



# The Major Transitions in Evolution—A Philosophy-of-Science Perspective

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Over the last thirty years, the study of major evolutionary transitions has become a thriving research program within evolutionary biology. In addition to its obvious scientific interest, this research program raises interesting philosophical questions. These fall into two categories: conceptual and ontological. The former category includes questions about what exactly an evolutionary transition is, what form an evolutionary explanation of a transition should take, and whether a general theory that applies to all transitions is possible. The latter category includes questions about the status of the higher-level units to which evolutionary transitions give rise (e.g., organism, superorganism, or individual), and about the nature of the resulting hierarchical organization. Tackling these questions requires an integrative approach that draws on both biology and the philosophy of science.

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## 1. INTRODUCTION

The contemporary interest in “major evolutionary transitions” (METs) can be traced to the pioneering works of Buss (1987), Maynard Smith and Szathmáry (1995), and Michod (1999). Though these authors’ approaches differed considerably, both in respect of the empirical phenomena they were concerned with and in the type of explanation they sought, they converged on a number of key points. These included: (i) that a series of evolutionary transitions has occurred in the history of life on earth that radically re-shaped subsequent life forms; (ii) that some or all of these transitions involved formerly free-living entities coalescing into larger groups, giving rise to a new level of hierarchical organization; and (iii) that explaining how and why these transitions occurred represents an outstanding task for evolutionary biology. In the last twenty-five years many evolutionists have risen to the task, and the study of METs has flourished into a thriving research program, generating much interesting work, empirical and theoretical.

While it is self-evident that METs are of considerable scientific interest, it is perhaps less obvious why they should be of philosophical interest. And yet they are, as attested by the large body of literature on METs authored or co-authored by philosophers of science (Griesemer, 2000; Okasha, 2005, 2006; Godfrey-Smith, 2009; Calcott and Sterelny, 2011; Birch, 2012, 2017; Godfrey-Smith and Kerr, 2013; Clarke, 2014; O’Malley and Powell, 2016; Ryan et al., 2016; Currie, 2019). In this literature we can detect two distinct sorts of philosophical question, which might be called “conceptual” and “ontological,” respectively. Examples of the former include questions about how exactly an evolutionary transition should be defined; what form an evolutionary explanation of an MET should take; how concepts such as kin selection, multi-level selection and the “gene’s eye view” apply to METs; and whether an overarching theory of evolutionary transitions is possible.

Examples of the latter include questions about what status the new biological units that arise from METs have (e.g., are they organisms, superorganisms, or individuals?); and about the nature of the hierarchical organization that results from the transitions (e.g., is it a hierarchy of parts and wholes? does it have a privileged level or are all levels of equal status?). Tackling these questions requires an integrative approach that draws on both biology and the philosophy of science. The aim of this article is to provide an overview of these questions, to defend particular answers to some of them, and to illustrate by example how philosophical analysis can shed light on this important area of evolutionary biology.

## 2. CONCEPTUAL QUESTIONS

### 2.1. What Is an MET?

There is a some disagreement in the literature about what exactly counts as a major evolutionary transition, as a number of commentators have pointed out (Queller, 1997; McShea and Simpson, 2011; Herron, 2021). In their 1995 book, Maynard Smith and Szathmáry offered a 2-fold characterization of an MET. The first was that an MET involves a “change in the way that information is stored and transmitted.” In line with this characterization, their list of METs included events such as the transition from RNA to DNA as store of genetic information, and the origin of human language. However, Maynard Smith and Szathmáry also offered a second characterization of an MET, noting that in many cases, “entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it” (p.8). This fits with the idea that an MET is essentially bound up with an increase in hierarchical complexity; that is, it involves the formation of a new higher-level biological unit from a group of lower-level units (Michod, 1999; Bourke, 2011). Consider cases such as the evolution of the eukaryotic cell by the symbiotic union of two prokaryotes; the evolution of multi-cellular eukaryotes from their unicellular ancestors; the evolution of obligate symbioses, e.g., lichens; and the evolution of eusocial insect colonies. In each of these cases, the end result of the transition is that a new higher-level entity exists, built up out of smaller, formerly free-living entities.

There has been considerable debate about which of these characterizations of an MET is “better,” and what the relation between them is. [Alternative characterizations have also been suggested, such as that of Robin et al. (2021) who argue that ecosystem effects need to be explicitly included in the definition]. In an update of his views, Szathmáry (2015) offers a spirited defense of the two-dimensional characterization of an MET found in his earlier work with Maynard Smith, arguing that it is a “feature not a bug” (p. 10105). His reason for saying this appears to be the apparent link between changes in how information is stored or transmitted and the evolution of new higher-level units; indeed in many cases the former seems to be a prerequisite for the latter to go to completion. Thus for example, the evolution of multi-cellularity necessitated a system of (within-organism) epigenetic inheritance in which cellular phenotypes could be transmitted across mitosis, thus allowing differentiation and division-of-labor to evolve; while the evolution of eusocial

animal societies required a system of signaling and social learning in order for the colony to function as a unit. Thus on Szathmáry’s view, the two-dimensional characterization of an MET is not an undesirable ambiguity but has a genuine point, since there is a close empirical link between the two dimensions, despite their conceptual independence.

