

## Major Problems in Evolutionary Transitions: How a Metabolic Perspective Can Enrich our Understanding of Macroevolution

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### Abstract

The model of major transitions in evolution (MTE) devised by Maynard Smith and Szathmáry has exerted tremendous influence over evolutionary theorists. Although MTE has been criticized for inconsistently combining different types of event, its ongoing appeal lies in depicting hierarchical increases in complexity by means of evolutionary transitions in individuality (ETIs). In this paper, we consider the implications of major evolutionary events overlooked by MTE and its ETI-oriented successors, specifically the biological oxygenation of Earth, and the acquisitions of mitochondria and plastids. By reflecting on these missed events, we reveal a central philosophical disagreement over the explanatory goals of major transitions theory that has yet to be made explicit in the literature. We go on to argue that this philosophical disagreement is only reinforced by Szathmáry's recent revisions of MTE in the form of MTE 2.0. This finding motivates us to propose an alternative explanatory strategy: specifically, an interactionist metabolic perspective on major transitions. A metabolic framework not only avoids many of the criticisms that beset classic and revised MTE models, but also accommodates missing events and provides crucial explanatory components for standard major transitions. Although we do not provide a full-blown alternative theory and do not claim to achieve unity, we explain why foregrounding metabolism is crucial for any attempt to capture the major turning points in evolution, and why it does not lead to unmanageable pluralism.

### Introduction

The history of life on Earth presents as a series of historically contingent events with unpredictable consequences. However, we can attempt to explain the large-scale trajectories of life by targeting major turning points in evolution and connecting them all by a common theoretical thread. The most widely subscribed contemporary model of major events in evolution was devised by John Maynard Smith and Eörs Szathmáry (1997; Szathmáry and Maynard Smith 1995). They called it 'major transitions in evolution' (MTE) and believed it to explain the origins of apparent hierarchy in the organization of life-forms. Szathmáry's recent overhaul of the classic model in the form of MTE 2.0 (Szathmáry 2015) has set the stage for a timely re-examination of the philosophical foundations of MTE theory.

In this paper, we outline MTE, discuss some of its most significant theoretical and empirical criticisms, and consider whether revised MTE models that focus on evolutionary

transitions in individuality (ETIs) have succeeded in evading these criticisms. We then examine the implications of major events that are missed by MTE and its ETI-oriented successor theories—particularly the biological oxygenation of Earth, and the acquisitions of mitochondria and plastids. These events, we argue, are not easy to exclude from any account of major transitions, including those focused on ETIs. By reflecting on these missed events, we reveal a basic philosophical disagreement over the explanatory goals of major transitions theory. This philosophical disagreement has yet to be made explicit in the literature and is not addressed in Szathmáry's recent revision of classic MTE. Identifying this underlying tension helps make sense of the very different approaches to MTE that have emerged since the classic model was introduced. We argue that not only is MTE in both its classic and revised forms incomplete, but that it represents a fundamentally problematic approach to major transitions.

This analysis, in turn, motivates our alternative perspective on major transitions—one that focuses on neither replication nor increasing hierarchical complexity (as MTE does), but rather on metabolism and the intra- and intercellular interactions it entails. Although we do not provide a full-blown theoretical alternative, we do show that when metabolism as an interactive force is afforded a more central place in philosophical and scientific theorizing about major transitions, many of the problems that beset MTE are diminished. We conclude that even though a metabolic perspective will *not* in fact deliver a unified model of major transitions, it nevertheless succeeds in directing philosophical attention toward crucial neglected events and the explanatory strategies necessary to construct a broad-scale picture of major turning points in life's history.

## 1. Major Transitions in Evolution: MTE 1.0

MTE is a descriptive and explanatory account of changes in the informational and organizational forms of life across evolutionary history. The model's primary thesis is that major transitions in biological organization are effected by changes in modes of replication and inheritance, particularly changes in the ways in which genetic information is organized. Furthermore, it argues that 'the transitions must be explained in terms of immediate selective advantage to individual replicators' (Szathmáry and Maynard Smith 1995: 227). Maynard Smith and Szathmáry are particularly focused on explaining why natural selection operating on lower-level units did not prevent the formation or cause the decomposition of higher-level units (1997: 7).<sup>1</sup>

The first four events in MTE concern unicellular life and its pre-cellular origins (see Table 1). The model begins with the compartmentalization of replicating molecules, which refers to the RNA-world hypothesis and its 'replicator first' account of the origins of life. This primordial event is followed by transitions within the compartment to cooperating chromosomes, and then a division of labour between replicating and protein molecules so that the former now code for the latter. Prior to this event, RNA performed both roles of replicator and enzyme. These three transitions configure the original cell, which is recognizably prokaryotic. The eukaryote cell – the second major cell type, with distinct compartments for different functions – emerges more than a billion years afterwards. The other half of the eight transitions all concern much later evolutionary features of multicellular organisms: obligate reciprocal sexuality (not just occasional sex, as in many unicellular eukaryotic groups, or one-way 'sex' as in prokaryotes), cellular differentiation in

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<sup>1</sup> We agree with one of our referees that much evolution, especially but not only at the molecular and biochemical level, is non-adaptive. However, given the selectionist cast of MTE, our current paper will address only selection-driven aspects of major turning points.

multicellular organisms, social groups of multicellular organisms, and finally, human communication. A ninth transition is supposedly underway to a society that stores and transmits information electronically (Maynard Smith and Szathmáry 1997: 309), but this event (shown in broken border in Table 1) is not part of the classic eight-level model.

**Table One:** MTE's Major Transitions

<b>Transition</b>	<b>Original state</b>	<b>New state</b>
<b>One:</b> Origin of life	Uncontained replicating molecules	Groups of molecules in compartments
<b>Two:</b> Origin of chromosomes	Independent replicators within compartments	Cooperatively replicating replicators
<b>Three:</b> Origin of the genetic code	RNA functioning as both replicator and enzyme	DNA as the informational molecule coding for proteins
<b>Four:</b> Origin of eukaryotes	Prokaryotic cell ('limited complexity')	Eukaryotic cell ('increased complexity')
<b>Five:</b> Origin of obligate sexuality	Asexual or facultatively sexual microbes	Obligately sexual organisms (probably multicellular)
<b>Six:</b> Origin of multicellularity	Unicellular or facultatively multicellular organisms	Obligately multicellular organisms with developmental cell differentiation
<b>Seven:</b> Origin of obligately social groups	Individual multicellular organisms	Obligately social organisms with developmental and cultural differentiation of organisms
<b>Eight:</b> Origin of language	Primates and early humans communicating with protolanguage	Humans using symbolic verbal language with true grammar and unlimited representative capacity
<b>Nine:</b> Origin of electronic cultural transmission	Cultural transmission of information in oral and written forms	Cultural transmission of information in electronic forms

Each transition in MTE is meant to exhibit a change from autonomous replication to some form of cooperative group replication. The loss of reproductive independence is the primary defining criterion for major transitions. There are also vague commitments to increased division of labour (1997: 210) and new modes of inheritance. But what most philosophical and theoretical biologists pay attention to in MTE is the emergence of new units of selection – the transitions in individuality that occur when one level of individuality gives way to another (Calcott and Sterelny 2011a).

## 2. General Criticisms of MTE

Despite its widespread influence in the macroevolutionary literature, MTE is known to have serious problems. Some of these problems are general and theoretical, having to do with the lack of unity amongst events included in MTE, and the model's propensity to encourage a fallacious 'ladder-of-life' or otherwise progressivist view of evolutionary history. Other problems are more specific and empirical, having to do with missing events. Although we will focus on the latter, we will show in novel ways how these missing events reinforce the

more general problems with MTE that have already been identified. Additionally, we will explain why recent ETI-based attempts to improve the model, though making significant advances over the original, have conceptual and methodological limitations preventing a full account of major shifts in the history of life. Szathmáry (2015) himself has recognized this shortfall, and has recently crafted a revised version of MTE, which he labels '2.0' (Table 2). We will discuss this revisionary effort as well, and show how it too is encumbered by a set of problems very similar to those of MTE 1.0 and subsequent ETI-oriented revisions.

### ***Disunity***

Szathmáry and Maynard Smith recognized that their initial model did not theoretically unify the diverse events it included. They believed, however, that increasing knowledge would reveal each stage to be of the same kind. In their view, 'There is sufficient formal similarity between the various transitions to hold out the hope that progress in understanding any one of them will help illuminate the others' (Szathmáry and Maynard Smith 1995: 23). But as closer scientific and philosophical attention has been paid to each transition in the original model, fundamental differences between each event have become more salient.<sup>2</sup>

As several critics have pointed out, some of the transitions require alternative justifications for their inclusion. The transition to human society and language (Transition 8) is one of the most problematic, since human societies are not clear units of selection in their own right, let alone units of selection that represent a different stage of hierarchy than other evolved social groupings. The division of labour between genes and proteins (Transition 3) and the switch to obligate sexuality (Transition 5) also require additional, theoretically disparate justifications for their inclusion, because they too are not obviously transitions in individuality. As Daniel McShea and Carl Simpson lament,

We cannot find any theoretical unity in the Maynard Smith and Szathmáry history of major transitions...One could argue that theoretical unity is not their goal ... But then what is the point of collecting these transitions together? Can it be just their importance as milestones on the road to us? (McShea and Simpson 2011: 31)

McShea and Simpson conclude, and numerous commentators agree (e.g., Ågren 2014), that the events carved out by MTE are a hodgepodge of 'miscellaneous transitions with no obvious unity beyond their salience for us' (2011: 31).

