit in the literature. In this section we consider attempts to characterize levels, and show their shortcomings.

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[2] In general, it is important to distinguish between different questions regarding levels that can be asked in the context of the levels of selection debate, such as: (1) Is nature ordered into a hierarchy of levels of organization? (2) Does selection act on the various levels of this hierarchy? (3) Is multilevel selection an important cause of the emergence of the levels of organization? As will become clear later, we hold that each of these questions should be considered separately.

3.1 Okasha's definition

While most philosophers and scientists who appeal to levels of organization in the context of the multilevel selection debate do not explain what they mean by these levels, an important exception is Okasha ([2006]). He devotes one section (pp. 40-46) to hierarchical organization in his landmark book *Evolution and the Levels of Selection*. This is because Okasha considers the hierarchical organization of nature to be one of the three factors that together give rise to the levels-of-selection problem (the other two are the abstract nature of natural selection and the existence of phenomena that defy explanation in terms of organism-level selection; Okasha [2006], 10-12). He characterizes this hierarchical organization as follows: "Each organism is composed of organs and tissues, which are themselves made up of cells; each cell contains a number of organelles and a cell nucleus; each nucleus contains a number of chromosomes; and on each chromosome lie a number of genes. Above the level of the organism we find entities such as kin groups, colonies, demes, species, and whole ecosystems" (Okasha [2006], 10).

Okasha observes that although this picture is intuitive, it can be misleading in its simplicity, as it is not clear which levels should be included and why, nor how they correspond to levels of selection (Okasha [2006]). To address this, Okasha draws from McShea ([2001]) and Sober and Wilson ([1998]), and argues that *fitness-affecting interactions* among parts is the defining feature that distinguishes genuine hierarchical levels from arbitrary or nonrelevant sets of parts. What this means is that the parts at a level have to interact in a way that affects their individual fitness (usually defined in terms of the number of offspring an individual produces). Organisms thus can form a level of selection, since they interact with one another in fitness-affecting ways. Similarly, the cells that compose organisms (in some circumstances) interact in ways that increases or decreases the fitness of the individual cells.

While fitness-affecting interactions may be necessary, Okasha finds the criterion too permissive. Referring to McShea ([2001]), Okasha argues that entities at a level should also be *homologous* with organisms in a free-living state, either extant or extinct (Okasha [2006]).[3] This is because Okasha wants to rule out entities such as tissues and organs from forming a level. Okasha does not explain what "homologous" precisely means in this context, but presumably it should be understood in terms of sameness due to shared evolutionary ancestry (cf. Love [2007]; Ramsey and Peterson [2012]). Homology is standardly used to relate organs in different species, showing their shared ancestry. For example, human arms and bird wings are homologous limbs: if we trace the chain of ancestors of these species back in time, human arms and bird wings turn out to both be forms of the ancestral vertebrate forelimbs. Okasha, however, is not relating different traits in different species to ask whether they are homologous, but is instead relating traits in one species with whole free-living organisms of another species. On his view, organs and

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[3] McShea ([2001]) does not aim at defining levels of selection; rather, Okasha takes McShea's general account of parts—and levels of parts nested within parts—and applies it to the context of levels of selection. We return to McShea's account later in the paper (see section 5.1.). It should also be noted that McShea's account of levels does not include homology as a strict criterion (McShea, [2001], [2002], McShea and Venit [2001])

tissues are not levels of selection because they are not homologous with free-living organisms, whereas cells and organisms are.[4]

3.2 Problems with Okasha's definition

Okasha's proposal leads to a tidy and prima facie plausible way of defining the levels. However, as we will now show, this approach is unsatisfactory for making sense of levels of selection.

First of all, a significant portion of the levels of selection debate concerns levels that are lower than the cell, for example the level of genes or chromosomes. If we follow the approach of Okasha and include the homology requirement, it is not clear if genes and chromosomes can be seen as forming levels. There is no obvious sense in which they are homologous to extant or extinct organisms—whether they are homologous to entities such as viroids or hypercycles depends on the precise definitions of 'homologous' and 'organism', as well as empirical questions about early evolution that are still largely unsettled. However, whether genes and chromosomes in present-day organisms form levels of selection should not depend on such considerations, but rather on the processes in the evolutionary system of interest. Thus, the homology requirement seems to have the unintended consequence of making the status of levels of selection lower than the cell contingent on considerations that are not directly relevant to the selection processes at those levels.

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[4] It is not clear whether the homology criterion is needed here, as one could argue that tissues and organs and the somatic cells that compose tissues or organs do not have a fitness value (see, e.g., Michod [2005]), and thus do not engage in fitness-affecting interactions. Only germ-line cells have this capacity.