However, against Szathmáry, others have worried that the notion of a major transition has simply become too broad, sometimes seeming to include any evolutionary event that an author deems “important” enough by whatever yardstick they choose (McShea and Simpson, 2011). My own view is that an MET is best defined in terms of Maynard Smith and Szathmáry’s second characterization, that is, as the evolution of a higher-level biological unit out of formerly-free living units. Thus we should set aside the idea that an MET involves a change in how information is transmitted / stored. This means paring the original list of METs to exclude: the origin of the genetic code; the transition from RNA to DNA; the origin of sex; and the origin of human language. This more austere approach seems preferable for three reasons. Firstly, it avoids the murky notion of “the way in which genetic information is transmitted,” and sidesteps the question of how exactly changes in mode of information transmission relate to the evolution of higher-level units. Secondly, it offers the best hope that METs will constitute what philosophers call a “natural kind,” that is, a set of events (or objects) that are objectively similar to each other as opposed to an arbitrary grouping (Herron, 2021). Thirdly and relatedly, restricting the definition of an MET in this way fits best with the aim of finding a general theory of METs, a hope that animates much of the literature on the topic (e.g., Bourke, 2011; Szathmáry, 2015).

### 2.2. Complexity and Directionality

Evolutionists have often disagreed on whether the evolutionary process possesses an inherent directionality, leading to certain outcomes with a high degree of predictability. The pre-Darwinian idea that evolution is progressive in the sense of making things “better,” e.g., by leading from “lower” to “higher” organisms, has long been abandoned (Ruse, 1996); but vestiges of that idea persist in the widespread notion that evolution by natural selection leads to an increase in complexity, adaptiveness, self-organization, organismic autonomy, or some other quantity (Gould, 2002; Brandon and McShea, 2010). Despite widespread acceptance of the point that natural selection is a brute causal mechanism that lacks foresight, and the recognition that chance events play a crucial role in evolution, the idea that evolution is in some sense directional is still very much alive.

This general issue plays out in an interesting way in relation to the evolutionary transitions. There is a straightforward sense in which an MET leads to an increase in what is sometimes called “vertical” complexity, i.e., degree of hierarchical structuring, since by definition, an MET leads to a new level in the biological hierarchy that was not there before. Given that numerous METs have in fact occurred, it follows that hierarchical complexity, as measured by levels of nesting, has increased over time. However, this obvious point does not settle the question of whether METs are an example of evolution’s directionality, for two reasons.

Firstly, it is possible that the increase in hierarchical complexity may have been non-monotone, i.e., there were periods of decline; secondly, since the earliest life forms exhibited the lowest possible level of hierarchical complexity, passive diffusion alone would have led it to increase (Gould, 1988).

The question, then, is whether there is any inherent tendency for METs to occur, that is, for lower-level biological units to form themselves into larger units; and if so, why? The fact that METs have occurred repeatedly—the transition to multi-cellularity alone is believed to have occurred at least sixteen times (King, 2004)—may suggest a positive answer; and the fact that most METs have given rise to functionally complex higher-level units suggests that natural selection, rather than drift and mutation alone, was likely to have played a key role. [In the case of multi-cellularity, the relevant selective pressure may simply have been the survival advantage of being bigger (Bonner, 1988)]. But on the other hand, prokaryotes are the most abundant life-forms on earth, and the vast majority of prokaryotic lineages have not undergone evolutionary transitions, but rather have persisted for long periods of time in something close to their ancestral and ancient form. So the empirical facts do not speak unambiguously either way.

Despite this, a positive answer to this question often seems presupposed in the literature on METs, though it is rarely made explicit. One example of this is the widespread assumption that an MET represents a limit case of the evolution of cooperation / altruism, such that intermediate levels of pro-sociality represent staging posts en route to a full transition (see Birch, 2012 and Bourke, 2011, p.200-1 for critical discussion of this assumption). Thus Stearns (2007) has tentatively suggested that humans may be “stalled” part-way through a major transition from individuals to groups, thanks to intervening conditions. However, caution is needed here. Though it may well be true that the evolution of a new higher-level biological unit is facilitated by the existence of cooperative / altruistic interactions between the smaller units, this does not in itself prove that an evolutionary transition is in any sense an inevitable outcome of the spread of cooperation among smaller units. It is also equally possible that METs are rare singularities that require quite specific ecological conditions and / or fortuitous events (Boomsma, 2009), and that intermediate levels of cooperation among smaller units are evolutionarily stable, rather than being staging posts en route to a transition (Herron et al., 2013). The indisputable utility of the principles of social evolution in helping us to understand the evolutionary pressures at work in an MET should not seduce us into assuming that there is an inherent tendency for high levels of pro-sociality to lead to an MET. It may well be that an MET represents something qualitatively different from the evolution of altruism.