Beyond the diversity of transitional episodes in MTE is the additional problem that it lumps historically contingent events with trends that are likely to occur across alternative plays of the 'tape of life', and from which law-like macroevolutionary generalizations may be inferred. For instance, the emergences of language and information technological culture (Transitions 8 and 9, respectively) look to be non-replicable, one-off events—in contrast, say, to the transitions from unicellular eukaryotes to multicellular eukaryotes, and from the latter to eusocial colonies of multicellular organisms (Transitions 6 and 7). These hierarchical transitions appear to be evolutionarily robust outcomes given their independent origins in disparate phylogenetic groups, and can be read as part of a trend in the history of life toward increasing maximum hierarchy (Knoll and Bambach 2000; McShea 2001). Including both historically contingent events and robust trends in the MTE list further undermines its theoretical unity, because these different types of outcome necessitate different explanatory strategies (Powell 2009). Explanations of contingent turning points in the history of life advert to improbable events that are unlikely to be repeated in alternative life histories, whereas explanations of robust trends refer to law-like regularities that yield counterfactually stable patterns in macroevolution. Crucially, evolutionary contingency underwrites a pluralism of processes and mechanisms that precludes theoretical unification (Beatty 1995),

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<sup>2</sup> In addition, although MTE treated its core concepts – such as genetic information, individuality and hierarchy – as unproblematic, subsequent philosophical analyses have raised significant complications with them.

and perhaps even what we might call 'manageable' forms of pluralism (see concluding Section).

To avoid ontological and theoretical disunity, many evolutionary theorists discard the inconsistencies and contingent outlier events in MTE to home in on those that represent incontestable ETIs. Richard Michod, for example, sees transitions in individuality as crucial to understanding the history of evolution on this planet:

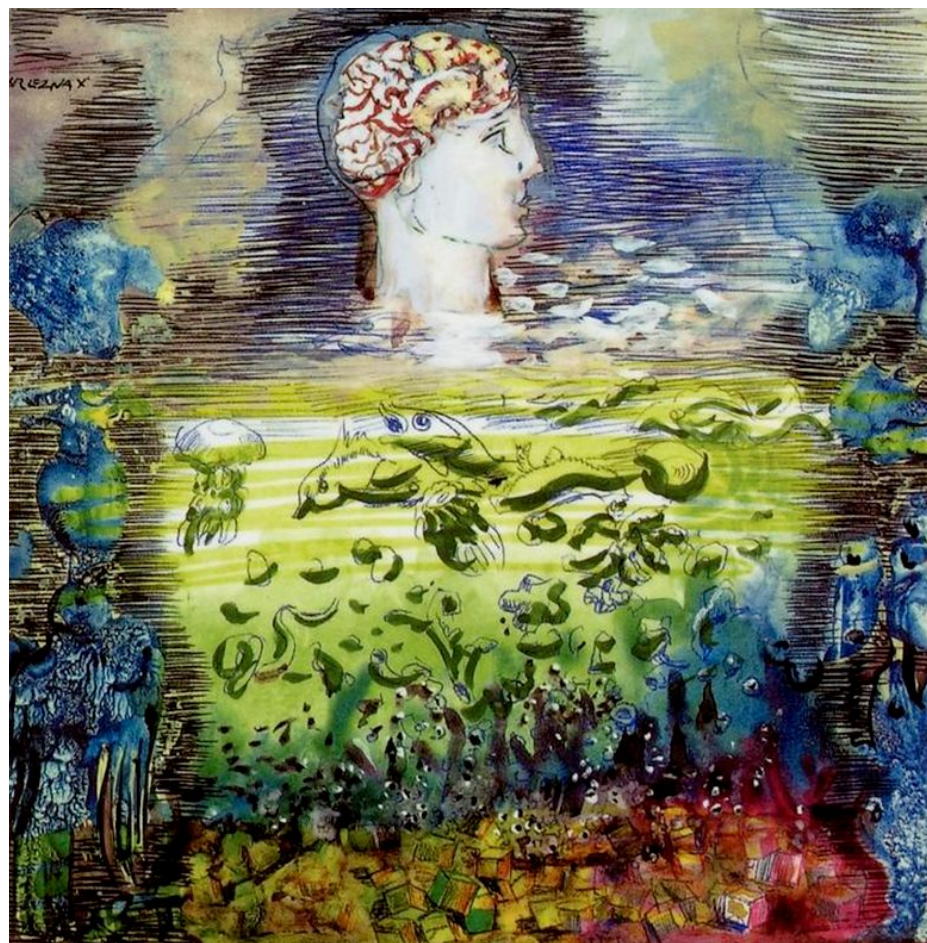
The major landmarks in the divergence of life and the hierarchical organization of the living world are consequences of a series of ETIs: from genes to gene networks to the first cell, from prokaryote to eukaryote cells, from cells to multicellular organisms, from asexual to sexual populations, and from solitary to social organisms. (Michod 2005: 967)

On this view, major transitions are explained by selection favouring increases in hierarchical complexity despite fitness conflicts between levels of selection (Grosberg and Strathmann 2007). Accordingly, the goal of MTE is to provide a Darwinian explanatory framework that can account for each transition in individuality, thereby explaining how biological hierarchy evolved despite evolutionary tensions between levels (e.g., Okasha 2005; Bourke 2011). Some theorists have argued that the replication conflicts associated with major transitions necessarily had non-selective origins (Brandon and Fleming 2015), even if the solutions to those conflicts were shaped and maintained by selection; yet even such non-selective accounts have assumed that ETIs are the key explananda. By focusing on ETIs, incongruous events can be removed from the MTE model. However, this leaves another general problem that McShea and Simpson point to: namely, that certain transitions are chosen merely because they are 'milestones on the road to us,' or to complex multicellular life more broadly.

### *Ascent Interpretation*

Because MTE traces a series of evolutionary stages that culminate, both temporally and hierarchically, in uniquely human capacities, 'ascent' interpretations of the model are virtually inevitable. Although earlier transitions in hierarchy have a broader phylogenetic distribution, the final transitions (Transition 8, and potential Transition 9) occur only at the human 'apex' of complexity. According to Maynard Smith (1988: 229), 'human society is the final level of complexity so far achieved by living organisms.' This is very clear when represented visually. The image on the cover of the 1997 edition of MTE (Figure 1) needs only an explicit ladder to match the iconography of 'Great Chain of Being' (*scala naturae*) conceptions of 'evolution', which were popular well into the nineteenth century for their depictions of evolution proceeding in a progressive, ladder-like fashion from monad to man. Although hierarchical theories of nature based on the perfection of organic form are seldom subscribed to nowadays, theories of progressive evolution grounded in increasing complexification are still widely embraced (Ruse 1996). MTE is just one prominent example of efforts to discern and explain a progressive signal in the history of life.

**Figure One:** The cover to *Major Transitions in Evolution* (1997). Increasing complexity and size over evolutionary time are read from the bottom of the image to the top. Image courtesy of Oxford University Press.



To be clear, Maynard Smith and Szathmáry do not argue for an ascent interpretation of evolution. In a section titled ‘The Fallacy of Progress’, they offer both empirical and theoretical reasons ‘for rejecting a *simple image* of progress on a linear scale’ (1997: 4 – emphasis added). They reject the notion that selection has a ‘built-in’ tendency toward complexification, and they point out that life is a branching tree, not a ladder of progress.<sup>3</sup> Yet, as Stephen Jay Gould (2002: 373-374) remarks in a different context, ‘iconography often provides a powerful guide to conceptual frameworks because pictures frequently make explicit what our psyches fail to acknowledge in the verbal mode.’ The key explananda chosen by Maynard Smith and Szathmáry end up forming a progressive model because all early events build up to complex multicellularity and, ultimately, to uniquely human evolutionary achievements.

It is one thing to say that human complexity is a legitimate explanatory target for scientists and philosophers. It is much more questionable and anthropocentrically ad hoc to structure a *general* account of evolutionary history such that humans emerge as the most ‘evolutionarily advanced’ species or at the pinnacle of a complexification trend, on the basis of loosely defined notions of complexity and information. Part of the problem stems from difficulties defining and operationalizing the underspecified notion of complexity both in general (McShea 1991) and as it relates to human traits (McShea and Simpson 2011). A less widely appreciated problem arises from focusing almost exclusively on certain types of complexity—in particular, on structural complexity in genomes, morphology, and behavior—

<sup>3</sup> However, see Sigmund and Szathmáry (1998: 439) for what appears to be an endorsement of “‘progress’...as a series of major transitions in evolution’; note also that MTE 2.0 still culminates in human language and society.

which appear to license narratives of onward and upward trajectories even if obvious outliers (like human capacities) are removed. While certainly of biological interest, none of these classic loci of complexity is necessarily the best or only basis from which to assess major evolutionary events or shifts in the organization of life. Below we will not only suggest an antidote to tendencies to construct misleading narratives of increasing complexity, but also propose an approach to major evolutionary transitions that is not about hierarchies of complexity at all.

### 3. Missing Events

These general problems with MTE – that it carves out a theoretically disunified list of events, with items selected because they represent stages on the way to human consciousness, language and society – could be partly sorted out by retaining only items that fit a strict notion of ETIs. This has proved the most attractive option for many evolutionary theorists (e.g., Michod 2005; Okasha 2005; Bourke 2011). A much stronger case can be made that ETI-based models are ontologically unified (but see below), and because ETIs are broadly phylogenetically distributed, such accounts are less susceptible to ‘ascent’ interpretations. The trouble, however, is that such a selective purging of the MTE list, if intended to salvage a theory of major transitions, still leaves a third major problem that has seldom been reflected on by MTE critics: namely, two kinds of missing events: (1) missing events that do not fit the ETI criterion, but which are so transformative from a macroevolutionary perspective that they must be included, and (2) missing events that fit the ETI criterion, but which nevertheless have been excluded from MTE. There are many events of these two types that could be considered, but we will focus on the oxygenation of the Earth, the acquisition of the mitochondrion, and the serial acquisitions of plastids. Our analysis of these missing events is not simply for the purpose of complaining about their absence. Reflections on these missing events compel us to reassess the philosophical goals of major transitions theory and to propose an alternative perspective on major transitions.