Moreover, the homology requirement as expressed by Okasha is too strong for higher levels as well. According to Okasha ([2006], p. 41), entities at *all levels* should be homologous to free-living organisms. This means that we cannot even include the levels of (kin) groups or colonies as genuine levels, since groups of organisms (e.g., a group of vervet monkeys) are not organisms themselves (though in some cases, like eusocial insects, we might label them superorganisms), nor are they not homologous to free-living organisms—or at least it is far from clear how we should understand such homology.

The homology criterion is also too strong in the following sense: It is possible that we may find on other planets, or even on Earth, entities that are fundamentally different from all other organisms we have encountered so far (and thus not homologous with them), but nevertheless are subject to evolution by natural selection. The homology criterion would rule out groups of such entities as candidates for higher-level selection, which seems arbitrary. Selection is a causal process that depends on the local features (the local environment and the particles and groups and their traits) of the evolutionary system, and should not be considered to depend on the existence of other species from across time and space.

Thus, although the approach based on homology and fitness-affecting interactions is initially appealing, it fails to capture a notion of levels of organization that would be adequate for debating levels of selection. Okasha seems to acknowledge this, as he ends his discussion of hierarchical organization by briefly suggesting that various other kinds of hierarchies can also lead to questions of multilevel selection (Okasha [2006], p. 46). However, it would be helpful if levels of selection could be characterized in a more precise way. This is the task to which we now turn, first by considering existing definitions of levels elsewhere in philosophy of science.

3.3 Definitions of levels in philosophy of science

Levels of organization have also been discussed in philosophy of science outside the context of levels of selection (Eronen and Brooks [2018]). In this section, we will consider whether some of the existing accounts of levels could help in making sense of levels of selection.

One of the earliest and most elaborate approaches to levels of organization is Wimsatt's "local maxima" account (Wimsatt [1994]; [2007]). According to Wimsatt, levels of organization have several characteristic (but not necessary) features: (1) They are compositional (there are whole things at higher levels and their parts at lower levels), (2) they are constituted by entities of similar size and dynamic properties that primarily interact with each other, (3) they appear as peaks or local maxima when regularity and predictability is plotted against a (size) scale, (4) processes at higher levels take place at slower rates than processes at lower levels, (5) higher levels are dynamically autonomous from lower levels, and so on (the full list includes 18 features).

The problem with this approach is twofold (Craver [2007]; Eronen and Brooks [2018]): First, most of the criteria are very liberal and/or not precisely defined. For example, it is not clear how one could measure or calculate the amount of regularity and predictability at different scales, or more generally, how exactly those terms should be understood or defined here. Second, it is difficult to see how the various criteria could work in harmony to yield a neat or useful picture of levels. For instance, the parts of an organism or a cell can be very heterogeneous, and therefore do not form a level of entities of similar size and properties, creating a conflict between criteria (1) and (2). Levels of selection may often have some of the characteristics laid out by Wimsatt, but his account in its present form is too vague and open-ended for clarifying the debate on levels of selection.

Another way of characterizing levels of organization is to draw from the notion of hierarchical *control* or *constraint* (e.g., Korn [2002]; Pattee [1973]), the idea being that a higher-level entity, such as an organism, imposes constraints on the behavior of lower-level entities, such as cells. However, as the quotes in section 2 suggest, the key feature of levels of selection is composition, not control. For example, it is not clear in what sense a group of organisms as a whole controls or imposes constraints on the behavior of the individual organisms, and questions of multilevel selection can arise even if there is no such control. On the other hand, endocrine glands control hormone levels in the body, and thus can be seen as constituting a higher level of hierarchical control, but this does not seem to be a good reason to treat endocrine glands as a level of selection. Thus, levels of hierarchical control are not well suited for defining levels of selection.

An alternative approach to levels that is at least prima facie more promising in this context is the account of *levels of mechanisms*, developed by Craver ([2007]) and Bechtel ([2008]), and in spite of recent criticism (e.g., Eronen [2015]), still widely popular among philosophers. The idea is that there are whole mechanisms at the higher levels, and their components (or working parts) inhabit lower levels. In this way, levels can be defined without appealing to external criteria such as homology. Another appealing feature of levels of mechanisms is that they are local and case-specific, and do not require assuming levels that extend beyond a specific mechanism or system. However, the idea of a mechanism is problematic in the context of levels of selection. For example, it would be odd to construe a group of organisms as a mechanism, and the individual organisms in that group as components or working parts. Similarly, a species can hardly be seen as a mechanism. It may be possible to stretch the definition of a mechanism so that it covers these kinds of cases, but in our view this is unnecessary. As we will argue below, it is more plausible and fruitful to view mechanistic levels and levels of selection as distinct notions of hierarchical organization.

4 How Levels of Selection Should be Understood

In the absence of an account of the levels of biological organization that can serve as a foundation for the levels of selection, an alternative approach is needed. Here we present such an approach and argue that talk of "levels of selection" involves two distinct notions of hierarchical organization that need to be pulled apart and explicated.