The underlying problem here, I suggest, is parallel to one that arises in other discussions of evolutionary directionality, namely that it is not entirely clear how to operationalize the thesis that there is an inherent tendency for METs to occur and thus an inherent tendency for vertical complexity to increase. It is not obvious what empirical data, even if we had it, would settle this question. Even if vertical complexity could be measured unambiguously, any observed trend is compatible with the hypothesis of an inherent tendency toward increase

or with the opposite hypothesis, so long as “constraints” and “countervailing forces” can be invoked. Hypotheses about evolutionary directionality thus suffer from a severe form of what philosophers call “underdetermination by the data.” However, we need not despair entirely. Some progress on the question could be made if a well-established “theory of evolutionary transitions,” of the sort envisaged by Szathmáry (2015), were developed. Such a theory could plausibly help to identify the relevant selective pressures and ecological conditions that push a biological system toward an MET, and could help resolve the question of whether an MET is a predictable, or at least somewhat likely, outcome in any biological system characterized by a high degree of cooperative or altruistic interactions.

### 2.3. A General Theory?

Should we hope for an overarching theory that can explain all the known METs? Or should we be content with a series of piecemeal explanations? The answer to this question depends on two things. The first is the extent to which the different evolutionary events that we call “METs” are objectively similar, or constitute a natural kind; for if they do not, then it would be misplaced to seek a general theory. The second is whether, even if the METs do constitute a natural kind, a common set of explanatory principles can be identified that applies to them all. These two issues are related but distinct.

So long as we define an MET in the way recommended above, as the evolution of a higher-level biological unit from smaller, formerly free-living units, the objective similarity requirement seems likely to be met, at least to a reasonable degree. Most evolutionary events do not involve the formation of new higher-level units; so singling out the ones that do, and co-classifying them, surely picks out a genuine kind. Obviously there are still differences between the METs; no two evolutionary events are going to be similar in all respects. Queller’s distinction between “fraternal” and “egalitarian” transitions is relevant here; in fraternal cases, the lower-level units that form a larger unit are themselves closely related (e.g., single-celled to multi-celled eukaryotes); while in the egalitarian cases, the lower-level units are unrelated and may be from different species (e.g., the union of two prokaryotic cells into a eukaryotic cell) (Queller, 1997, 2000). This is an important distinction, as different evolutionary pressures will apply in each case; but it is still compatible with METs being a natural kind composed of two sub-kinds. This at least seems like a plausible working hypothesis.

Could a common set of principles explain all of the transitions? This is a trickier issue. Since by definition, all METs involve “the same” thing, namely the formation of higher-level units from collections of smaller units; and since natural selection was presumably implicated in this, it is tempting to assume that basic Darwinian principles will illuminate the METs. And to an extent they do, as a number of authors have noted (Maynard Smith and Szathmáry, 1995; Bourke, 2011). For example, we know that there must have been a short-term selective advantage to the smaller units in order for them to form a collective; that the collective would not necessarily be stable owing to defectors pursuing their own interests; that mechanisms for aligning the

interests of the smaller units (e.g., kinship, policing, division-of-labor) could alleviate this problem (Frank, 2003); and that higher-level selection (between collectives) would need to trump lower-level selection (between units within a collective) in order for the collective to evolve adaptations of its own (Michod, 1999). These and other principles, stemming from general evolutionary theory, are likely to be relevant to all METs.

However—and this is why the issue is tricky—“relevant” is not the same as “useful” nor “explanatorily fundamental.” Explanations of METs at this level of abstraction, while not wrong, may not tell us what we want to know. Consider for example the evolution of the first proto-cell, the first eukaryotic cell, and the first eusocial insect colony. These events do have something in common, but it may be that focusing on the commonality obscures, or at least does not help answer, important biological questions. A full understanding of any one of these transitions requires a detailed description of the sequence of actual stages involved, not just an abstract analysis of the evolutionary forces at work. This, in turn, reflects the fact that explanations in terms of evolutionary advantage, while important, are not the only sorts of explanation in biology (hence the widely-appreciated need to integrate the study of function with the study of mechanism). In the case of the proto-cell, for example, we certainly want to know why it was advantageous for replicating molecules to become compartmentalized; but we also want to know how the compartments were formed; what their structure was; what the sequence of stages was that led to compartmentalization; and how and why one stage evolved into another. The answers to these questions may well be specific to the origin of the proto-cell, and will not necessarily have close analogs in the other METs.

Relatedly, there is a risk when studying METs of over-emphasizing the similarities between different transitions, or simply assuming ahead of time that they can all be explained in the same way. This is not a hypothetical point, since there has been a certain tendency to over-apply the social evolution framework (or simple models belonging to that framework such as the prisoner’s dilemma.) Thus for example, Rainey et al. (2014), in an article entitled “Microbes are not bound by sociobiology,” argue persuasively that terms and concepts from social evolution theory, such as “cheating” and “public good” have been misappropriated in studies of bacterial sociality with harmful consequences. In particular, Rainey et al. (2014) object to the practice of using the term “public good” to refer to any extracellular metabolite secreted by a microbe, irrespective of whether it is actually costly to produce or beneficial to others. An *a priori* commitment to the idea that a collective action problem is central to every MET appears to be the source of this confusing practice.

In short, there are clear thematic commonalities among the various METs, and we can point to general evolutionary principles that likely apply in all cases (though in light of the Rainey’s point above, we should take care not to pre-judge this). But precisely because of their generality, such principles will yield rather coarse grained explanations. The real issue, therefore, is not whether a general theory of METs of some sort can be found, but whether the principles of such a theory could be

suitably general to apply to all METs *and* suitably specific to yield explanations at the right “grain” to answer the biological questions that interest us. The jury is still out on this question.