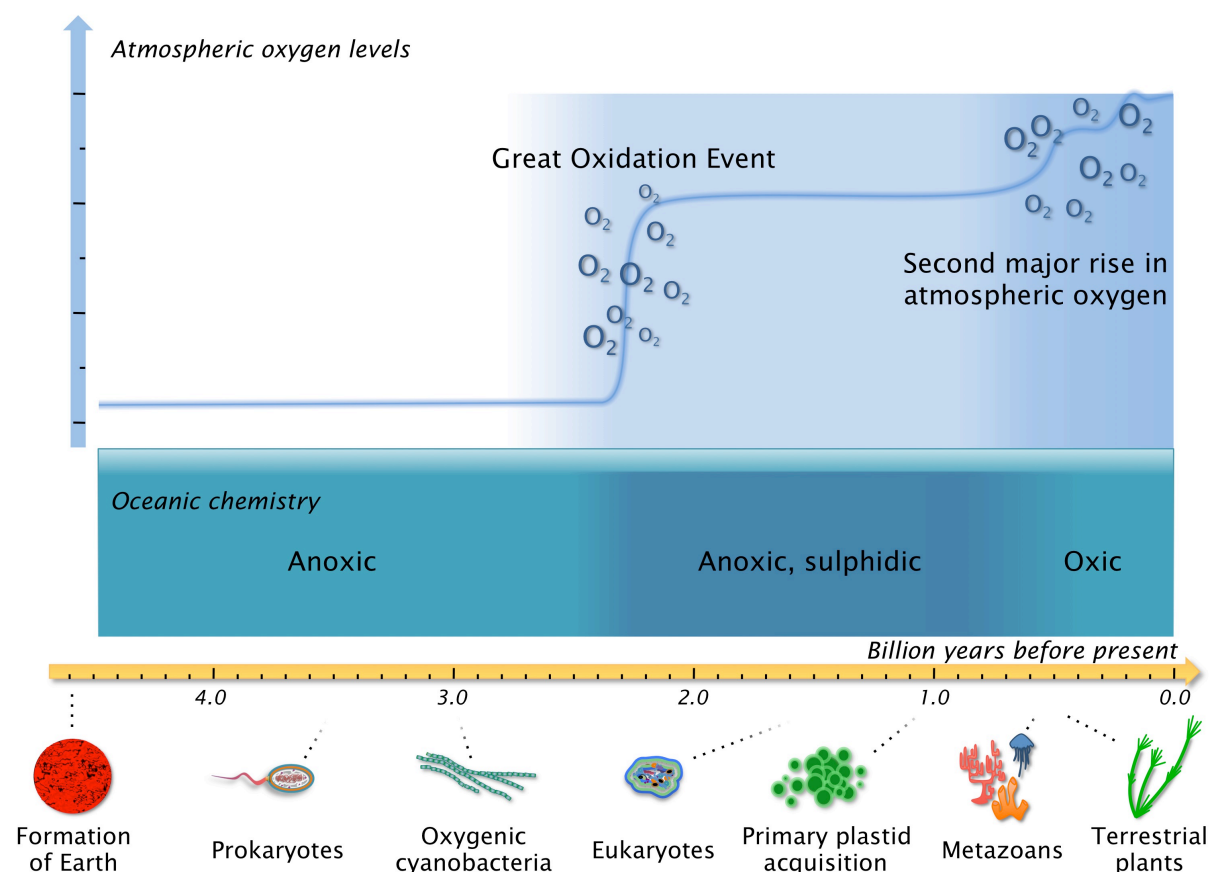
#### *Oxygenation of the Earth*

The evolution of oxygenic (oxygen-producing) photosynthesis brought about major changes to the evolution of life, and yet barely gains a mention even as background within MTE. Phototrophy refers to the use of light to generate energy biologically; photoautotrophy is when this process co-occurs with carbon fixation. The latter is often called ‘primary production’ because it is the basis of all the nutrient chains that rely on the initial production of organic carbon. A specialized and highly skilled form of phototrophy is called ‘photosynthesis’, which only in some photosynthesizing organisms produces oxygen (Bryant and Frigaard 2006). While many eukaryotic oxygenic photosynthesizers are known today (e.g., plants, algae, various other unicellular eukaryotes), the ancestry of their photosynthetic machinery can be traced back to ancient cyanobacteria possibly as long as 3.0 billion years ago (Crowe et al. 2013). Oxygen is the waste product produced by these photosynthesizers, which evolved a beautifully complex system of photoresponse and electron transport to oxidize water and fix carbon. The original oxygenic photosynthesizers, cyanobacteria, are abundantly extant today in diverse forms.

Oxygenic photosynthesis only became possible via the combination of the two separate photosystems that had enabled anoxygenic photosynthesis, which had been around since nearly the beginning of life on Earth (Hohmann-Marriott and Blankenship 2011). There are different evolutionary explanations of how the two photosystems combined to form one extended process that was able to split water (Knoll 2003; Allen and Martin 2007). But the

key point is that although this novel photosystem did not generate a new level of individuality, it transformed the entire biological world (Figure 2).

**Figure Two:** The rise of oxygen and the evolution of aerobic life. Oxygen levels are on a logarithmic scale. Timing for both oxygen levels and organismal origins is still undergoing revision, but each major rise in oxygen is correlated with the proliferation of new oxygenic photosynthesizers: cyanobacteria, and eukaryotes with primary plastids (algae, plants). Redrawn by Michel Durinx, with the top part based on Donaghue and Antcliffe (2010). Adapted with permission from Macmillan Publishers, *Nature*, © 2010.



Because oxygen was initially toxic for most existing organisms, oxygenic photosynthesis imposed powerful new selection pressures on nearly all of life on Earth. Some organisms developed more than the ability to tolerate free oxygen: they evolved aerobic respiration to take advantage of it. Metabolic productivity is typically significantly higher when oxygen is involved than it is in anaerobic regimes. By providing a powerful oxidant (oxygen), oxygenic photosynthesis changed the chemical environments available to life, and with them evolutionary possibility. Due to the rise of oxygen in the atmosphere and eventually oceans, cellular metabolic networks underwent enormous expansion, with hundreds of new reactions and metabolic pathways coming into existence (Raymond and Segrè 2006). The effects of cyanobacterial metabolism on the rest of life were massively amplified when recently evolved eukaryotic cells, already in possession of mitochondria, acquired cyanobacteria as photosynthesizing organelles. These photosynthesizing eukaryotes further transformed primary production both in the sea in the form of algae, and later, on land as plants. The additional ecological transformations wrought by plants are deemed by some theorists to be part of a major transition (e.g. Knoll and Bambach 2000). Increased oxygen



generated by all these new photosynthesizing organisms created new adaptive possibilities, including transitions to the more hierarchically complex forms of life to which MTE is particularly attuned. The origins of complex multicellular organisms coincide with this second global increase in biotic oxygen production (see Figure 2).

The biological conversion of an anoxic world into an oxic one constitutes a world-changing evolutionary transition that explains a great deal about life as we know it. According to some biogeochemists, '85% of Earth's and life's evolution has merely been an adjustment to more oxygen' (Buick 2008: 2741). Whether understood ecologically or evolutionarily, oxygenic photosynthesis 'might well be regarded as the central event in the history of life, because it liberated biology from hydrothermal vents and other [restricted] environments ... allowing organisms to spread across the planet.' (Knoll 2003: 4-5).

Surprisingly, oxygenic photosynthesis has not figured in the standard or revised ETI versions of MTE. One might object to its inclusion on the grounds that the great oxygenation event was simply an abiotic event that made certain biological MTEs possible. This objection is misguided. The evolution of oxygenic photosynthesis is not an abiotic event with biotic consequences: it is a biotic event with momentous biotic consequences. It fits any general criterion for being 'major' and it is as biological as any of the standard MTEs. Oxygenic photosynthesis is a biological innovation that altered in a sustained way the selective regimes and evolutionary trajectories of the main branches of the tree of life (Figure 2).

But the main reason that oxygenic photosynthesis has not been incorporated into MTE theory is, presumably, because it does not fit the ETI schema at the heart of the revised model, for it did not create a new level of individuality. We agree that if MTE in its classic form has anything going for it, it is this attention to transitions in individuality. However, we will show that other major events that *do* fit this central ETI rationale have been problematically excluded from MTE.

### ***Acquisition of the Mitochondrion and the Origin of Eukaryotes***

It may come as some surprise to learn that Maynard Smith and Szathmáry did not include the acquisition of the mitochondrion as anything major in their classic model, since many theorists see this event as a paradigm transition in individuality (Calcott and Sterelny 2011a)). The reason for this absence, however, is that MTE emphasizes the origin of eukaryotes (eukaryogenesis) by mutational processes, and not by cell merger – despite recognizing additions of once free-living organisms to the eukaryote cell.<sup>4</sup> Placing the explanatory emphasis on genomic replication, MTE maintains that the crucial difference between eukaryotes and prokaryotes is that the former can begin replicating their chromosomes at multiple places in the genome (1997: 7). So according to MTE, eukaryotes originated and were recognizably eukaryotic *prior* to the acquisition of the mitochondrion, which MTE conceives as an evolutionarily minor addition to an already major transition. This view contrasts with 'exogenous' theories of eukaryogenesis, according to which a prokaryotic cell (an archaeon) happened to engulf a bacterial cell and maintain it internally—an endosymbiotic event that preceded and stimulated all the subsequent architectural changes in eukaryote cells.<sup>5</sup> Yet by committing to a non-ETI-based hypothesis of eukaryogenesis, the theoretical thread connecting MTE events further unravels.

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<sup>4</sup> When Maynard Smith and Szathmáry visualize the differences between prokaryotes and eukaryotes, they deliberately omit the mitochondria (and other acquired organelles) because 'on the scenario that seems to us most plausible, these intracellular structures originated later in time than the [other distinctively eukaryotic] structures' (1997: 122). See our discussion below of Szathmáry's (2015) recent thoughts on this topic.

<sup>5</sup> For details of these competing hypotheses of eukaryote origins, see O'Malley (2010).