4.1 Two notions of hierarchical organization

First of all, it is clear that the idea that levels of selection are based on fitness-affecting interactions plays a central role in the debate (see section 3). We propose to define such levels in a minimalistic or deflationary way, without appealing to the problematic homology criterion and any other further criteria for levels.[5] This leads to a very liberal picture where entities engaging in fitness-affecting interactions will

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[5] McShea and Venit ([2001]) also propose a similarly minimalistic approach to levels based on compositional hierarchies. However, their account is not intended to capture levels of selection, and does not refer to fitness-affecting interactions. We discuss the relationships between these two notions of levels in section 5.1.

constitute a “level,” and collectives wholly or partially composed of such entities will constitute a higher “level.” With this approach, levels no longer need to correspond to the classical levels of organization as described in the quotes in section 2. Thus, the “levels” defined based on fitness-affecting interactions are conceptually detached from any broader idea of hierarchical levels of biological organization. More precisely, we suggest that these levels can be characterized as follows (see also section 5.3 for more explanation):

> **Levels of fitness-affecting interactions**: When entities engage in fitness-affecting interactions, they form a level. When these entities have parts that also engage in fitness-affecting interactions among each other, the parts form a *lower* level with respect to the entities. Similarly, when entities that engage in fitness-affecting interactions are parts of a collective that also engages in fitness-affecting interactions with similar collectives, those collectives form a *higher* level with respect to the first level.[6]

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[6] The ‘similarity’ in this characterization should not be understood too strictly. Relatively dissimilar collectives could engage in fitness-affecting interactions, such as groups of different sizes. However, traditionally in the debate the focus has been on similar things interacting at each level (e.g., cells at a lower level, multicellular organisms at a higher level). Also, the notion of entities that engage in ‘fitness-affecting interactions’ is chosen here to follow Okasha ([2006]) and Sober and Wilson ([2008]) , but the characterization could also be formulated based on some other notion that plays a similar role, such as Darwinian individuality (Godfrey-Smith

One can then use these pairwise comparisons to determine a local rank ordering of levels. For example, genes are lower than organisms and lower than groups of organisms, whereas organisms are lower than groups of organisms, but higher than genes. Thus, the order is group, organism, gene. We do not share the worry of Okasha that levels based on fitness-affecting interactions are too permissive (see section 3.1): Identifying a level of selection does not automatically mean that there are traits that can be explained by these levels of selection. It could be that while there are multiple levels in a particular system, only one has selection of sufficient strength to evolve adaptations. Or it could be that the traits selected for at a particular level have too low a heritability to lead to an evolutionary response to selection.[7]

The other notion of hierarchical organization that is central in the debates on levels of selection is what is referred to as the "levels of the biological hierarchy" or "levels of organization" in the literature, consisting of, e.g., the level of molecules,

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[2009]) or evolutionary individuality (e.g., Clarke [2016]) —we return to this in sections 4.3 and 5.2.

[7] In order for our characterization to be broadly applicable, fitness needs to be understood in a very general sense, and not just as a feature of organisms. However, this is in line with how fitness is typically treated in the multilevel selection debate. For example, Okasha ([2006], p. 11) writes: "cells give rise to other cells by cell division, genes to other genes by DNA replication, groups to other groups by fission (among other ways), species to other species by speciation, and so on. Thus the Darwinian concept of fitness, that is, expected number of offspring, applies to entities of each of these types."

cells, individuals, populations, and species. Entities at higher levels of organization (e.g., cells) are typically thought to be composed of entities at lower levels (e.g., molecules). However, although the parts and collectives in levels of organization *can* engage in fitness-affecting interactions, they do not have to. For example, most of the molecules that compose cells (e.g., actins or lipids) do not engage in such interactions.

As we argued above, it is difficult to precisely characterize levels of organization, and extant accounts of levels of organization are not well suited for capturing levels of selection. However, if we pull these two notions of hierarchical organization apart, we see that they can play distinct roles in the debate. The first notion (levels of fitness-affecting interactions) is crucially important for analyzing questions of multilevel section in specific cases, whereas the second (levels of organization) can be useful in addressing more general questions, such as how a specific case of multilevel selection maps onto a broader framework of levels of organization, or how higher-level selection contributes to the emergence of a new level of organization. In order to see how this works, and how treating these two notions of hierarchical organization separately helps to clarify the debate, let us first take a closer look at the structure of the levels of selection problem.