## 2.4. Hierarchical vs. Genic Explanations

A number of authors have pointed to a distinction between “genic” and “hierarchical” approaches to the METs (Buss, 1987; Queller, 1997). On the genic side, we find authors such as Maynard Smith and Szathmáry (1995), Bourke (2011, 2014), and West et al. (2015); on the hierarchical side, we find Buss (1987), Michod (1999) and Szathmáry (2015). The distinction is one of preferred explanatory approach and / or conceptual toolkit. The genic approach is reductionistic in spirit, borne of the general conviction that Darwinian evolution should be explained in terms of direct selective advantage to individual replicators. Applied to the METs, this suggests that the key thing we need to understand is what the selective advantage to the lower-level units was from forming a larger unit. The hierarchical approach, by contrast, is anti-reductionistic, emphasizing emergent properties of wholes and the role of multi-level selection in driving evolutionary outcomes. To explain an MET, on this approach, we need to understand why selection between higher-level units was able to dominate selection within them, thus allowing higher-level units to evolve into functionally integrated units.

In his review of Maynard Smith and Szathmáry’s (1995) book, Queller (1997) argued that we need not choose between the genic and hierarchical approaches—“we can, indeed must, have it both ways” (p. 187). Queller argued that Buss’s “failure to do his genetic sums” had led him to questionable conclusions about the evolution of multi-cellularity, but that the hierarchical approach nonetheless “leads to the right questions,” such as what an organism is (p.187). Queller is surely right that the genic vs. hierarchical issue is something of a false dichotomy, since there is no obvious respect in which the two are incompatible; and in general, a pluralism of explanatory schemes is often a good thing in science (Birch and Okasha, 2015). However, we should distinguish between two different ways of “having it both ways,” that is, of trying to combine genic and hierarchical approaches to the METs.

The first way is to adopt the genic approach for some METs and the hierarchical approach for others. Consider again the distinction between fraternal and egalitarian transitions. Though Queller (1997) does not suggest this, a natural idea is that fraternal transitions are best explained using the genic approach and egalitarian transitions using the hierarchical approach. For the hallmark of a fraternal transition is the high relatedness between the lower-level units, and the consequent potential for kin selection to operate. Thus in the transition to multi-cellularity, for example, one well-known scenario posits a proto-group of cells that arose from the products of mitosis remaining physically attached to their parent cell; since its constituent cells would then be clonally related, simple kin selection logic then explains how the proto-group could evolve into a cooperative unit. By contrast, in an egalitarian transition, such as the formation of the eukaryotic cell by the symbiotic union of unrelated prokaryotes, a different sort of explanation is needed; kin selection cannot be part of the story (Bourke, 2011). Plausibly,

the explanation will appeal to the group-level advantage from combining replicating units of different sorts in a single group. Such an explanation is broadly “hierarchical,” in the sense that it appeals essentially to emergent or group-level properties; and it explains the transition by invoking a between-group selective process.

The second way of trying to reconcile the two approaches is different. Rather than applying the genic approach to some METs and the hierarchical approach to others, perhaps one and the same MET can be explained using either approach? This is a reconciliation of a different sort; it ties in with the broader idea, familiar since Dawkins (1976) “necker cube” analogy, that a single evolutionary process may usefully be viewed from multiple perspectives. Since in an MET, the higher-level unit comes to be functionally organized thanks to the alignment of the fitness interests of the constituent gene-level sub-units (Bourke, 2014), it stands to reason that the MET can be viewed from either a genic or hierarchical perspective. In support of this second reconciliation, we should note that even in a fraternal transition, where the genic approach is most natural, the end result is still an increase in hierarchical complexity; and even in an egalitarian transition, where the hierarchical approach is most natural, it remains true that without a direct selective advantage to each of the (unrelated) lower-level replicators, they would never have voluntarily entered into a group-living arrangement in the first place. Thus elements of both explanatory frameworks, genic and hierarchical, do seem applicable to all METs.

This second way of reconciling the genic and hierarchical approaches to the METs might be regarded as a special case of the well-known idea that inclusive fitness and multi-level selection are “equivalent” formulations of social evolution theory, despite having been pitted against each other in the past. This “equivalence thesis” has been widely endorsed in the social evolution literature, though with some dissenters. [Supporters of the equivalence thesis include Queller (1992), Frank (1998, 2013), Kerr and Godfrey-Smith (2002), Lehmann et al. (2007), Marshall (2011); dissenters include Hölldobler and Wilson (2009), van Veelen (2009), Nowak et al. (2010), Traulsen (2010)]. Since the genic approach is intimately bound up with inclusive fitness, and the hierarchical approach with multi-level selection, it is tempting to regard the equivalence thesis as supplying a theoretical underpinning for the idea that any MET can in principle be explained using either a genic or a hierarchical approach.