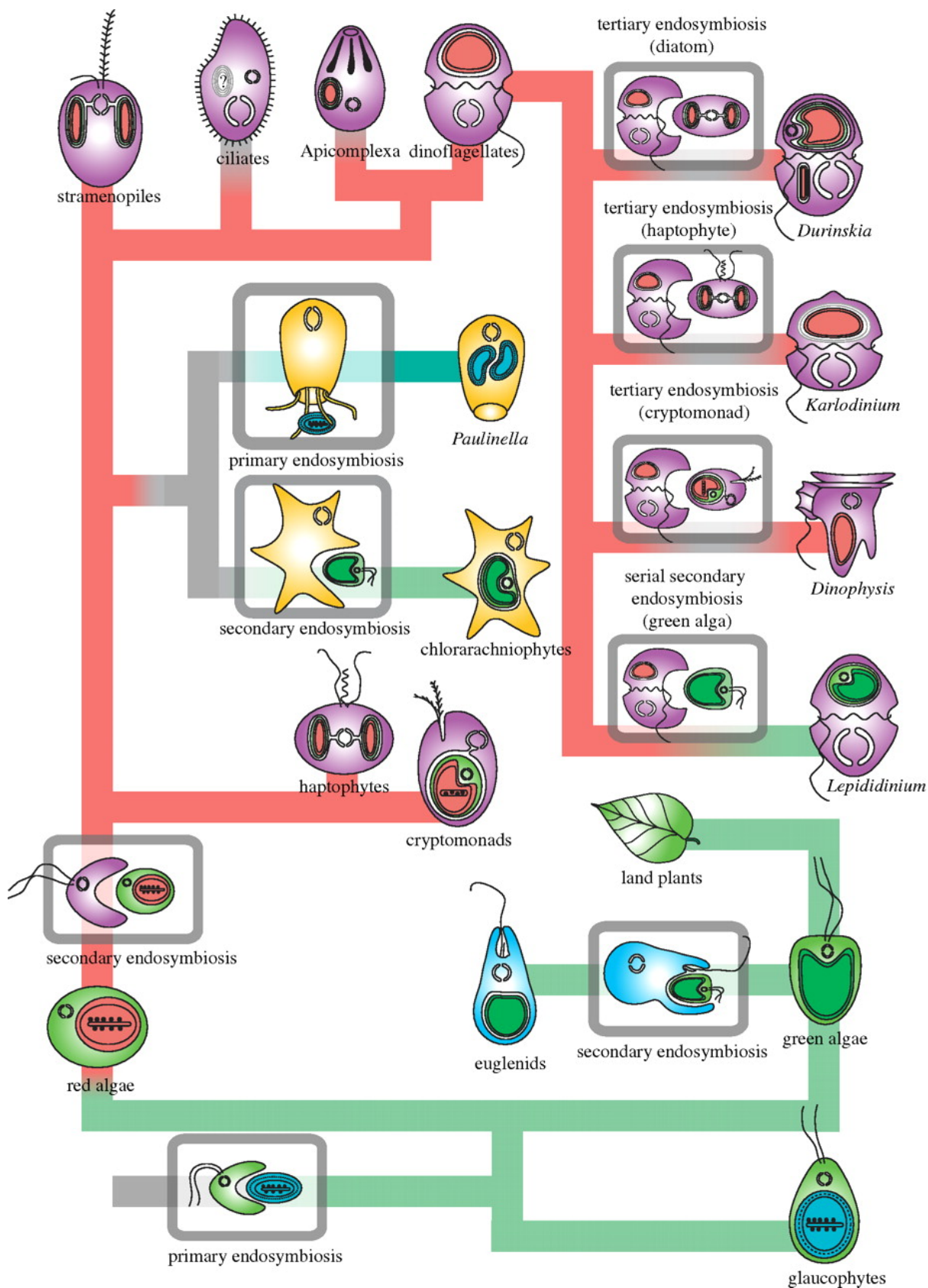
Despite Maynard Smith and Szathmáry side-lining the 'mitochondria-first' hypothesis, and Szathmáry (2015) continuing to be agnostic about it in MTE 2.0, many philosophers and theoretical biologists now discuss MTE as if eukaryogenesis were initiated exogenously by cell merger (e.g., Calcott and Sterelny 2011b; McShea and Simpson 2011; Queller 2000). The transition from prokaryote cell types to the eukaryote cell type is thus told today almost exclusively as a story of how two very different cells with separate evolutionary interests became one Darwinian individual. Certainly, if ETIs are the unifying criteria for MTE, and if the origin of eukaryotes is viewed as a major evolutionary transition, then this is the appropriate way to conceptualize eukaryogenesis.

However, even though MTE has been implicitly revised by ETI theorists to adopt the mitochondrion-driven version of eukaryogenesis, one would think that if ETIs were of such central theoretical importance to the revised model, then other evolutionarily significant events in which two organisms become one would loom large on the transitions-theoretic radar. But although major endosymbiotic events have occurred numerous times in evolutionary history and have had profound evolutionary and ecological consequences, they have garnered limited recognition by the majority of philosophers of biology and recent MTE theorists – at least in part because they did not feature in the original MTE list, which the revision process merely purged of non-ETI events.

### ***Plastid Acquisitions***

Plastids are eukaryotic organelles that are ancestrally cyanobacteria. The most well-known is the chloroplast, which is the photosynthesizing entity in the original cyanobacterial-eukaryote fusion. This fusion perfectly fits the criteria for a transition in individuality. The host was an ancestral eukaryote with a mitochondrion, a cytoskeleton and all the other eukaryotic accoutrements. Because of the eukaryotic cytoskeleton, this cell was able to ingest cells and other particles. One of these ingested cells was a photosynthesizing bacterium: the ancestral cyanobacterium already encountered in the discussion of photosynthesis. Once this acquisition occurred, over a billion years ago, eukaryote cells took up further endosymbioses in a phylogenetically impressive way (Figure 3). The primary plastid acquisition is rarely mentioned in MTE, and it is never discussed as a major transition; this is equally true of subsequent revisions that assume an ETI focus. Maynard Smith and Szathmáry seem to have believed that primary and secondary plastid endosymbioses had no theoretical importance, and this belief appears to have been shared by later ETI theorists. In MTE 2.0 however, plastid acquisition makes a surprise appearance (Szathmáry 2015; Table 2). Our analysis will first address reasons for including these endosymbioses, and second, discuss some problems with the way in which MTE 2.0 has included them.

**Figure Three:** Primary, secondary and tertiary plastid endosymbioses (Keeling 2010). Image used with permission from The Royal Society (London).



We think it is a matter of some importance that the primary plastid endosymbiosis was not ‘merely’ a transition in individuality. Just as significantly, it further transformed the biogeochemical world and the space of evolutionary possibility, because many of these new plastid-bearing organisms (the algae and then the plants) became major contributors to the

ongoing oxygen balance of our atmosphere today. This balance is significantly higher than when cyanobacteria were solely responsible for biogenic oxygen production (Figure 2). Rising oxygen levels due to the metabolic outputs of plastid endosymbioses ultimately enabled the radiation of morphologically, ecologically, and behaviourally complex animals in the Cambrian (Sperling et al. 2013). Endosymbioses proved so successful or at least causally feasible – depending on how adaptationist a story one tells – that some plastid-bearing eukaryotes did it again, and yet again (Figure 3; Keeling 2010; Archibald 2009).<sup>6</sup>

These events – primary, secondary and tertiary endosymbioses – are ETIs that feature a huge diversity of organisms and multiplicity of events, many of which had important evolutionary and biogeochemical consequences.<sup>7</sup> They involved not only algal and plant contributions to the Earth's increased oxygen levels (Figure 2), but also to carbon and nitrogen budgets in the ocean, on land and in the air. Why are they not major transitions in evolution? Even if MTE got it wrong, why haven't ETI revisionists 'corrected' the model as they appear to have done with the mitochondrion acquisition event? Szathmáry (2015: 5) has recently regretted the earlier exclusion of the primary plastid acquisition, and he believes it is now possible 'to justify the promotion of plastids to major transition rank'. We agree this inclusion is warranted. However, we do not think the way in which plastids are now accommodated resolves the problems that arise from relying solely on an ETI-based or information-based justification. In fact, further consideration of such acquisitions prompts a more thoroughgoing revision than even MTE 2.0 achieves.

#### **4. From Transitions to Turning Points: MTE 2.0 and the Philosophical Foundations of MTE Theory**

So far we have shown how MTE is best understood as a scattershot selection of events that are neither the most major evolutionary events nor even all the major ETIs. What potential solutions are there? The revisionist approach, as we have noted, is to purge all inconsistent events from the list and retain only events that constitute 'genuine' ETIs. But this would mean including *all* known transitions in individuality, and it is not clear how 'major' some of these transitions are (e.g., tertiary plastids). Furthermore, if transitions in individuality are what drive up levels of hierarchical complexity, as the revisionist model supposes, then this might imply that tertiary plastid endosymbioses should be regarded as the 'culmination of evolution' – the utmost hierarchy of previously independent units of selection becoming integrated into a single unit. To make matters worse, some MTE reformers believe that every interspecific mutualism ('ecological fusions', in which evolutionary fates are entwined) would need to be included in a revised model consisting of ETIs alone (e.g., Kerr and Nahum 2011: 128-9), and (still worse) that ETIs must also include the myriad of events in which non-kin mobile genetic elements are integrated into genomes (e.g., Ågren 2014). Including these smaller events is clearly a mistake if 'major' transitions are being sought, even if the criteria for being 'major' remain rather fuzzy.

These problems indicate to us that whatever major transitions are, shifts in individuality cannot be the sole criterion for their designation. In response, one might hold that an evolutionary event is a major transition only if it implicates an ETI *and* has major evolutionary consequences. This approach would have the advantage of excluding less

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<sup>6</sup> Secondary and tertiary endosymbioses are events in which green and red algae acquire a second or even a third photosynthesizing organism (another alga) in addition to the one they already had, or after losing their original plastid (Figure 3).

<sup>7</sup> Plastid endosymbioses are still occurring, with a new primary plastid acquisition well underway in *Paulinella chromatophora* (Figure 3).

consequential ETIs, but also the disadvantage of missing profoundly significant evolutionary innovations that any account of major transitions would be hard-pressed to exclude, such as the evolution and proliferation of oxygenic photosynthesis.

Szathmáry's new scheme as presented in MTE 2.0 (Table 2) makes several important modifications to the list of major events. Of considerable significance are events that have been added, including the primary plastid acquisition; events that have been expanded upon, such as multicellularity, which now includes symbioses; and events that have been removed, most notably sex. Szathmáry now conceptualizes the primary plastid acquisition as an ETI that contributed to the increasing complexification of eukaryotes, and he also now pays more attention to the mitochondrion acquisition during eukaryogenesis (whether it happened earlier or later in the transition). Both of these revisions are justified by ETI explanations plus accompanying informational rationales (genomic restructuring, and the physical separation of transcription and translation that accompanied the emergence of the nucleus in eukaryotic cells).