4.2 Targets of selection and the multilevel selection problem

The issue of levels of selection can be seen as having two (interconnected) main components: The targets (or units) of selection problem and the multilevel selection problem (see also Lloyd [2017]). [8] The first problem is defining and determining what

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[8] According to Brandon ([1982]; see also Hull [1980]), “units of selection” should refer to replicators (i.e., the entities that produce copies of themselves, usually genes),

are the targets (or units) of selection*:* What biological entities are subject to selection, and how does this selection lead to an evolutionary response? We can ask whether genes constitute a target of selection, and if so, how such selection should be understood. It is widely thought that genes can compete among each other within an organism for representation in the next generation. Meiotic drive, for example, can be seen as a case of genic selection: genes compete by "cheating" in the meiotic lottery, gaining a greater than 0.5 probability of making it into the gametes.

This analysis of the targets of selection is different from the second component, questions about multilevel selection. Questions of the latter kind arise when we take into account that organisms (or other targets of selection) are sometimes assembled into groups that may also be targets of selection. In other words, some targets of selection bear a particle-collective relationship to one another, where the collective consists of particles that engage in fitness-affecting interactions. This creates a tension between selection acting at the two different levels. The question of multilevel selection then becomes: How should we understand and model the interplay between selection at the two levels, the level of the particles (the parts) and the level of the collectives? For example, does selection at the lower level (e.g., organisms) swamp the effects of selection at the higher level (e.g., groups of organisms)? This problem is tackled by theories about how to conceptualize and model selection in cases in which there are entities that compose collectives, where

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and "levels of selection" should refer to interactors (i.e., the entities that interact with the environment in a way that results in differential reproduction). In our framework, the problems of targets of selection and multilevel selection both concern interactors, and thus are about "levels of selection" in Brandon's terminology.

there is arguably selection among individuals within the collectives, but also among the collectives.

The most widely discussed form of tension between levels of selection occurs in cases where there is selection against altruistic behavior at the organismic level, but for altruism at the group level (i.e., for groups containing altruists). If the group-level selection is strong enough, the altruistic phenotype can increase and become a stable feature of the species (Sober and Wilson [1998]). There are, of course, countless debates over what altruism fundamentally is (Ramsey [2016]) and whether it evolves via group selection, and not another mechanism like reciprocity or kin selection (Nowak et al. [2010]; Abbott et al. [2011]; Ramsey and Brandon [2011]).

Navigating these debates is far beyond the scope of this paper. What is important is that for the purposes of these debates, the levels can be fully understood in terms of levels of fitness-affecting interactions as characterized in 4.1. The lower level of selection consists of individuals that engage in interactions that affect their fitness, and the higher level consists of the collectives that have those individuals as parts. For example, if the question of interest is whether natural selection acts on groups of vervet monkeys, the relevant levels are the level of individual vervet monkeys and the level of collectives (groups of vervet monkeys). To settle this question, it is not necessary to posit or define a more general “level of individual organisms,” or a more general “level of groups.” It is also not necessary to appeal to criteria such as homology, or to rely on a broader framework of levels of biological organization.

4.3 Multilevel selection theories from a deflationary perspective

This minimalistic or deflationary approach to the levels of selection helps to clarify the debates over multilevel selection. Let us start with the widely accepted distinction between two kinds of multilevel selection: multilevel-selection-1 (MLS1) and multilevel-selection-2 (MLS2) (Damuth and Heisler [1988]). In MLS1, the individuals (or particles) are the central units in the selection processes and the central question is the following: How does selection at the higher level of groups (or collectives) affect the differential reproduction of the individuals that make up those groups? In MLS2, groups (or collectives) themselves are the units of interest and the question is instead: How does selection at the level of groups (or collectives) affect the differential reproduction of the groups? It is clear that the “levels” here can be defined locally, following our deflationary approach. The lower level consists of the individuals that engage in interactions that affect their fitness, and the higher level consists of the collectives that are made up of those individuals. No broader framework of levels of organization is needed for distinguishing between MLS1 and MLS2 (although notions such as ‘individuals’ or ‘fitness-affecting interactions’ may of course be subject to further debate and clarification; see the end of this section and section 5.2).

With this in mind, let us take a closer look at the multilevel theory of selection in its classic or standard form (e.g., Sober and Wilson [1998]; Wilson [1975]; Wilson and Sober [1994]; Wilson and Wilson [2008]). This theory is presented as a theory of selection occurring at multiple levels of organization in the biological hierarchy, and is often accompanied with pictures of this hierarchy, where we see, for example, the level of genes, individuals, groups, and populations (e.g., Wilson and Wilson [2008]). The core idea is then that “selection not only acts on individuals but can act (simultaneously) on multiple levels of biological organization" (Kramer and Meunier [2016]).