However, some care is needed here. It is true that there is a *formal* equivalence between inclusive fitness and multi-level selection, in the sense that in *some* models for the evolution of a pro-social behavior, it is possible to do the evolutionary analysis in either multi-level terms, by partitioning fitness variation into within-group and between-group components, or in inclusive fitness terms, by partitioning fitness into direct and indirect components. However it is unclear whether this is true of all models, in part because the equivalence results rely on approximations including weak selection (Lehmann and Rousset, 2014); and in part because the multi-level analysis presupposes the existence of group structure while the inclusive fitness analysis does not (Birch and Okasha, 2015). Moreover, formal

equivalence is not the same as causal-explanatory equivalence (Okasha, 2016). For the aim of evolutionary analysis is not simply to predict the outcome of evolution, or to compute a correct expression for allele frequency change, but rather to produce causal explanations. One of two “formally equivalent” approaches may yield a better causal representation of the evolutionary processes at work in a particular biological system. So it would be overhasty to conclude, from the formal equivalence results alone, that inclusive fitness and multi-level selection are necessarily equivalent in respect of their causal adequacy; and by the same token, we cannot conclude that genic and hierarchical approaches to the METs are always of equal explanatory power. The equivalence thesis, therefore, does not discriminate between the two ways of reconciling the genic and hierarchical approaches.

To conclude, Queller’s idea that the genic and hierarchical approaches both have something to contribute to the study of METs is correct. But there is more than one way of trying to effect a reconciliation between the two approaches. It may yet turn out that the genic approach is better suited to studying some METs while the hierarchical approach to others; alternatively, it may turn out that any MET can be fruitfully studied using either approach.

## 2.5. METs and the Levels of Selection

It is interesting to consider how the study of METs relates to the traditional “levels of selection” (or “units of selection”) discussion in evolutionary biology. The latter discussion traces to Darwin (1859) and achieved prominence in the second half of the 20th century through works by Williams (1966), Lewontin (1970), Hamilton (1975) and Dawkins (1976, 1982), among others; it thus pre-dates the contemporary work on METs. Yet clearly there is a conceptual connection between METs and levels of selection. For in an MET, formerly free-living individuals become integrated into a larger unit; so there is the potential for natural selection to act at two different levels (Okasha, 2005; Wilson, 2010). As Buss (1987) first emphasized, for an evolutionary transition to be successful, it is necessary for higher-level selection to “trump” lower-level selection; typically this requires the evolution of mechanisms, such as policing, to regulate the selfish tendencies of the lower-level units and / or to align their evolutionary interests. Thus it is unsurprising to find that many themes from the traditional levels of selection discussion, such as altruism versus selfishness, individual versus group interests, and the importance of genetic relatedness, re-appear in the literature on METs.

In some ways, the MET research program has breathed new life into the levels of selection discussion. Some biologists have wanted to dismiss the traditional levels discussion as a storm in a teacup, arguing that in practice, individual selection is all that really matters in biology, whatever about other theoretical possibilities. [Thus for example, Waddington (1975) described the debate over group selection as “a rather foolish controversy”]. Others have dismissed the debate as largely semantic. But in the light of the METs, these dismissive attitudes are hard to defend, for two reasons. Firstly, group selection appears implicated in many if not most of the METs (though a kin selection / inclusive

fitness perspective may be equally valid in some of these cases, as discussed above). Given that METs clearly have occurred, the evolutionary importance of group (or multi-level) selection can hardly be denied. Secondly and more importantly, the METs remind us that even paradigm biological individuals can be regarded as groups or collectives, once we take a sufficient long time-horizon. Multi-celled organisms and eukaryotic cells, for example, are both collective entities that evolved out of smaller free-living biological units. Thus once we adopt the expanded evolutionary perspective that is necessary to understand the METs, the view that “individual selection is all that matters in practice” clearly cannot be sustained; and indeed the very notion of an “individual” is called into question.

Despite their conceptual kinship, there is one important difference between the study of METs and the traditional levels of selection debate. The latter debate dealt with selection and adaptation at *pre-existing* hierarchical levels, and largely set aside the question of the origin of the biological hierarchy itself (Griesemer, 2000; Okasha, 2005). Thus consider for example how Lewontin (1970) formulated the “units of selection” question in his highly influential article. Lewontin began by observing that there are three essential requirements for the process of evolution by natural selection: variation, associated differences in fitness, and heredity. He then observed that in principle, biological units at various hierarchical levels, above and below that of the individual organism, could satisfy these three requirements. Thus for Lewontin, the “units of selection” question stemmed from two factors: (i) the abstract nature of the fundamental Darwinian requirements; and (ii) the fact that biological units form a nested hierarchy. There is nothing wrong with Lewontin’s formulation per se, but it is incomplete in one important respect. For clearly, hierarchical organization is not simply a brute fact about the living world: the earliest life-forms were not hierarchically complex. Thus there must be an evolutionary story to be told about how the biological hierarchy evolved in the first place; and the METs form a key part of that story.