**Table Two:** MTE 2.0 (our schematic rendering of Szathmáry 2015. See his Table 1 for details).

<b>MTE 1.0</b>	<b>MTE 2.0</b>
<b>One:</b> Origin of life	<b>One:</b> Origin of protocells
<b>Two:</b> Origin of chromosomes	
<b>Three:</b> Origin of the genetic code	<b>Two:</b> Origin of prokaryotic cells
<b>Four:</b> Origin of eukaryotes	<b>Three:</b> Origin of eukaryotic cells (mitochondrion acquisition as one contributor; sex now part of this transition)
<b>Five:</b> Origin of obligate sexual reproduction	<b>Four:</b> Plastid endosymbioses (recursive)
<b>Six:</b> Origin of multicellularity	<b>Five:</b> Origins of 'spectacular' multicellularity and multicellular symbioses (recursive)
<b>Seven:</b> Origin of obligately social groups	<b>Six:</b> Origins of animal eusociality (recursive)
<b>Eight:</b> Origin of language	<b>Seven:</b> Origin of language

Is there anything more to say about why major ETIs (such as the primary plastid acquisition) were excluded from MTE 1.0 and subsequent ETI-based revisions, and why they now appear in MTE 2.0? A closer look at these different treatments reveals a fundamental tension between two very different theoretical approaches to major transitions. We believe that the central reason why the primary plastid was excluded from MTE 1.0 and ETI revisions is that despite creating a new evolutionary individual with planet-wide consequences, the endosymbiotic acquisition of cellular organelles was thought to be 'already covered' by the acquisition of the mitochondrion (e.g., Bourke 2011). This earlier event had already brought about the transition to an obvious hierarchical level, namely the eukaryote

cell. The same logic explains the curious way in which multicellularity is treated in all versions of MTE: although the transition from single-celled eukaryotes to multicellular eukaryotes occurred numerous times in the history of life (e.g. in plants, animals, fungi and protists), 'the' transition to multicellularity is listed only once, and generically, in both classic and revised MTE models. Likewise, the transition from multicellular organisms to eusocial colonies, which also occurred several times, is treated in precisely the same generic fashion.

In MTE 2.0 Szathmáry introduces the notion of a 'recursive' transition possibly to capture this type-token relationship. By 'recursive' transitions, he seems to mean transitions that are of a generic type and recur in different forms—and thus have different token instantiations—at different periods in life's history. For instance, plastid acquisition appears to be treated as a generic event in MTE 2.0. Tertiary plastids and the ongoing primary plastid transition in *Paulinella* (see Figure 3) are categorized as 'limited' instances of the plastid transition because of how few lineages were affected by these particular events. The same is true of the numerous events Szathmáry groups in MTE 2.0 under 'the' transition to multicellularity, which now includes obligatory symbioses between organisms.

What these generic characterizations reveal is that MTE, as classically conceived, and as conceived by many theorists today, including MTE 2.0, is primarily concerned with identifying *types* of transitions, rather than singular transitions that had profound consequences for the evolution of life on earth but which are not tokens of natural kind-like transitions. Consequently, unique biological innovations that transformed the organization of life on Earth, such as oxygenic photosynthesis, are not included in standard and revised models. Likewise, on this type-oriented approach, including additional tokens of natural kind-like transitions, such as the primary plastid or other instances of transition 'recursion', would be superfluous once the relevant transition type (e.g. cell merger or multicellularity) has been identified. As we saw, although Szathmáry relents and includes plastids in MTE 2.0, secondary or tertiary plastid acquisitions (like other tokens of recursive transitions) are treated as recurrences of a type that happen to be limited in phylogenetic scope. One fallout of this natural kinds-like approach to major transitions is the linear, progressive-looking model that we see in MTE, ETI revisions and in MTE 2.0. 'Ascent' iconographies are an inevitable result of such type-oriented models, because they ignore or abstract away the broader phylogenetic base of ETIs. This is even more problematic for models that culminate in human culture and communication—a questionable transition that is retained in MTE 2.0.

We conceive of the MTE project very differently. In our view, the purpose of any account of major evolutionary transitions is to sketch an answer to the following Big Question: "How did the biological world get here from there?" We are not alone in holding this conception of the explanatory goals of major transitions theory. Calcott and Sterelny maintain that the goal of major transitions theory is to produce what they call a "Big Picture" of life's history (2011: 15). This view can also be attributed, albeit implicitly, to theorists who have been critical of the parochial focus of MTE (e.g. Gould 1997), to researchers who have offered alternative lists of events (e.g. Knoll and Bambach 2000), and perhaps even to one of the pioneers of classic MTE who prior to MTE 2.0 called for broader perspectives on major transitions (Lenton et al. 2004; Szathmáry and Fernando 2011).

We are suggesting that all the problems with MTE 1.0, ETI revisions, and MTE 2.0 indicate that the type-oriented approach is a profoundly mistaken way of approaching major events in the actual trajectory of life on Earth. Because the actual trajectory of life is sensitive only to events in the world, and because some of these events may not be instances (tokens) of natural kinds, the type approach runs into serious difficulties. These difficulties stem not only from theoretical disunity, but also—and more fundamentally—from giving up on the grander explanatory ambitions of major transitions theory. MTE in its revised and original forms carves out only one small slice of the Big Question (namely, hierarchy), and then

carves out only one part of an answer to that one small slice of that one Big Question. The result is an incomplete—and potentially misleading—picture of life's history.

A proponent of existing MTE approaches might respond that such highly idealized approaches are the key to successful science, particularly in relation to complex subject matters such as the history of life on Earth. Departing from a natural kinds-like account of major transitions, so this logic goes, would result in a haphazard and unscientific approach to macroevolution. But although we accept that a heavily idealized, natural kinds-like approach to major transitions can sometimes be desirable, we have shown above how it overlooks other equally important types of events that it should aim to explain, and will show below how the received view overlooks crucial explanatory components of the types of events that it does aim to explain. These limitations come about by presupposing that the formation of higher-level individuals with a single reproductive fate is the key explanandum in the history of life, and by assuming that the best way of understanding the emergence of these higher-level kinds is to explain how replication conflicts are solved.

We reject both of these assumptions. In what follows, we argue that both replication and metabolism are of fundamental explanatory importance. But in order to avoid a semantic turf war over the phrase 'major transitions', which has come to be strongly associated with a unity-seeking approach grounded in ETIs, we will rebill the broader range of explanatory targets of major transitions theory as 'major turning points'. We do not deny that the evolution of hierarchy is an important explanatory target. We do not deny that some ETIs are major turning points. However, if the aim of major transitions theory is to give an account of game-changing events that have shaped the large-scale organization of life on earth—that is, to sketch an answer to the Big Question—then we think the theoretical limitations of a strict ETI-based approach – or even a slightly more relaxed one such as MTE 2.0 – are too severe.

## 5. A Metabolism-Based Perspective

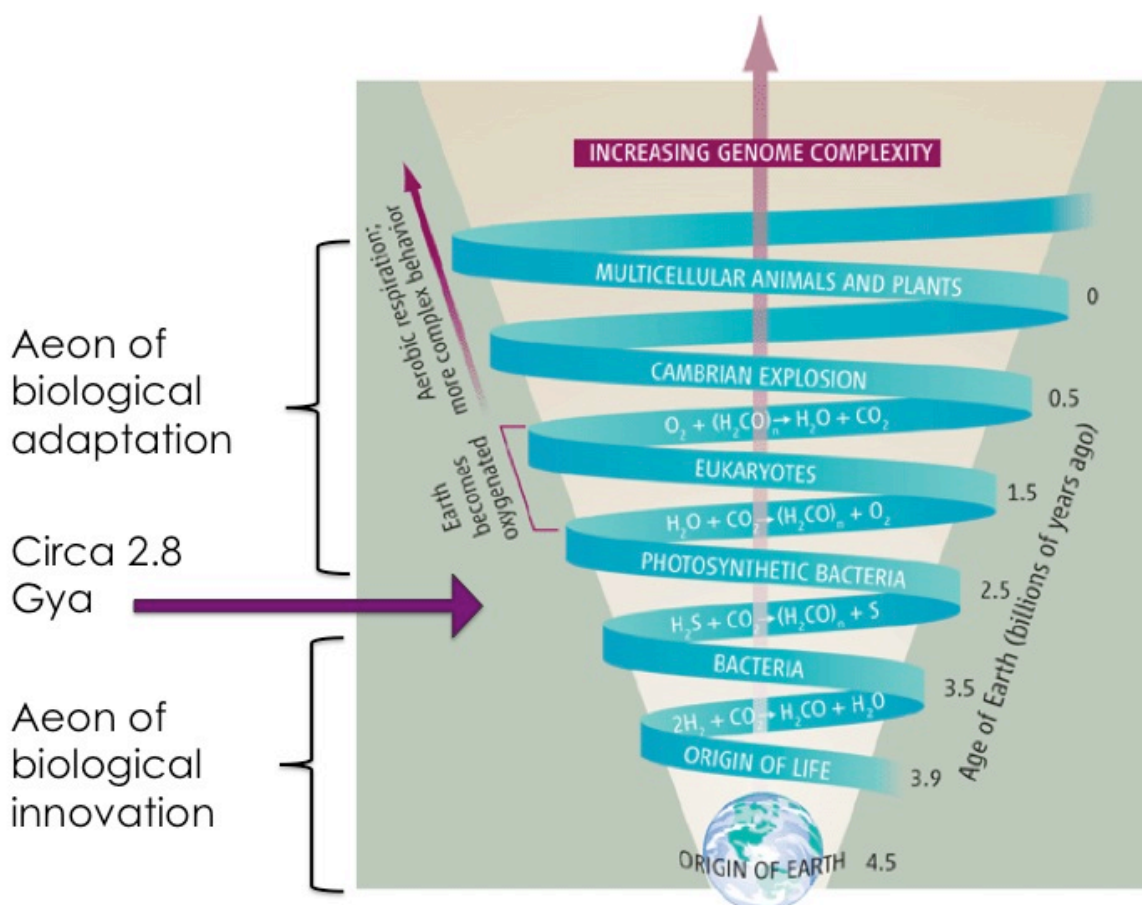
One way to overcome some of the major problems with MTE is to develop a supplementary perspective that is less hierarchical, less focused on multicellular events, less replication oriented, and in particular, more metabolic. Metabolism is the biologically structured conversion of energy and carbon, or, put another way, the cell's method for remaining stably out of electrochemical equilibrium (i.e., death). There is no life without metabolism. Although there are plenty of non-metabolizing replicating entities (e.g., viruses), all living cells rely on the production of the chemical adenosine triphosphate (ATP), which is the major energy currency of cells. To produce ATP, cells require chemical reactions and/or light to drive energy transfers, and membranes to allow the build-up and dissipation of electrochemical gradients. Thermodynamics constrains what biological energy choices are possible, in which conditions. But even so, biology works around less favourable thermodynamic potentials to create liveable situations out of low-energy environments and overcome thermodynamic barriers. Making a metabolic living occurs via photosynthesis and redox couplings. The latter are based on chemical interactions between reducing electron donors and oxidizing acceptors. Diverse pathways of reduction and oxidation have combined in individual microorganisms or groups of them to produce the biogeochemical cycles – such as oxygen, carbon and nitrogen – that maintain life on the planet (Falkowski and Godfrey 2008).