In our framework, we can interpret this rendering of multilevel selection theory as consisting of two elements: (1) The idea that not only individuals (particles) but also collectives can be targets of selection (either in the sense of MLS1 or MLS2), and (2) methods to analyze the dynamic interplay between the "level" of the groups and the "level" of the individuals that make up those groups. These elements can be perfectly captured and modeled in the minimalistic framework that we have described above: The lower level consists of particles that engage in interactions that affect their fitness, and the higher level consists of collectives of those particles. There is no need for a framework of levels of organization beyond this minimalistic idea.[9] The broader notion of levels of organization is needed only if we are interested in examining how (if at all) the levels of fitness-affecting interactions in this specific case map onto levels of organization, but this is a distinct and supplementary question. Multilevel selection could in principle occur in a world with just individuals and collectives that are subject to natural selection, with no further hierarchical organization.

Similar considerations apply to Okasha's ([2006]) account of multilevel selection. His starting point is to analyze multilevel selection with the help of the Price equation, with which selection can be broken down into two components, one

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[9] Of course, this two-level picture can be expanded, as it is possible that the particles themselves are composed of parts that engage in fitness-affecting interactions, or that the collectives form further higher-level collectives. However, neither these further "levels" nor the original two levels need to correspond to traditional levels of organization.

reflecting selection among individuals within groups (the particle level), and the other reflecting selection between groups (the collective level). He then points out that selection at the collective level requires either covariance between the traits and fitness of entities at that level (MLS2), or covariance between collective traits and individual fitnesses (MLS1). However, this is not yet enough, as this covariance could be a byproduct of selection processes at the individual level. Thus, according to Okasha, what is also required is that the covariance is due to a *causal* relationship: In other words, that the collective ("higher-level") trait has a *causal influence* on collective ("higher-level") fitness (or on individual fitnesses, in case of MLS1). These causal influences are usually studied with contextual analysis, essentially a form of multivariate regression (Goodnight, Schwartz, and Stevens [1992]; Heisler and Damuth [1987]; see also Earnshaw [2015]).

Okasha correctly points out that this kind of multilevel selection requires the hierarchical organization of the entities involved. However, his characterization of hierarchical organization is unnecessarily convoluted, appealing to considerations such as homology with free-living organisms (see section 3.1). Our approach provides a much more straightforward way of capturing the relevant kind of hierarchical organization: All that is needed is a level of particles ("lower level") and of collectives ("higher level"), which can be defined as levels of fitness-affecting interactions, and then the methods of studying multilevel selection (e.g., contextual analysis) can be applied to these levels. This captures Okasha's intuition that the "criteria by which hierarchical levels are defined should be relatively liberal" (p. 43). In this way, we provide a clear and consistent framework for understanding levels in Okasha's approach to multilevel selection. The same holds for other formal models of multilevel selection (e.g., Simon et al. [2012]; Traulsen and Nowak [2006]).

Our deflationary framework is also well suited for understanding the notions of levels involved in discussions of evolutionary transitions (Maynard Smith and Szathamary [1995], Michod, [1999]; [2005]; see also Buss [1987]). Whereas in the multilevel selection debate the focus is on the dynamics between levels that are already in place, in the evolutionary transitions debate the central question concerns how new levels emerge (Griesemer [2000]): For example, how did single-celled organisms evolve into multicellular organisms, thereby forming a new level of organization?

Detailed models of these processes of evolutionary transitions have been developed, the most elaborate of which is probably the evolutionary transitions of individuality (ETI) theory of Michod ([1999]; [2005]). The basic idea of this model is that a process of evolutionary transitions involves a decline in the individual fitness of the particles (as they engage in altruistic and cooperative behavior) and a corresponding increase in the fitness of the collectives. This eventually results in the fitness being completely transferred to the higher level, as is the case with multicellular organisms, where we find extensive cooperation and division of labor (e.g., between germ cells and somatic cells). In this way, the emergence of individuality at the higher level can be explained. These processes can be understood in terms of MLS1 and MLS2: At first, multilevel selection is of the MLS1 kind as the relevant fitness is that of the particles, whereas at the end of the transition only the higher-level collectives have fitness, so MLS2 becomes the right model (Michod [2005], Okasha [2006]; see also Bourrat, [2015]).

Clearly, also in this approach (and other similar models of evolutionary transitions), the “levels” can be understood in the deflationary sense in terms of particles and collectives, and there is no need to appeal to more general levels of organization. Instead, levels of organization have a different role in this debate: They function as the basic explanandum (and correspondingly, levels in our deflationary sense have a role as part of the explanans). In other words, models of evolutionary transitions aim to provide an explanation for the levels of organization that we observe in nature. However, the traditional levels of organization are merely a starting point, and there is no reason to expect that evolutionary transitions would be restricted to only those levels (see section 5.1). This sharp distinction between levels of selection and hierarchical levels of organization also helps to understand how ETI theory (Michod [1999]; [2005]) can make novel empirical predictions and hypotheses concerning levels: ETI models can rely on a deflationary notion of levels of selection in order to derive testable hypotheses about levels of organization in the broader sense.

