The Major Transitions in Evolution – a philosophy-of-science perspective

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ABSTRACT

In the wake of the pioneering works of Buss (1987), Maynard Smith & Szathmáry (1995) and Michod (1999), the study of major evolutionary transitions is now 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.

Keywords: major transitions, evolution, philosophy of science, organism, conflict, cooperation, multi-level selection

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 occured 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 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; Godfrey-Smith and Kerr, 2013; Clarke, 2014; O'Malley and Powell, 2016; Ryan, Power and Watson, 2016; Birch, 2012. 2017; 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

32 be defined; what form an evolutionary explanation of an MET should take; how concepts such as kin
33 selection, multi-level selection and the "gene's eye view" apply to METs; and whether an overarching
34 theory of evolutionary transitions is possible. Examples of the latter include questions about what status the
35 new biological units that arise from METs have (e.g. are they organisms, super-organisms or individuals?);
36 and about the nature of the hierarchical organization that results from the transitions (e.g. is it a hierarchy of
37 parts and wholes? does it have a privileged level or are all levels of equal status?). Tackling these questions
38 requires an integrative approach that draws on both biology and the philosophy of science. The aim of
39 this paper is to provide an overview of these questions, to defend particular answers to some of them, and
40 to illustrate by example how philosophical analysis can shed light on this important area of evolutionary
41 biology.

2   CONCEPTUAL QUESTIONS

42 ### 2.1   What is an MET?

43   There is a some disagreement in the literature about what exactly counts as a major evolutionary transition,
44 as a number of commentators have pointed out (Queller 1997, McShea and Simpson 2011, Herron 2021).
45 In their 1995 book, Maynard Smith and Szathmáry offered a two-fold characterization of an MET. The
46 first was that an MET involves a "change in the way that information is stored and transmitted". In line
47 with this characterization, their list of METs included events such as the transition from RNA to DNA as
48 store of genetic information, and the origin of human language. However, Maynard Smith and Szathmáry
49 also offered a second characterization of an MET, noting that in many cases, "entities that were capable of
50 independent replication before the transition can replicate only as part of a larger whole after it" (p.8). This
51 fits with the idea that an MET is essentially bound up with an increase in hierarchical complexity; that is, it
52 involves the formation of a new higher-level biological unit from a group of lower-level units (Michod
53 1999, Bourke 2011). Consider cases such as the evolution of the eukaryotic cell by the symbiotic union of
54 two prokaryotes; the evolution of multicellular eukaryotes from their unicellular ancestors; the evolution
55 of obligate symbioses, e.g. lichens; and the evolution of eusocial insect colonies. In each of these cases,
56 the end result of the transition is that a new higher-level entity exists, built up out of smaller, formerly
57 free-living entities.

58   There has been considerable debate about which of these characterizations of an MET is "better", and
59 what the relation between them is. (Alternative characterizations have also been suggested, such as that of
60 Robin *et al.* (2021) who argue that ecosystem effects need to be explicitly included in the definition.) In an
61 update of his views, Szathmáry (2015) offers a spirited defense of the two-dimensional characterization of
62 an MET found in his earlier work with Maynard Smith, arguing that it is a "feature not a bug" (p. 10105).
63 His reason for saying this appears to be the apparent link between changes in how information is stored
64 or transmitted and the evolution of new higher-level units; indeed in many cases the former seems to
65 be a prerequisite for the latter to go to completion. Thus for example, the evolution of multicellularity
66 necessitated a system of (within-organism) epigenetic inheritance in which cellular phenotypes could
67 be transmitted across mitosis, thus allowing differentiation and division-of-labour to evolve; while the
68 evolution of eusocial animal societies required a system of signaling and social learning in order for the
69 colony to function as a unit. Thus on Szathmáry's view, the two-dimensional characterization of an MET is
70 not an undesirable ambiguity but has a genuine point, since there is a close empirical link between the two
71 dimensions, despite their conceptual independence.