A metabolic perspective is thus a highly 'interactionist' approach, in the sense that it takes into account complex networks of energy exchange, from electron trades within and between cells right up to global geochemical interchanges. It is fairly common to claim that 'Earth's redox state is an emergent property of microbial life on a planetary scale' (Falkowski et al. 2008: 1034). The evolution of microbial metabolic capacities has influenced the

evolution of all life on Earth, and metabolic innovations are therefore good candidates for major evolutionary events in their own right, as well as for explaining key MTE transitions that have been given replication-based explanations.

A general interactionist metabolic perspective on evolutionary history can be seen in Figure Four. Marine biogeochemists Paul Falkowski and Linda Godfrey ([2008]) highlight just two major aeons of evolution (Figure 4). The first is the ‘aeon of biological innovation’, during which all existing electron transfer mechanisms and metabolic pathways coevolved and eventually combined to form the biogeochemical cycles that sustain life today. We might consider the evolution of each of these novel metabolic pathways to be a major turning point. The second era is an ‘aeon of biological adaptation’ in which those previously evolved metabolic pathways proliferated in diverse lineages and underwent adjustments to fit new morphologies, cell types, and environmental conditions. Although these innovations involve ‘mere’ modifications of existing biochemistry rather than the *de novo* metabolic innovations of the first aeon, many of them can still be considered major turning points because of how earlier metabolic capacities in this second aeon are transformed by cell-biological restructuring (e.g., the mitochondrion and the chloroplast). One significant theoretical upshot of this ‘two aeons’ approach to major transitions is that it implies that the vast majority of major evolutionary shifts occurred neither in animals, nor even in eukaryotes, as is often presupposed—but rather, in prokaryote modes of life.

**Figure Four:** Two major aeons of evolution (modified from Falkowski 2006). ‘Gya’ stands for ‘billion years ago’; the date for the origin of photosynthesis may need to be pushed back (see Crowe et al. 2013). Image reprinted with permission from AAAS.





Although we believe this bullet ultimately has to be bitten, once we begin to reflect further on some of this cell-biological structure, and particularly the membrane restructuring that occurred at various points in the history of life, a second, more specifically bioenergetic model of major metabolic turning points comes into view. This framework is vigorously argued for in the work of evolutionary biochemists and molecular biologists Nick Lane and William Martin. Starting with the origin of life and focusing on major diversifications in the subsequent 3.8 billion years, these theorists set out a bioenergetic perspective that is built on the necessity of chemiosmotic coupling for living systems (Lane et al. 2010; Lane and Martin 2012). Chemiosmotic coupling involves membranes separating high and low electrochemical potential. When protons (or sodium ions) from the high concentration translocate across the membrane, this drives ATP generation. As Lane remarks, 'the beauty of chemiosmotic coupling is that it transcends chemistry' (2014: 6) by 'tricking' it into allowing growth and reproduction. This trick occurs by subverting balanced chemistry with imbalanced proton gradients, which then power growth and other processes via ATP. Lane, Martin and similarly minded researchers focus on major bioenergetic transformations due to membrane upgrades at various turning points: minimally, the origin of life, the divergence of Bacteria and Archaea, the origin of eukaryotes, and the origin of eukaryotic photosynthesizers (Lane 2011). We will discuss each of these briefly as we expand below on the general implications of a broad metabolic view of major evolutionary turning points.

Whether general or more specifically bioenergetic, a metabolic perspective on evolutionary turning points makes explanatory contributions to classic and revisionist MTE theory. First, by focusing on the metabolic mechanisms that have driven the biogeochemistry of life on Earth, it includes key missing events in its ontology of major turning points, including the oxygenation of Earth, the mitochondrial-based origins of eukaryotes, and plastid acquisitions. The two main endosymbiotic events can not only be explained in metabolic terms—i.e., in terms of selection for metabolic functions, or the 'lateral' co-option and integration of existing metabolic innovations—but they also constitute major metabolic events in their own right. Characterizing these outcomes as major metabolic events, rather than as major ETIs with proximate metabolic explanations, helps underscore and make sense of their ramifications for the future history of life on earth. Metabolic approaches are more effective than replication-oriented accounts in explaining metabolically established endosymbioses. Genes, it could be argued, merely 'followed' these mergers.

A metabolic perspective also identifies other strong candidates that classic and revisionist MTE models overlook, such as the primeval evolutionary divergence of prokaryotes into the bacterial and archaeal domains (Sojo et al. 2014; Knoll and Bambach 2000). These groups are characterized by distinct varieties of membrane-based metabolic innovation that affect not only the organisms possessing the innovations, but also the energetic environments of many other lineages and thus the evolutionary pathways available to them. One could argue that this divergence is the most fundamental major transition, because in important respects all life today is either archaeal or bacterial. From that perspective, eukaryotes are 'merely' a special kind of archaeon, especially if current views about eukaryotes being a group lodged firmly within the Archaea continue to gain traction (Koonin and Yutin 2014; Spang et al. 2015; Embley and Williams 2015). Even for more conservative views that are committed to preserving the evolutionary uniqueness of eukaryotes, the Archaea-Bacteria divergence is a major event that cries out for explanation, and it is therefore somewhat surprising that MTE 2.0 does not attempt to provide one. Although there are many aspects of this ancient turning point (before 3gya) that remain to be clarified, a compelling bioenergetic explanation has been proposed by Lane and colleagues (Sojo et al. 2014). This account foregrounds how early cells with porous membranes were totally dependent on external proton gradients for energy. Different populations of these cells

found divergent solutions to plugging their membranes and endogenously generating proton gradients, thus giving rise not only to robustly self-contained cellular life but also to the divergence between Bacteria and Archaea. No one, in contrast, has proposed that this event can be described or explained as an ETI.

Second, a metabolic perspective offers powerful resources for explaining evolutionarily several major transitions that *are* identified by MTE, without appealing to problematic notions like 'genetic information'. For example, a metabolic perspective helps to explain not only the diversification but also the origins of the prokaryotic cell. Metabolism lies at the heart of compartmentalization (Transition 1 in MTE 1.0), since metabolic reactions must be contained in order to avoid diffusion, and only contained metabolism can support genetic replication and biosynthesis. The metabolic benefits from compartmentalization are likely to have spurred the transition from unlinked replicating molecules to cooperative chromosomes (Transition 2 in MTE 1.0; part of Transition 1 in 2.0), because selection could begin to operate on the more or less successful proliferation of the compartmental contents rather than individual selfish elements (Koonin and Martin 2005). Acknowledging the interdependence of metabolism and replication also helps to resolve polarized metabolism-first/replication-first debates over life's emergence (Fry 2011).

A metabolic perspective gives further reasons for inclining toward the mitochondrion-driven explanation of eukaryogenesis – an explanation to which MTE 2.0 now gives near parity – while identifying and explaining other major endosymbiotic events overlooked by classic MTE and its ETI successors, such as the primary plastid acquisition. Lane and Martin identify increased energy production from the addition of mitochondrial membranes as central to genome complexification (a key metric of complexity in MTE), because the expression of large genomes is energetically costly (Lane and Martin 2010). More membrane potential freed eukaryotes from the metabolic constraints that even now preclude the genomic expansion and internal complexification of bacteria. Moreover, the levels of selection problem introduced by the acquisition of the ancestral mitochondrion was not only generated by metabolic factors (namely, energetically and replicatively selfish endosymbionts), but may also have initially been solved through metabolic regulation (Blackstone 2013). A similar case can be made for plastids (Allen and Raven 1996). The evolution of sexual cycles (Transition 5 in MTE 1.0; no longer a separate transition in MTE 2.0) can be explained as a mechanism to control energetically selfish mitochondria (Blackstone 2013); this energetic explanation might be a reason to retain this event, rather than to discard it as MTE 2.0 now does. Further, not only did metabolic innovation make each origin of multicellularity possible, but also a key selective advantage to multicellularity is metabolic, in that it reduces the surface area limitations and intracellular transport distances that constrain large unicellular organisms (DeLong et al. 2010). It is also feasible to argue that all the various complex behaviours found in large motile organisms, especially animals, are ultimately the gift of a generous metabolic budget. However, we do not believe that a metabolic account is best deployed in the service of explaining generic transitions. Rather, each token origin of multicellularity (or major behavioural innovation) should be examined separately.

In short, a metabolic perspective supplies both mechanistic and selectionist explanations that are indispensable for any account of major turning points in evolution. Understanding the selective reorganization of metabolic energy generation is crucial to explaining a great deal about the origins of genetic replication and complexification, as well as aspects of morphological complexity (Wallace 2010), including intracellular morphology. Behavioural complexity, sometimes suggested as a type of major evolutionary innovation that needs explanation beyond genes and metabolism (e.g., Worden et al. 2015), is at the very least dependent on prior metabolic achievements. Metabolic considerations do not, of course, fully explain how fitness conflicts between levels of nested replicators are resolved—this

matter remains within the province of ETI theory—but metabolic regulation of genetic elements will be part of those explanations, too (e.g., Blackstone 2013).