The upshot of our analysis is that there are two distinct notions of hierarchical organization implicit in the debate, and that studying and modeling the levels of selection in each specific case requires levels only in the deflationary sense of particles and collectives, and *not* in the sense of levels of biological organization. The latter notion is needed only if one wants to map the specific case onto a more general framework of levels, and this is a different and separate scientific goal.

It is important to note that although we have followed Okasha ([2006]) and Sober and Wilson ([1998]) in treating fitness-affecting interactions as the key criterion for levels of selection, this is by no means universally accepted. Instead of fitness-affecting interactions, levels of selection can also be characterized based on, for example, Darwinian or evolutionary individuality (Godfrey-Smith [2009]) or functional non-aggregativity (Bourrat [2021). Our aim here is not to give a final definition for levels of selection or to defend the fitness-affecting interactions account, but to argue that there are two different notions of levels at play in the debate, and that levels of selection need not align with levels of organization. This general point will hold even if levels of selection are characterized in a different way, for the reason that the notion of levels of selection and the notion of levels of organization have different epistemic goals: The former concerns natural selection acting at different levels in nested structures, whereas the latter aims to capture general compositional features of biological organization. Additionally, levels of selection can act as causal explanations for the formation and maintenance of features of the levels of organization. Thus, it is prudent to characterize and treat levels of selection separately from levels of organization.

5 Implications for the Levels of Selection Debates

The existence and nature of multiple levels of selection have been discussed for decades. Much of this discussion has been fruitful, but in our view intertwining discussions of the levels of selection with those of the hierarchy of levels of organization has contributed to a loss of clarity. There are at least three important implications of our claim that we should sharply distinguish the levels of selection from the levels of organization. We will consider each in turn below.

5.1 Collective-particle theory can be pursued independently from the levels of organization

The idea that levels of selection correspond to levels of organization may tacitly guide the debate, or even research, towards certain "classic" levels, such as the level of genes, organisms, populations, and species. This stems from the fact that no definition is typically given for levels of organization. Instead, a list of levels is offered with little or no justification for what is included in the list. Such a list suggests that the likely targets of selection are found at these levels. However, the logic of multilevel selection does not require that targets of selection are located on anything corresponding to traditional levels of organization.

Indeed, many recently discussed candidates for multilevel selection are not easily placed on a level of organization. Consider, for example, biofilms. Biofilms are complex communities of bacteria (Clarke [2016]). They are neither cells nor multicellular organisms, but rather something in between, a distinct form of biological organization. Therefore, the level of selection at which we find biofilms (if there is indeed one) does not correspond to any of the standard levels of organization. The same applies to modular organisms (Tuomi and Vuorisalo [1989]), siphonophores (Dunn and Wagner [2006]), the genome (Durand and Michod [2010]), and mitochondria (Taylor et al. [2002]). The classic hierarchy of levels has served as a guide in finding candidates for multilevel selection, but it is clearly an incomplete guide. Leaving it behind could help direct research toward more untrodden paths and new cases of multilevel selection.

One possible objection to our argument that levels of selection are distinct from levels of organization is that our deflationary characterization of levels in section 4.1 seems to assume a notion of levels of organization, as it makes reference to parts (lower level) and collectives (higher level). Our response is that our approach indeed assumes the basic notions of parts and collectives and corresponding local hierarchies, but these should not be confused with the traditional levels of organization (see also McShea and Venit [2001]). For our purposes, parts and collectives can be understood in a very broad and unrestrictive way, for example along the lines of McShea and Venit (McShea [2002]; McShea and Venit [2001]): a part is an entity that is relatively well integrated internally and relatively well isolated from its surroundings, and such parts can integrate with other parts to form collectives that are in turn relatively well isolated from their surroundings (see also Simon [1962]).

However, regardless of the precise definition, the crucial point is that the assumption that there are compositional hierarchies in nature does not require assuming that there are levels in any further sense that goes beyond these hierarchies (Craver [2007]; Eronen [2020]; McShea and Venit [2001]). There is no denying that there are part-whole or part-collective relationships in nature, but ‘levels of organization’ are characteristically understood as something more than just hierarchies of part-collective relationships (Craver [2007]; Eronen and Brooks [2018]), and it is a matter of ongoing debate whether the notion of ‘levels organization’ is needed or how it should be understood (see Brooks, DiFrisco & Wimsatt [2021] and the next section).

5.2 No general definition of levels of organization is needed for the levels of selection

Based on our discussion in section 4, there seems to be no need for a definition or characterization of levels of organization when discussing levels of selection. It is sufficient to identify the actual empirical instances of the particles and collectives of interest. As is illustrated by the discussion of the homology criterion in section 3, attempts at characterizing levels in a more general way easily leads to a picture of levels that is ill-suited for understanding levels of selection, and will create more conceptual confusion than clarity.