This implies that the link between METs and the traditional levels of selection issue is more complex than it seems; it is not just a case of themes from one discussion re-appearing in the other. One useful way to look at it is the following. In the traditional levels discussion, hierarchical organization is treated as “exogenous,” something that is part of the assumed background against which evolutionary explanations are constructed but does not receive any explanation itself (Okasha, 2021). In the literature on METs, by contrast, hierarchical organization is “endogenized,” since the aim is precisely to offer an evolutionary account of how biological units came to form a nested hierarchy in the first place. In philosophical terms, hierarchical organization thus moves from being part of the *explanans* to being part of the *explanandum*. Looked at this way, we have an instance of a common pattern in evolutionary biology, in which features that were once part of the assumed biological background against which evolutionary explanations take place (e.g., sexual reproduction, gamete dimorphism, and fair meiosis) are progressively endogenized as the science advances, leading to an increase in theoretical generality (Okasha, 2021).

Finally, the study of METs forces us to re-examine certain issues from the traditional levels of selection discussion. One such issue is how best to formulate the basic Darwinian principles. Dawkins (1976, 1982) introduced the concepts of “replicator” and “vehicle” as part of his abstract analysis of the elements of Darwinian evolution; Hull (1980) later suggested the term “interactor” in lieu of vehicle. Though these concepts have their merits, and certainly clarified aspects of the traditional levels debate, they arguably lack generality, for they help themselves to something that needs to be explained. Thus Dawkins characterized a replicator as an entity with high “copying fidelity” that passes on its structure intact to its descendants; while Hull characterized an interactor as an entity that “interacts as a cohesive whole with its environment.” However, recent work on METs teaches us that high copying fidelity and organismic cohesion are evolved attributes. The first replicators would have had low copying fidelity, as the mechanisms that ensure copying fidelity did not then exist [This is the source of “Eigen’s paradox” as discussed by Maynard Smith and Szathmáry (1995)]. Similarly, the first multi-celled organisms were unlikely to have been particularly cohesive, as they were probably mere clusters of cells that arose when daughter cells failed to fully separate from their parents, and thus would have lacked any group-level functional organization. If we want evolutionary theory to be able to explain how attributes such as high-fidelity replication and organismic cohesion evolved initially, we had better not build these attributes into the concepts that we use to formulate the basic Darwinian principles. This is another conceptual moral of the METs.

### 3. ONTOLOGICAL ISSUES

The term “ontology” has a dual meaning in philosophy. It can refer to the traditional sub-branch of philosophy that tries to answer the question “what things exist in the world?” It can also refer to the objects of study of some particular field of enquiry, as when we say that electrons belong to the “ontology of particle physics,” for example. It is this second sense of the term that is relevant here. The study of METs raises interesting questions concerning the ontology of evolutionary biology; these have to do with the nature of biological entities, hierarchical organization, and part-whole structure.

#### 3.1. Hierarchical Organization

It is a commonplace that the entities studied in biology vary greatly in size, from biomolecules at one extreme to ecosystems at the other, and that these entities form a hierarchy of sorts, with larger ones composed of smaller ones. This observation long predates the MET research program, of course. Though there have been attempts to theorize systematically about hierarchical organization (e.g., Salthe, 1985), most descriptions of the biological hierarchy are fairly casual. A typical description is: “gene–chromosome–cell–tissue–organ–organelle–multi-celled organism–kin group–colony–ecosystem.” Clearly there is something right about this description, but it raises a number of awkward questions. What is the criterion for being a level in this hierarchy? Where do species and clades fit in? Is there a unique biological relation that relates entities

at adjacent levels (e.g., gene to chromosome and organism to kin group)? Is it a problem that some entities in the above list (e.g., organisms) are functionally organized but others (e.g., ecosystems) are not? Should we think of the hierarchy as one of (what philosophers call) part-whole inclusion? (That is, do the larger entities contain the smaller ones as their “parts” in the same way that other macroscopic objects, e.g., cars, contain parts)? Do all biological entities belong to a single hierarchy?

Some progress with these questions was made by Eldredge (1985), who argued that there are in fact *two* biological hierarchies: ecological and genealogical. In the former, the relation that “binds” a number of lower-level units into a single higher-level unit is ecological interaction, while in the latter it is genealogical relatedness. Thus, entities such as species and monophyletic clades belong in the genealogical hierarchy, while entities, such as colonies and social groups belong in the ecological hierarchy. Interestingly, Eldredge argues that a multi-celled organism belongs in both hierarchies (and is the only entity that does); the reason is that the cells within a single organism are clonally derived from a single zygote, so form a monophyletic group of cells; and they also interact ecologically, for example via cell-cell signaling, and have a common fate. Thus organisms stand at the intersection of the genealogical and ecological hierarchies.

The study of METs brings further clarity to the nature of hierarchical organization in biology. As emphasized above, an MET by definition gives rise to an entity at a previously unoccupied hierarchical level, so can be thought of as a means by which *some* of the hierarchical structuring in the biota evolved. The qualification “some” is needed for two reasons. Firstly, the hierarchical organization that results from an MET corresponds to Eldredge’s ecological hierarchy, not his genealogical hierarchy. This point is obvious when we consider the egalitarian transitions, whose hallmark is precisely that higher-level units are formed out of unrelated smaller units. It is also obvious once we note that entities such as species and clades are not the product of METs. Secondly and less obviously, even once entities belonging to the genealogical hierarchy are excluded, the hierarchy that results from METs is more restricted than that given in some descriptions of “the” biological hierarchy, such as the illustrative one at the start of this section. In particular, tissues and organs do not belong; for although they are composed out of cells, they did not evolve by groups of free-living cells combining themselves into a larger unit, but by differentiation among the parts of an already existing multi-celled organism. In short, to belong in the hierarchy that results from the METs, an entity needs to be “homologous with organisms in a free-living state, either extant or extinct,” to borrow a phrase of Dan McShea (2001); this explains why organelles and cells belong, but tissues and organs do not. This is not to deny that there could be a genuine point to a characterization of the biological hierarchy that includes organs and tissues as levels. But it is important to see that the logical basis for such a characterization, i.e., the implicit criterion for what counts as a level, would be quite different from that of the hierarchy that results from the METs.