We are not criticizing theorists who take metabolism as a satisfied background condition in order to explore how genetic conflicts are solved during hierarchical transitions. Maynard Smith and Szathmáry are right that problems of inheritance needed to be overcome if genomes and morphologies were to become more complex. Our point, however, is that equally fundamental metabolic problems also had to be overcome. Indeed, an interactionist metabolic perspective goes some way toward making sense of, and theoretically unifying, the evolution and ecology of ETIs as well as non-hierarchical major turning points. Unlike replicationist accounts, a metabolic approach provides a coherent framework for understanding the sources of selection of many classic ETIs, as well as their world-shaping evolutionary impacts. And importantly, a metabolic perspective explains why standard ETIs are in fact major turning points, rather than merely assuming this by definition. Metabolic innovation is therefore treated in our proposed view both ontologically, as a series of major stages to be explained (e.g., oxygenic photosynthesis), and epistemically, as playing a central role in the explanation of other major shifts in the organization of life and their evolutionary consequences (e.g., eukaryogenesis).

Finally, insofar as the metabolic account shifts the focus onto prokaryotes – the most metabolically innovative organisms now and throughout the history of the planet – it avoids problems that beleaguer ascent interpretations of macroevolution, in which human capacities, and more broadly, morphologically complex life, sit at the pinnacle of a series of evolutionary transitions. Metabolic perspectives are not of course immune to ascent interpretations. Indeed, some theorists have placed human complexity at the apex of a bioenergetically driven trend of informational complexification (e.g., Wallace 2010). In our metabolically focused perspective, however, the photosynthesizing machinery of cyanobacteria holds a crucial slot as one of life's most complex and evolutionarily significant wonders, and embodies what might be the last great metabolic innovation. Placing prokaryotic innovation at the 'high table' of major transitions also serves as a useful counterweight to revised MTE models that focus exclusively on the evolution of hierarchical complexity, much of which, we have argued, cannot adequately be understood outside the metabolic context.

## **6. Objections to the Metabolism-Based Account**

But how satisfying is a metabolic account of evolutionary transitions for philosophers and theorists of evolution? Both classic and revised MTE models, although inconsistent in many respects, are consistent in seeing the evolution of new metabolic capacities and geochemical interactions as deserving no special attention. Philosophers of evolution have likewise focused very little on metabolism. One objection, alluded to earlier, might assert that the Great Oxidation Event is a transition that is not 'purely' biological because it includes geological and chemical factors, and hence that it does not qualify as an evolutionary transition. But evolution without ecology is not evolution at all, and focusing exclusively on genetic and morphological structures is a comparatively limiting framework. Szathmáry, prior to MTE 2.0, acknowledged the need 'to take a broader view [than the informational one] ... [by] linking major transitions to Earth history ... for example, the transition to oxygenic photosynthesis' (Szathmáry and Fernando 2011: 307-8). This expansion would produce an account of major transitions that integrates genes, metabolism and biological

structures with geochemistry, suggests Szathmáry.<sup>8</sup> David Queller likewise, in a discussion of ETI models, sees the designation of major transitions as unachievable by a strictly genetic approach:

The answers here must lie not in the fairly well-understood area of genetic transmission but in the much more complex challenges posed by environment (ecology) and in the much more complex ways that organisms respond to them (physiology) (Queller 2012: 1673).

This is what we mean by a metabolic perspective on major turning points being a more 'interactionist' approach than one focused on replication and morphology. Nevertheless, we do not see a great deal of this perspective in MTE 2.0. In fact, the various additions to MTE 2.0 go no further in this direction, apart from weighing up more carefully reasons to consider but not acquiesce to a metabolism-driven ETI-based explanation of eukaryogenesis (Szathmáry 2015). Other recent MTE theorists have stressed interactive approaches to MTE that sit better with the metabolic perspective we advocate here. For instance, Douglas Erwin (2015) has recently drawn attention to the connection between major transitions and public biological goods (including gene sequences and cells), which leads him to highlight a number of metabolically consequential events such as lateral gene transfer, symbiotic accounts of eukaryogenesis, chloroplast acquisition, and the great oxidation event.

Emphasizing metabolism (physiology) does not by any means ignore structure and replication—hallmarks of MTE. However, these features must be compatible with and sometimes explained by an account of metabolic innovations and interactions. Even when the evolution of individuality is given pivotal theoretical importance, what enables higher-level individuals to come into existence, persist and diversify is the evolution of metabolic capacities, both in individual cells and in the form of biogeochemical cycles. For theorists, metabolism has the appeal of being both very basic and very general—ranging in application from prebiotic to organismic to ecological entities (Morowitz et al. 2008)—as well as capturing a more theoretically unified series of events than is possible by focusing solely on replication and inherited information.

Another potential objection to our focus on metabolism draws on Mayr's (1961) famous distinction between 'proximate' and 'ultimate' biological causes. It holds that a metabolic perspective of major transitions is merely in the business of offering proximate explanations—that is, describing physiological and ecological conditions that make major transitions possible, but failing to explain why such shifts occurred in the way that they did. In contrast, so the objection goes, MTE and its successors aim to provide an 'ultimate' explanation of major transitions by describing the evolutionary forces driving them, while taking metabolic (and other proximate) factors as stipulated background (e.g., Bourke 2011). If this were correct, then placing metabolic views on an equal or competing explanatory footing with ETI-based theories would be wrong or misleading, since they address fundamentally different aspects of a complete evolutionary explanation of major transitions.

This objection is unfounded. A metabolic perspective on major turning points does not merely describe background conditions that make these evolutionary shifts possible—it explains the *adaptive motivations* for the major turning points themselves. One could just as well examine the ultimate metabolic factors that precipitated major turning points while taking replication conflict solutions as stipulated background. Our point is not that ETI-based explanations are dispensable, but rather that metabolic explanations are an indispensable part of the *ultimate* explanation of many major turning points, and thus of any complete

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<sup>8</sup> Andrew Knoll and Richard Bambach (2000) also propose an 'expanding ecospace' model that articulates a greater role for ecological transformations in major transitions, but their model mostly maps onto the classic MTE, culminating in 'technological intelligence' and thus similarly encouraging ascent interpretations.

evolutionary explanation of these events (see also Van Valen 1976). Holding that metabolism is merely a proximate cause of major evolutionary transitions is additionally problematic because the distinction between proximate and ultimate causes breaks down where 'proximate' factors shape selective environments (West et al. 2007; Laland et al. 2011). So yet another advantage of the metabolic perspective is that its interactionist view helps to reintegrate the artificial separation of proximate and ultimate causes by stressing the impact of major turning points on the selective regimes and organizational possibilities of large swaths of the tree of life.

Perhaps the biggest problem with the proposed account is that a focus on metabolism would not foreground quite so readily the evolution of hierarchy, which is what most commentators have found interesting in evolutionary transitions. A useful discussion of this contrast can be found in Kim Sterelny's (1999) comparison of Gould's (1997) model of evolutionary 'modes' with Szathmáry and Maynard Smith's transitions. Gould's framework emphasizes a 'bacterial' (read: prokaryotic) view of evolution, with life quickly reaching and remaining ever thereafter in a bacterial mode. Gould does not highlight any specific 'major' transitions and argues against directionality, because 'life has always been, and will probably always remain until the sun explodes, in the Age of Bacteria' (1997: 33). Here we take Gould to mean the 'Age of Prokaryotes' and attribute his word choice to the non-technical nature of his target audience; accepting the Bacteria-Archaea divergence as a fundamental transition would have been grist for his epistemic mill. Thus there are clear differences between Gould's 'continuity' view of macroevolution and MTE's directional hierarchy-forming view. One might be tempted to see these two views of life as simply focusing on different explananda rather than reflecting any genuine theoretical dispute; yet for Gould, focusing on vertical complexity as the central explanandum in the history of life amounts to the 'elevation of a small and epiphenomenal consequence into a major and controlling cause [of macroevolution]' (1997: 169).

Gould's prokaryotic view of life moves the emphasis away from 'vertical complexity [as] ... the number of layers or nestings within a system ... cell, tissue, organ, organ system, organism' (Sterelny 1999: 467). Sterelny prefers the MTE approach because it provides a more directional model of change in biological organization (e.g., prokaryotes to eukaryotes; unicellular to multicellular organisms), thereby revealing an important signal that would be missed were we to adopt a metabolic rather than a morphological focus. MTE 2.0 continues this focus. Even recent non-selectionist accounts of major transitions, such as that of Brandon and Fleming (2015), share MTE's exclusive focus on the evolution of hierarchy.

But stratifying biological entities into levels can be problematic because these levels are neither universal nor discrete (*sensu* Potochnik and McGill 2012), despite biological wholes being clearly composed of parts. Problems with theorizing hierarchy are due in part to the continued success of prokaryotic life and the ubiquity of symbioses—some of the very motivations for adopting a metabolic approach. For example, unicellular organisms are simultaneously cells and organisms, and thus organisms are not necessarily composites of cells; more significantly, multicellular organisms are higher-level ecosystems or a different sort of organism when their microbial occupants are considered (Dupré and O'Malley 2009). These overlaps can be problematic for some theoretical purposes, such as identifying the relevant biological or evolutionary individual, which is crucial for ETI theory. Moreover, this lack of discreteness may pose problems for considering the transition types identified by MTE as natural kinds, since it is commonly held that overlapping natural kinds must form a discrete, nested hierarchy and should not involve smooth transitions between them (Ellis 2001). But most importantly, by focusing parochially on the complexity-increasing stratification of life over evolutionary time, MTE misses a broader, dynamically interactive

view of biological entities and their environments over evolutionary time. This view is more effectively captured by a metabolism-based approach to macroevolution.

As intuitive as it may seem to recognize levels in a traditional biological hierarchy, a metabolism-focused model moves the emphasis from these 'levels' to what keeps such structures together over physiological and evolutionary time, and why they exist in the first place. Metabolic innovation is not only the stuff of which many evolutionary transitions are made, but it also explains a great deal about cells, cellular collectives, ecological systems and evolutionary relationships. It furthers our understanding of units of adaptation, for example, and why they do not often map one-to-one onto genetically isolated lineages (consider, e.g., plants and their integral nitrogen-fixing bacteria).