This point is also supported by recent discussions of levels of organization in philosophy of science. It is an undeniable fact that nature is compositionally structured: Organisms are composed of tissues, tissues are composed cells, cells of cell parts, and so on. However, upon closer analysis, it turns out that this compositional organization is often too messy to fit into a neat mold of universal levels (Eronen [2015]; Potochnik and McGill [2013]): Things at a "level" (e.g., organisms) tend to be very heterogenous, and their components even more so (e.g., tissues, blood cells, bacteria). Are multicellular organisms at the same level as bacteria? Or are bacteria at the level of the cells that compose multicellular organisms? Are sterile worker bees at the same level as solitary bees, or at the level of the solitary bee's cells?

These problems are partly circumvented by the account of levels of mechanisms, where levels are defined on a case-by-case basis depending on the phenomenon of interest (Craver [2007], Craver and Bechtel [2007]; see, however, Eronen [2021]). However, as we pointed out in section 3.3, the notion of a mechanism is ill-suited for the context of levels of selection. If we then leave out the mechanistic framework and simply define local compositional levels on a case-by-case basis (see, e.g., Love [2012]; McShea [2002]; McShea and Venit [2001]), what remains is essentially just part-collective hierarchies. As discussed in the previous section, such hierarchies are important and also the basis for our account, but they consist just of part-whole or part-collective relationships, and do not amount to levels of organization in any substantive sense (Eronen [2013], [2015]; McShea and Venit [2001]). Thus, at least in this context, making levels local or case-specific does not save the notion of levels of organization but just leads back to part-collective hierarchies and a deflationary approach.

A possible objection is that even if our account can do away with levels of organization, it may still require some basic notion of biological entities or individuals. Indeed, our characterization of levels has the notion of "entities" as its starting point. However, it also adds the additional substantive constraint that these entities should engage in fitness-affecting interactions. Therefore, the notion of "parts" or "entities" can remain very general, for example, following the characterization of a "part" by McShea and Venit (which we describe in section 5.1).[10] The notion of fitness-affecting interactions (or some other similar constraint, such as Darwinian individuality or functional non-aggregativity; see section 4.3) ensures that only biological entities that are capable of reproduction and have a fitness value are included as candidates for forming levels of selection.[11]

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[10] It is not clear whether genes satisfy the criteria of McShea and Venit ([2001]), so in that context an even weaker definition of entities might be needed. This also reinforces our point that genic selection as multilevel selection differs in important ways from other cases of multilevel selections (see section 5.3).

[11] An anonymous reviewer pointed out that these "levels" based on fitness-affecting interactions or evolutionary individuality could also be seen as candidates for levels of organization in some non-traditional sense. In our view, such an account is not needed for analyzing the core problems of multilevel selection, but could certainly be

The debate over levels of organization is far from settled (see Eronen and Brooks 2018 for a review): Many authors have even argued that the whole concept of levels of organization is deeply problematic or useless (e.g., Guttman [1976]; Ladyman and Ross [2007]; Potochnik and McGill [2012]; Potochnik [2021]), whereas others still see potential in further developing and studying the concept (Brooks [2017]; Brooks and Eronen [2018], DiFrisco [2017]). We do not want to take stance on the future prospects of the concept of levels of organization in biology. Our main point is that there seems to be no reason why a notion of levels of organization would be needed to analyze multilevel selection. Moreover, if the debate on levels of selection implicitly relies on an ill-defined or unclear notion of levels of organization, it inherits all the conceptual problems of such a notion, leading to unnecessary confusion. Therefore, the levels of selection debate will benefit if it is detached from the conceptual framework of levels of organization.

5.3 The danger of over-generalizing

The traditional framework of the levels of biological hierarchy seems to suggest a uniform or homogeneous hierarchical organization. More specifically, theories of levels usually assume that although things at different levels are different in kind, the

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interesting and important for other purposes, such as capturing general patterns in the organization of nature. We also believe that our minimalistic framework can provide a good conceptual basis and starting point for developing such an account, and can therefore also be helpful for philosophers working on new approaches to levels of organization (see, e.g., Brooks [2019]; Brooks, DiFrisco and Wimsatt [2021]; DiFrisco [2017]; DiFrisco, Love and Wagner [2020]).

relationship between levels (the interlevel relationship) is the same across the entire hierarchy (see also Craver [2007], ch. 5). Thus, accounts of levels of organization tacitly suggest that, for example, the relationship between genes and cells is analogous to the relationship between cells and organisms, or organisms and groups, or groups and species. However, our approach highlights the fact that the precise relationship between specific particles and specific collectives needs to be determined on a case-by-case basis.