The point that the METs account for some but not all of the part-whole structure in the living world, combined with

Eldredge’s distinction, helps us toward a better understanding of, and a more principled way of describing, hierarchical organization in biology. It does not resolve all the questions though. One that remains concerns the existence or otherwise of a privileged hierarchical level.

### 3.2. A Privileged Level?

There are two ways of thinking about the hierarchical structure that results from the METs. According to the first way, entities occupying different levels differ in their vertical complexity, but apart from that there is nothing that distinguishes one level from other. The levels thus enjoy an equal ontological status, none being privileged over any other. According to the second way, the levels do not have equal status; rather, the highest level occupied, in any particular biological system, is privileged over all the lower levels. For only entities at the highest level count as “organisms” (or perhaps: “evolutionary individuals”) entities at lower levels relinquished that status when the transition took place. Thus a mitochondrion and a cell in a modern metazoan, for example, have a fundamentally different status from the metazoan itself (presuming that the metazoan is not part of an integrated colony that has itself resulted from an MET).

The first view is implicit in much of the traditional levels of selection discussion, discussed above (e.g., Lewontin, 1970). A key idea in that literature is that it is a mistake to focus exclusively on “the individual” when thinking about how Darwinian evolution works; natural selection can operate at other levels too, e.g., the group level, given that the fundamental requirements—variation, heredity, and multiplication—are satisfied by entities above and below that of the individual. This idea fits naturally with the view that the different levels in the biological hierarchy are on a par. The second view, by contrast, is implicit in the idea that an MET involves a change in the “level of individuality,” a characterization favored by certain theorists of the METs (e.g., Michod, 1999). According to this idea, during an MET the lower-level units relinquish their status as individuals, for they give up their free-living existence and evolve into parts of a larger unit; that larger unit then counts as a new, higher-level “evolutionary individual.” Thus, the attribute of “individuality” is lost by the smaller units but gained by the larger unit. This fits with the idea that the hierarchy generated by METs does have a privileged level, namely the highest occupied level in a given system.

Which of these views is preferable? It depends in part on the vexed question of what “individuality” is; this is a topic of much recent discussion (Pradeu, 2016). My own view is that a version of the second view is defensible, but that it is best expressed in terms of the concept of an *organism*, rather than that of an “evolutionary individual”; where an organism, roughly speaking, is an entity that exhibits adaptations, is functionally organized, and exhibits a certain “autonomy” or “agency.” That is, what happens during an MET is that there is a shift in the level of “organismality” entities that were formerly organisms lose that status, and a new organism evolves that is made up of parts that are homologous to the original, smaller organisms. Thus, there is indeed a privileged level in the hierarchy that results from the METs, namely the highest occupied level, for it is there and only there that we find organisms.

This version of the second view may seem hard to square with the popular idea that some METs have given rise to *superorganisms*, such as eusocial insect colonies. If this is true, surely there cannot be anything privileged about the organismic level in the hierarchy generated by the METs, and surely we cannot equate the organismic level with the highest occupied level? However, an important argument of Queller (1997) deserves mention here. Queller argues that the very notion of a superorganism should be rejected on logical grounds. If an entity, such as a honey bee colony, exhibits sufficient functional organization and a sufficiently low level of internal conflict to merit being called a superorganism, it is more consistent to simply describe it as an organism. As Queller puts it, “we designate something as an organism, not because it is  $n$  steps up on the ladder of life, but because it is a consolidated unit of design” (1997, p.187). If Queller is right about this, as I believe that he is, it follows that we can treat the organismic level as ontologically privileged in the hierarchy generated by the METs without falling into contradiction.

Finally, it is interesting to note that the issue here—privileged level or not—also arises in relation to the genealogical hierarchy, but in reverse form. The lowest level in the genealogical hierarchy is usually taken to be the species; the entities at higher levels are monophyletic clades of various sizes (traditionally assigned to different “ranks,” though these have been abandoned by modern “rank-free” approaches to phylogenetic systematics). Biologists concerned with classification and systematics have long disagreed about whether species have a different ontological status to higher taxa or not. One traditional view is that species are “real” biological units whereas higher taxa are merely “conventional;” this implies that the species level is a privileged level in the genealogical hierarchy. But an alternative view holds that species are merely the “basal taxonomic units;” that the concept of monophyly can apply at the species level; and that all monophyletic clades, including species, are equally “real.” Here is not the place to try to resolve this (somewhat murky) issue; the point to note is simply the analogy with the parallel issue concerning the hierarchy that results from the METs.