72　　However, against Szathmáry, others have worried that the notion of a major transition has simply become
73　too broad, sometimes seeming to include any evolutionary event that an author deems "important" enough
74　by whatever yardstick they choose (McShea and Simpson 2011). My own view is that an MET is best
75　defined in terms of Maynard Smith and Szathmáry's second characterization, that is, as the evolution of a
76　higher-level biological unit out of formerly-free living units. Thus we should set aside the idea that an MET
77　involves a change in how information is transmitted / stored. This means paring the original list of METs
78　to exclude: the origin of the genetic code; the transition from RNA to DNA; the origin of sex; and the
79　origin of human language. This more austere approach seems preferable for three reasons. Firstly, it avoids
80　the murky notion of "the way in which genetic information is transmitted", and sidesteps the question
81　of how exactly changes in mode of information transmission relate to the evolution of higher-level units.
82　Secondly, it offers the best hope that METs will constitute what philosophers call a "natural kind", that is,
83　a set of events (or objects) that are objectively similar to each other as opposed to an arbitrary grouping
84　(Herron 2021). Thirdly and relatedly, restricting the definition of an MET in this way fits best with the aim
85　of finding a general theory of METs, a hope that animates much of the literature on the topic (e.g. Bourke
86　2011; Szathmáry 2015).

2.2　Complexity and directionality

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

97　　This general issue plays out in an interesting way in relation to the evolutionary transitions. There is
98　a straightforward sense in which an MET leads to an increase in what is sometimes called "vertical"
99　complexity, i.e degree of hierarchical structuring, since by definition, an MET leads to a new level in the
100　biological hierarchy that was not there before. Given that numerous METs have in fact occurred, it follows
101　that hierarchical complexity, as measured by levels of nesting, has increased over time. However this
102　obvious point does not settle the question of whether METs are an example of evolution's directionality, for
103　two reasons. Firstly, it is possible that the increase in hierarchical complexity may have been non-monotone,
104　i.e. there were periods of decline; secondly, since the earliest life forms exhibited the lowest possible level
105　of hierarchical complexity, passive diffusion alone would have led it to increase (Gould 1988).

106　　The question, then, is whether there is any inherent tendency for METs to occur, that is, for lower-level
107　biological units to form themselves into larger units; and if so, why? The fact that METs have occurred
108　repeatedly – the transition to multicellularity alone is believed to have occurred at least sixteen times (King,
109　2004) – may suggest a positive answer; and the fact that most METs have given rise to functionally complex
110　higher-level units suggests that natural selection, rather than drift and mutation alone, was likely to have
111　played a key role. (In the case of multicellularity, the relevant selective pressure may simply have been
112　the survival advantage of being bigger (Bonner, 1988)). But on the other hand, prokaryotes are the most
113　abundant life-forms on earth, and the vast majority of prokaryotic lineages have not undergone evolutionary

114 transitions, but rather have persisted for long periods of time in something close to their ancestral and
115 ancient form. So the empirical facts do not speak unambiguously either way.

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

132   The underlying problem here, I suggest, is parallel to one that arises in other discussions of evolutionary
133 directionality, namely that it is not entirely clear how to operationalize the thesis that there is an inherent
134 tendency for METs to occur and thus an inherent tendency for vertical complexity to increase. It is not
135 obvious what empirical data, even if we had it, would settle this question. Even if vertical complexity
136 could be measured unambiguously, any observed trend is compatible with the hypothesis of an inherent
137 tendency towards increase or with the opposite hypothesis, so long as "constraints" and "counterveiling
138 forces" can be invoked. Hypotheses about evolutionary directionality thus suffer from a severe form of
139 what philosophers call "underdetermination by the data". However, we need not despair entirely. Some
140 progress on the question could be made if a well-established "theory of evolutionary transitions", of the
141 sort envisaged by Szathmáry (2015), were developed. Such a theory could plausibly help to identify the
142 relevant selective pressures and ecological conditions that push a biological system towards an MET, and
143 could help resolve the question of whether an MET is a predictable, or at least somewhat likely, outcome in
144 any biological system characterized by a high degree of cooperative or altruistic interactions.

145 2.3   A General Theory?

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

152   So long as we define an MET in the way recommended above, as the evolution of a higher-level biological
153 unit from smaller, formerly free-living units, the objective similarity requirement seems likely to be met, at
154 least to a reasonable degree. Most evolutionary events do not involve the formation of new higher-level
155 units; so singling out the ones that do, and co-classifying them, surely picks out a genuine kind. Obviously
156 there are still differences between the METs; no two evolutionary events are going to be similar in all

157 respects. Queller's distinction between "fraternal" and "egalitarian" transitions is relevant here; in fraternal
158 cases, the lower-level units that form a larger unit are themselves closely related (e.g. single-celled to
159 multicelled eukaryotes); while in the egalitarian cases, the lower-level units are unrelated and may be from
160 different species (e.g. the union of two prokaryotic cells into a eukaryotic cell) (Queller, 1997). This is an
161 important distinction, as different evolutionary pressures will apply in each case; but it is still compatible
162 with METs being a natural kind composed of two sub-kinds. This at least seems like a plausible working
163 hypothesis.