This becomes clear when we compare some paradigmatic cases of multilevel selection (see also Wilson [2003]). Groups are made up of individual organisms in a straightforward way: A set of individual organisms that have fitness-affecting interactions is how a group is defined. However, when it comes to the level of genes, things get far more convoluted. In *some contexts* genes can also be seen as groups in an analogous way, for example, when the focus is on the evolutionary transition from macromolecules (e.g., hypercycles) to the genome or the cell (Michod [1983]; Durand and Michod [2010]). However, when it comes to genic selection in the context of the multilevel selection debate (see, e.g., Okasha [2006]), the higher level is typically considered to be the level of multicellular organisms (e.g., humans), in which case the relationship between the lower level (genes) and the higher level (organisms) becomes much less straightforward.[12] In this case, groups of genes do not simply constitute the higher level of selection as in group selection; instead, genes are located

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[12] The term ‘genic selection’ is ambiguous, as there are in fact many distinct concepts that fall under that rubric (see, e.g., Lloyd 2017; Walton [1991])—here we primarily refer to applying multilevel selection models to genes, treating them as particles that are targets of selection (Okasha [2006]).

in "in the deepest recesses of [the compositional] hierarchy" (Griesemer [2006], p. 219). The relationship between genes and organisms such as humans is extremely complex, and very different from the relationship between organisms and groups.

Thus, in many contexts in the multilevel selection debate, the interlevel relationship between genes and organisms is very different from the interlevel relationship between organisms and groups, in ways that are relevant for natural selection (see also Griesemer [2005] and Wilson [2003]). This difference is muddled by expressions such as "an individual can be regarded as a population of genes" (Wilson and Sober [1994], 591), which are common in the literature, and stem from the assumption of a uniform framework of levels. Similar problems apply to the level of species: Whatever species are, they are not just lots of organisms (or groups of organisms) interacting in fitness-affecting ways (Lloyd and Gould [1999]).

It is due to considerations of this kind that we characterized levels of fitness-affecting interactions in the way we did in section 4.1. The simple idea that particles that interact in fitness-affecting ways form a lower level, and collectives of those particles form a higher level, does not fit some standard forms of multilevel selection, such as genic selection and species selection. In these cases, the higher-level entities are not just collectives of interacting particles, but something more (e.g., evolutionary individuals with a division of labor among the components; Clarke [2016]; Michod [2007]). It is for this reason that our characterization only requires that the particles that interact in fitness-affecting ways are parts of a collective that also engages in fitness-affecting interactions with similar collectives. Thus, it is not required that the lower-level particles that engage in fitness-affecting interactions completely make up the higher-level collective, but rather that they form a subset of the parts of the higher-level collective. This leaves room for different kinds of relationships between the lower- and higher-level entities. In particular, the level of genes can also be covered. Even though genes do not completely make up entities that are targets of selection (except perhaps in the context of evolutionary transitions), they are *among* the parts of such entities (i.e., organisms). The same applies to some other cases that do not easily fit the original definition, such as mitochondrial selection (Taylor et al. [2002]): Mitochondria do not completely make up cells, but are parts of them, and mitochondria engage in fitness-affecting interactions. The case of organisms and groups also falls under this definition as a special case where *all* of the parts of the higher-level collective engage in fitness-affecting interactions.

Our characterization captures the essential features of levels that are relevant for multilevel selection: It is not crucial that the particles completely make up the collectives, or that the levels correspond to some predefined levels of organization. What is essential is that the particles (that engage in fitness-affecting interactions) are contained (“nested”) within collectives (that engage in fitness-affecting interactions). When this is the case, a tension can arise between selection acting on the different levels, leading to interesting questions of multilevel selection.

Importantly, this minimalistic framework helps only to identify levels of selection, but doesn’t specify the biological details of each case. The exact relationship between particles and collectives differs greatly between cases such as genic selection, mitochondrial selection, group selection, and species selection, and these differences can have implications for the models used (see Okasha [2006] on genic selection and Gould and Lloyd [1999] on species selection). What we want to emphasize is that the particle-collective relationship needs to be studied on a case-by-case basis with explicit attention to the differences and the biological details. This requires detaching the questions of multilevel selection from the framework of traditional levels of organization.

6. Conclusions

In this paper, we have tried to answer the question: *What are the 'levels' in levels of selection?* After ruling out proposals such as defining levels of selection based on current accounts of levels of organization, we have argued that the debate concerns two notions of levels that need to be disentangled. First, there are local particle-collective levels, which are sufficient for capturing the notion of levels that is relevant for theories of multilevel selection. Second, there is the more general notion of levels of biological organization, which has been under fire in recent years (e.g., Eronen [2015]; Potochnik and McGill [2012]; Potochnik [2021]). In the context of multilevel selection, questions related to these levels of organization (e.g., at which levels of organization do we find the entities that are involved in multilevel selection in the first sense?) are secondary and supplementary to the question whether multilevel selection occurs in a given case. As we have argued in the last section, taking this approach and detaching levels of selection from a more general framework of levels of biological organization would bring much-needed clarity to this debate.

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