### 3.3. METs and Part-Whole Structure

Our final ontological issue follows directly from the previous one; it concerns the nature of the part-whole structure (or hierarchical organization) to which METs give rise. Consider again the idea that an MET involves a higher-level entity gaining organismic status and lower-level entities giving up that status. If this conceptualization is right, it suggests that an organism cannot have parts that are themselves organisms; this is an example of what philosophers call an “exclusion principle.” Indeed this principle follows directly from the definition of an organism found in Queller and Strassmann (2009), which is motivated by their study of METs. They define an organism as “the *largest* unit of near-unanimous design,” where the “unanimity” of a biological unit means that its constituent parts exhibit a lot of cooperation but little conflict (p. 3144, my emphasis). As Godfrey-Smith (2009) notes, Queller and Strassman’s definition implies that if

an entity is an organism, any parts or sub-units that it contains are not organisms.

Is the part-whole exclusion principle plausible? In many cases it is. An amoeba is clearly an organism; but the chromosomes and mitochondria that it contains are not. A metazoan is clearly an organism; but the cells within it are surely not. However, in other cases the principle seems less obviously true. Think for example of the gut bacteria in each of us; they are clearly organisms, and one might well think that they are parts of us. Or think of one of the partners in an obligate symbiosis, such as the fungal partner in a lichen, for example. On the face of it, there is nothing obviously wrong with the idea that the lichen itself and the fungus are both organisms, the latter being part of the former. Finally, consider a honey bee colony. There is a strong case for regarding the whole colony as an organism, as noted above; but it seems counter-intuitive to say that the individual bees are not organisms, as the exclusion principle would require. [Indeed as Godfrey-Smith (2009) notes, Queller and Strassmann (2009) say in one place that the individual bees *are* organisms, thus, implicitly contradicting their own definition].

How should we resolve this issue? There are three possible options. The first is to simply reject the exclusion principle, i.e., to claim that some *bona fide* organisms do contain other organisms as parts, even if most do not. I see no decisive objection to this; though it is interesting to note that according to a venerable philosophical tradition, there is an important sub-category of natural kind terms, known as *sortals* or *substance sortals*, that are thought to satisfy the part-whole exclusion principle (Grandy and Freund, 2021). (The sortal to which an entity belongs is to meant to tell us the “fundamental sort” of thing it is, and to settle questions about the entity’s identity and persistence over time). If the term “organism” in evolutionary biology violates that principle, despite functioning much like a sortal term in other respects, this would be a philosophically significant finding. The second option is to retain the exclusion principle and try to explain away the apparent counterexamples. Thus in the lichen example, we would need to argue either that the lichen is not a single organism or that its fungal partner is not; and similarly for the honey-bee colony. One possible motivation for this view is the idea that in both these cases, the MET has not gone to completion (and may never do so). That is, the lichen and the honey bee colony do not count as organisms, precisely *because* their constituent parts have not fully relinquished their organismic status, in the way that the cells of a metazoan, or the mitochondria of a eukaryotic cell, have done.

The third possible option is to argue that being an organism is a matter of degree, not an all-or-nothing matter. This is quite plausible, given the gradualness of evolution. Even if an MET does produce a new higher-level entity that is clearly an organism, there will likely be a transitional phase, or gray area, when the entity’s organismic status is moot. Moreover, as noted in section 2.4, such a phase could reflect a stable equilibrium, so is not necessarily a temporary staging post en route to a “full” transition. This option opens the door to arguing that some entities, such as lichens and honey bee colonies, are partly though not wholly organismic. Also, this allows a modified version of the part-whole exclusion principle to be retained, restricted to



entities that are fully organismic. The modified principle thus says that no entity that enjoys *full* organismic status can have parts that also enjoy that status.

The choice between these three options raises difficult issues, both philosophical and scientific. (The main scientific issue is how we should understand the concept of organism in the light of the METs; the main philosophical issue is whether or not we should treat the part-whole exclusion principle for organisms as sacrosanct, and why). My own view is that the second and third options are both defensible, and on balance preferable to the first option; but I know of no consideration for or against any of the three options that strikes me as decisive.

## 4. CONCLUSION

Evolutionary biology has long been a source of fascination for philosophers. There are two main reasons for this. The first is that evolutionary biology promises to shed light on topics of perennial philosophical interest, such as human nature, altruistic vs. selfish behavior, and the tension between individual self-interest and group welfare. The second is the prevalence of conceptual issues within evolutionary biology that are ripe for philosophical analysis, such as the rationale for using purposive language, the nature of biological classification, and the relation between proximate and ultimate explanations.

Set against this background, it is unsurprising that recent philosophers of biology have turned their attention to the

study of METs, given their evident scientific importance. However to a practicing biologist, it may not be obvious why philosophers think they have something to contribute to this area. The aim of this article has been to explain why this is so. We have distinguished two types of philosophical question—conceptual and ontological—that are thrown up by the MET research program; we have identified a number of questions of each type and suggested answers to some of them. While these answers are inevitably provisional, my hope is that the reasoning behind them illustrates the potential for fruitful interplay between philosophers and biologists working in this area.

## AUTHOR CONTRIBUTIONS

SO carried out the research and wrote the article.

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