164   Could a common set of principles explain all of the transitions? This is a trickier issue. Since by definition,
165 all METs involve "the same" thing, namely the formation of higher-level units from collections of smaller
166 units; and since natural selection was presumably implicated in this, it is tempting to assume that basic
167 Darwinian principles will illuminate the METs. And to an extent they do, as a number of authors have
168 noted (Maynard Smith and Szathmáry 1995, Bourke 2011). For example, we know that there must have
169 been a short-term selective advantage to the smaller units in order for them to form a collective; that the
170 collective would not necessarily be stable owing to defectors pursuing their own interests; that mechanisms
171 for aligning the interests of the smaller units (e.g. kinship, policing, division-of-labour) could alleviate
172 this problem (Frank 2003); and that higher-level selection (between collectives) would need to trump
173 lower-level selection (between units within a collective) in order for the collective to evolve adaptations of
174 its own (Michod 1999). These and other principles, stemming from general evolutionary theory, are likely
175 to be relevant to all METs.

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

191   Relatedly, there is a risk when studying METs of over-emphasizing the similarities between different
192 transitions, or simply assuming ahead of time that they can all be explained in the same way. This is not a
193 hypothetical point, since there has been a certain tendency to over-apply the social evolution framework (or
194 simple models belonging to that framework such as the prisoner's dilemma.) Thus for example, Rainey *et al.*
195 (2014), in an article entitled "Microbes are not bound by sociobiology", argue persuasively that terms and
196 concepts from social evolution theory, such as "cheating" and "public good", have been misappropriated
197 in studies of bacterial sociality with harmful consequences. In particular, Rainey *et al.* (2014) object to
198 the practice of using the term "public good" to refer to any extracellular metabolite secreted by a microbe,
199 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 versus 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 Bourke (1987), Maynard Smith and Szathmáry (1995) and West et al. (2015); on the hierarchical side, we find Buss (1987), Michod (1999) and Szathmáry (2019). 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 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 multicellularity, 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 versus 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 egalitation 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 multicellularity, 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 eukayortic 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

243 explanation is broadly "hierarchical", in the sense that it appeals essentially to emergent or group-level
244 properties; and it explains the transition by invoking a between-group selective process.

245   The second way of trying to reconcile the two approaches is different. Rather than applying the genic
246 approach to some METs and the hierarchical approach to others, perhaps one and the same MET can be
247 explained using either approach? This is a reconciliation of a different sort; it ties in with the broader idea,
248 familiar since Dawkins (1976) "necker cube" analogy, that a single evolutionary process may usefully
249 be viewed from multiple perspectives. Since in an MET, the higher-level unit comes to be functionally
250 organized thanks to the alignment of the fitness interests of the constituent gene-level sub-units (Bourke,
251 2014), it stands to reason that the MET can be viewed from either a genic or hierarchical perspective. In
252 support of this second reconciliation, we should note that even in a fraternal transition, where the genic
253 approach is most natural, the end result is still an increase in hierarchical complexity; and even in an
254 egalitarian transition, where the hierarchical approach is most natural, it remains true that without a direct
255 selective advantage to each of the (unrelated) lower-level replicators, they would never have voluntarily
256 entered into a group-living arrangement in the first place. Thus elements of both explanatory frameworks,
257 genic and hierarchical, do seem applicable to all METSs.

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

268   However, some care is needed here. It is true that there is a *formal* equivalence between inclusive fitness
269 and multi-level selection, in the sense that in *some* models for the evolution of a pro-social behaviour, it
270 is possible do the evolutionary analysis in either multi-level terms, by partitioning fitness variation into
271 within-group and between-group components, or in inclusive fitness terms, by partitioning fitness into
272 direct and indirect components. However it is unclear whether this is true of all models, in part because the
273 equivalence results rely on approximations including weak selection (Lehmann and Rousset, 2014); and
274 in part because the multi-level analysis presupposes the existence of group structure while the inclusive
275 fitness analysis does not (Birch and Okasha, 2015). Moreover, formal equivalence is not the same as
276 causal-explanatory equivalence (Okasha 2015). For the aim of evolutionary analysis is not simply to predict
277 the outcome of evolution, or to compute a correct expression for allele frequency change, but rather to
278 produce causal explanations. One of two "formally equivalent" approaches may yield a better causal
279 representation of the evolutionary processes at work in a particular biological system. So it would be
280 overhasty to conclude, from the formal equivalence results alone, that inclusive fitness and multi-level
281 selection are necessarily equivalent in respect of their causal adequacy; and by the same token, we cannot
282 conclude that genic and hierarchical approaches to the METs are always of equal explanatory power. The
283 equivalence thesis, therefore, does not discriminate between the two ways of reconciling the genic and
284 hierarchical approaches.

285   To conclude, Queller's idea that the genic and hierarchical approaches both have something to contribute
286 to the study of METs is correct. But there is more than one way of trying to effect a reconciliation between

287 the two approaches. It may yet turn out that the genic approach is better suited to studying some METs
288 while the hierarchical approach to others; alternatively, it may turn out that any MET can be fruitfully
289 studied using either approach.

290 ## 2.5 METs and the levels of selection

291   It is interesting to consider how the study of METs relates to the traditional "levels of selection" (or
292 "units of selection") discussion in evolutionary biology. The latter discussion traces to Darwin (1859) and
293 achieved prominence in the second half of the 20th century though works by Williams (1966), Lewontin
294 (1970), Hamilton (1975) and Dawkins (1976, 1982), among others; it thus pre-dates the contemporary
295 work on METs. Yet clearly there is a conceptual connection between METs and levels of selection. For
296 in an MET, formerly free-living individuals become integrated into a larger unit; so there is the potential
297 for natural selection to act at two different levels (Okasha, 2005; Wilson, 2010). As Buss (1987) first
298 emphasized, for an evolutionary transition to be successful, it is necessary for higher-level selection to
299 "trump" lower-level selection; typically this requires the evolution of mechanisms, such as policing, to
300 regulate the selfish tendencies of the lower-level units and / or to align their evolutionary interests. Thus it
301 is unsurprising to find that many themes from the traditional levels of selection discussion, such as altruism
302 versus selfishness, individual versus group interests, and the importance of genetic relatedness, re-appear in
303 the literature on METs.

304   In some ways, the MET research program has breathed new life into the levels of selection discussion.
305 Some biologists have wanted to dismiss the traditional levels discussion as a storm in a teacup, arguing
306 that in practice, individual selection is all that really matters in biology, whatever about other theoretical
307 possibilities. (Thus for example, Waddington (1975) described the debate over group selection as "a rather
308 foolish controversy".) Others have dismissed the debate as largely semantic. But in the light of the METs,
309 these dismissive attitudes are hard to defend, for two reasons. Firstly, group selection appears implicated
310 in many if not most of the METs (though a kin selection / inclusive fitness perspective may be equally
311 valid in some of these cases, as discussed above). Given that METs clearly have occurred, the evolutionary
312 importance of group (or multi-level) selection can hardly be denied. Secondly and more importantly, the
313 METs remind us that even paradigm biological individuals can be regarded as groups or collectives, once
314 we take a sufficient long time-horizon. Multicelled organisms and eukaryotic cells, for example, are both
315 collective entities that evolved out of smaller free-living biological units. Thus once we adopt the expanded
316 evolutionary perspective that is necessary to understand the METs, the view that "individual selection is all
317 that matters in practice" clearly cannot be sustained; and indeed the very notion of an "individual" is called
318 into question.

319   Despite their conceptual kinship, there is one important difference between the study of METs and
320 the traditional levels of selection debate. The latter debate dealt with selection and adaptation at *pre-*
321 *existing* hierarchical levels, and largely set aside the question of the origin of the biological hierarchy itself
322 (Griesemer 1998, Okasha 2005). Thus consider for example how Lewontin (1970) formulated the "units
323 of selection" question in his highly influential paper. Lewontin began by observing that there are three
324 essential requirements for the process of evolution by natural selection: variation, associated differences
325 in fitness, and heredity. He then observed that in principle, biological units at various hierarchical levels,
326 above and below that of the individual organism, could satisfy these three requirements. Thus for Lewontin,
327 the "units of selection" question stemmed from two factors: (i) the abstract nature of the fundamental
328 Darwinian requirements; and (ii) the fact that biological units form a nested hierarchy. There is nothing
329 wrong with Lewontin's formulation per se, but it is incomplete in one important respect. For clearly,

330 hierarchical organization is not simply a brute fact about the living world: the earliest life-forms were
331 not hierarchically complex. Thus there must be an evolutionary story to be told about how the biological
332 hierarchy evolved in the first place; and the METs form a key part of that story.

333   This implies that the link between METs and the traditional levels of selection issue is more complex
334 than it seems; it is not just a case of themes from one discussion re-appearing in the other. One useful way
335 to look at it is the following. In the traditional levels discussion, hierarchical organization is treated as
336 "exogenous", something that is part of the assumed background against which evolutionary explanations
337 are constructed but does not receive any explanation itself (Okasha 2019). In the literature on METs, by
338 contrast, hierarchical organization is "endogenized", since the aim is precisely to offer an evolutionary
339 account of how biological units came to form a nested hierarchy in the first place. In philosophical terms,
340 hierarchical organization thus moves from being part of the *explanans* to being part of the *explanandum*.
341 Looked at this way, we have an instance of a common pattern in evolutionary biology, in which features
342 that were once part of the assumed biological background against which evolutionary explanations take
343 place (e.g. sexual reproduction, gamete dimorphism, fair meiosis) are progressively endogenized as the
344 science advances, leading to an increase in theoretical generality (Okasha 2019).

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

3 ONTOLOGICAL ISSUES

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

3.1 Hierarchical organization

369   It is a commonplace that the entities studied in biology vary greatly in size, from biomolecules at one
370 extreme to ecosystems at the other, and that these entities form a hierarchy of sorts, with larger ones

371   composed of smaller ones. This observation long predates the MET research program, of course. Though
372   there have been attempts to theorize systematically about hierarchical organization (e.g. Salthe 1985,
373   2002), most descriptions of the biological hierarchy are fairly casual. A typical description is: "gene–
374   chromosome–cell–tissue–organ–organelle–multicelled organism–kin group–colony–ecosystem." Clearly
375   there is something right about this description, but it raises a number of awkward questions. What is the
376   criterion for being a level in this hierarchy? Where do species and clades fit in? Is there a unique biological
377   relation that relates entities at adjacent levels (e.g. gene to chromosome, and organism to kin group)? Is
378   it a problem that some entities in the above list (e.g. organisms) are functionally organized but others
379   (e.g. ecosystems) are not? Should we think of the hierarchy as one of (what philosophers call) part-whole
380   inclusion? (That is, do the larger entities contain the smaller ones as their "parts" in the same way that
381   other macroscopic objects, e.g. cars, contain parts)? Do all biological entities belong to a single hierarchy?

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

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

410   The point that the METs account for some but not all of the part-whole structure in the living world,
411   combined with Eldredge's distinction, helps us towards a better understanding of, and a more principled
412   way of describing, hierarchical organization in biology. It does not resolve all the questions though. One
413   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 favoured 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" (Okasha 2021); 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.

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

3.3   METs and Part-whole structure

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

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

491   How should we resolve this issue? There are three possible options. The first is to simply reject the
492   exclusion principle, i.e. to claim that some *bona fide* organisms do contain other organisms as parts, even if
493   most do not. I see no decisive objection to this; though it is interesting to note that according to a venerable
494   philosophical tradition, there is an important sub-category of natural kind terms, known as *sortals* or
495   *substance sortals*, that are thought to satisfy the part-whole exclusion principle (Grandy and Freund 2021).
496   (The sortal to which an entity belongs is to meant to to tell us the "fundamental sort" of thing it is, and to
497   settle questions about the entity's identity and persistence over time.) If the term "organism" in evolutionary
498   biology violates that principle, despite functioning much like a sortal term in other respects, this would
499   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 grey 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 that 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 versus selfish behaviour, 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 practising biologist, it may not be obvious why philosophers think they have something to contribute to this area. The aim of this paper 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.

CONFLICT OF INTEREST STATEMENT

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