Understanding these organizational modes and their evolution requires a focus on 'horizontal complexity' rather than the vertical complexity emphasized in standard views of evolutionary transitions. By horizontal complexity, we simply mean the way in which organisms interact over evolutionary time with their environments, biotic and abiotic, in order to make a living. This horizontality occurs both in metabolic and genetic interactions. Rather than neat vertical food-chains leading ultimately to large animals, or tidy lines of vertical descent, our explanatory strategy focuses on vast networks of energy exchange that can often involve lateral gene transfers (Falkowski et al. 2008). In fact, metabolic advantage seems to be a major explanation of adaptive gene transfers (Ochman et al. 2000; Pál et al. 2005). A horizontal approach is necessary to explain the multiscale interactions that make the biological world what it is, because such interactions range over multiple 'levels' of organization, causally affecting one another without regard to hierarchy. Metabolism, as we have seen, is at once an intracellular and planetary phenomenon. And microorganisms, rather than being the small creatures that operate at the base of any trophic hierarchy, work as metabolic feedback loops that do not respect linear interactions between levels (Ducklow 1994). For example, growing recognition of the multiple roles of microbes in recycling organic carbon as well as producing it brought about a major shift in understanding how nutrient cycles operate over short and long periods of time.

It is of course still useful for many research questions to focus on nested systems. But recognizing that there is no absolute biological hierarchy opens up possibilities that nestedness is neither the only way, nor even the most useful way, in which to think about biological organization in order to gain a dynamic view of how life is organized. An interactive, metabolism-focused model of major evolutionary events may be 'flatter' and in a sense less intuitive, but it identifies types of organizational complexity that are missed by MTE and cites different mechanisms in their explanation. It is a helpful perspective at any phase of evolution, whether in the precellular, unicellular or multicellular world. It is less prone to evolutionary chauvinism than are hierarchical views that culminate in animal communication or focus on complex multicellularity. Metabolism can even be shown to underpin the evolution of cooperation above and beyond the major endosymbiotic acquisitions and symbioses discussed above.<sup>9</sup>

In its embrace of biochemistry, a metabolism-focused model of major turning points rebalances not only the historical philosophical trend to focus on genes and morphology, but also the classic MTE emphasis on replicators at the expense of ecology. As noted earlier, one

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<sup>9</sup> In bacterial biofilms and other collectives, the fruits of metabolic innovation can be exploited by surrounding cells (Benomar et al. 2015). These interactions, often of benefit to multiple species, provide the impetus for cooperative strategies designed to ensure that metabolic benefits are confined to biochemical co-operators. In cases where cooperation is intraclonal (Drescher et al. 2014), kin selection and metabolism offer complementary aspects of a unified ultimate explanation of cooperation. Metabolism is especially good for explaining how free-riding can be overcome in biological collectives (a focus of MTE), including multilineage consortia (Hillesland and Stahl 2010).

of the major contributors to the original MTE model, Szathmáry, initially made movements toward such an explanatory stance with an 'entwined environment-information' account of evolutionary transitions (Lenton et al. 2004: 914; Szathmáry and Fernando 2011: 307). We do not think MTE 2.0 realizes this ambition, but the aspiration still speaks to the potential of a metabolic perspective to realize a more interactionist account of major turning points than could be achieved by a theory that interprets the evolution of life exclusively in terms of individuals and the solution of replication conflicts.

Furthermore, if a central goal of MTE is to identify robust trends in the history of life, then a metabolic perspective will prove at least as valuable as a focus on replication and hierarchy. There is a macroevolutionary trend toward increasingly energetic metabolisms that necessarily underpins the trend toward larger body sizes (DeLong et al. 2010), and as shown above, metabolic 'motivations' drove many of the ETIs that comprise the trend in hierarchical complexification. If the trend in hierarchy is indeed robust, this may hinge on, and be explained in part by, the robust metabolic trajectories that underpin it. Thus, metabolic explanations are at least as central as replicationist explanations when it comes to explaining hierarchical trends and transitions, as well as the breaking of evolutionary constraints on genomic/morphological complexification (Lane et al. 2014). The fact that eukaryotes originated only once may speak to the contingency of this particular major turning point in the history of life, and thus perhaps to the contingency of all subsequent major evolutionary shifts that built on it. Nevertheless, given the iterated evolution of endosymbioses (Figure 3), and the robust trend toward increasingly energetic metabolisms driven in no small part by diverse prokaryotic innovation, we are inclined to think that eukaryogenesis may not be as contingent as its singular origin could suggest.

## **7. The Limits of a Metabolic Perspective on Major Transitions**

Much work remains to be done by anyone sympathetic to the interactionist metabolic remodelling of major transitions. Our primary suggestion here is that by examining evolution and the history of life more metabolically, philosophical attention can be refocused on what might be the genuinely explanatory major events in 3.8 billion years of evolution.

Although there are significant virtues to incorporating metabolic perspectives into philosophical reflections on life and its evolution, such perspectives also have limitations. It would clearly be a step too far, for example, to maintain that metabolic innovation could constitute or explain every important stage in evolutionary history, even if it makes many major non-metabolic events possible. Furthermore, because we have not offered an operational definition of major turning points as conceived metabolically, our approach might be seen as vulnerable to the charge that it (like MTE) identifies turning points by selecting intuitively compelling events, rather than by choosing an objective metric and letting the macroevolutionary data speak for itself. In this paper we have been concerned with establishing a minimal thesis, namely that metabolism is at least as important as genetic replication and morphological structures when it comes to understanding large-scale patterns in the history of life, and that it deserves a more prominent place in the philosophy of macroevolutionary theory. We see a notable and timely confirmation of this need in MTE 2.0, in which metabolism continues to be treated as a satisfied background condition.

Despite its epistemic virtues, in the end, even a metabolic perspective cannot succeed in forming a unified model of major turning points. It too would succumb to the charge that it either amounts to an unsystematic collection of descriptions of theoretically diverse events, or else overlooks certain major transitions. The fact remains that major turning points vary widely in their combinations of causes and in the nature of their effects, and there is no clear path to their theoretical unification, whether one is concerned with the events themselves or

their explanation. This remains the case even when metabolism is the focus. Metabolic events have theoretical continuity at the level of electron transfer and electrochemical imbalances across membranes, but the evolutionary consequences of new metabolisms are unpredictably varied. Furthermore, some plausible major turning points might be characterized as non-metabolic in nature even if they can ultimately be explained metabolically, while others can neither be described as metabolic innovations nor explained in metabolic terms (e.g. the division of labour between replicating and protein molecules). A metabolic account may fare better in some respects than MTE and its successors, but it would still produce a hit-and-miss catalogue of events.

### **Conclusion: Manageable Pluralism**

As we see it, the inability of a metabolic perspective to deliver a theoretically unified account of major transitions is not a failure. We do not expect theoretical unity underlying any full-bodied answer to the Big Question, because the diversity of formative mechanisms and events in the history of life calls for a diverse range of explanatory strategies. Indeed, Szathmáry (2015) now makes it clear that a narrow unifying principle is not and never was the goal of MTE (2015: 1). Simply trading in methodological or explanatory 'replicationism' for its metabolic equivalent in the service of theoretical unity would result in an equally imbalanced view of life and its history. Shifting the focus from major transitions to major turning points highlights the need to integrate replicationist and energetic explanatory strategies into a coherent view of life and its history. We are open to the possibility that these explanatory approaches might one day be unified, but for the moment we will have to settle for something less than a synthesis. Nevertheless, the utility of emphasizing a metabolic approach and questioning the old replicationist one is clear: we learn more about potential candidates for transitions, generate less biased answers to the Big Question, and gain some philosophical traction on the merits of working with disunified accounts.

With regard to that last point, finding reasons to reject a monistic unity-seeking approach to major transitions is not to resign ourselves to the idea that natural history is 'one damn thing after another', even if these two epistemic strategies are often posed as necessary alternatives (e.g., McShea and Simpson 2011: 22). We can deploy multiple explanatory frameworks accommodating a diverse range of evolutionary events, which can then be woven into a rich scientific narrative of key turning points in the actual trajectory of life on Earth. If explaining how common physical systems behave requires adverting to a plurality of theories and mechanisms (Sober 1997), then it should not be surprising if this turned out to be true as well for major turning points in evolution. The key question is not *whether* pluralism obtains, but whether a given case of pluralism is *manageable*. Pluralism is unmanageable if it entails an endless array of contingent evolutionary generalizations and mechanisms, which in turn necessitate an equivalently diverse range of biological explanations. In contrast, the pluralism we are contemplating for major turning points is manageable because it implicates a small number of regularities and mechanisms, and thus does not preclude our ability to theorize broadly across the relevant domain. More generally, such pluralism may be embraced without theoretical defeatism where (1) rigorous efforts at explanatory unification have proved unsuccessful, (2) there are good theoretical reasons to think that a monistic account will not suffice for the relevant domain, and (3) the resulting pluralism is manageable. In this paper, we have established (1) and (2) for major turning points in evolution, though (3) remains an open question. Our analysis suggests, however, that replicationist and energetic approaches together offer the prospect of a manageable pluralism with respect to the largest scale organizational patterns of macroevolution.



Our aim here has not been to offer a detailed list of metabolic events, but rather to urge the complementary and minimal thesis that metabolism be foregrounded in any account of major evolutionary turning points. Although it cannot be granted an all-encompassing explanatory status, a metabolic perspective enables a more interactionist understanding of macroevolution than a 'simple-to-complex' or more broadly replicationist strategy permits. A metabolic approach draws attention to neglected interactive evolutionary processes, such as symbioses, biogeochemistry, and niche construction—as well as neglected mechanistic explanations based on electron transfer, chemiosmotic coupling, and biogeochemical cycles. It supplies crucial elements of selectionist explanations in reliance on the ecology of metabolic interaction. In essence, a metabolic perspective reveals important aspects of evolution, and of evolutionary explanation, which are easy to overlook in the shadow of selfish replicator theory. It shows why it is misleading to equate major transitions in evolution with ETI types or even with event types at all, and why it is mistaken to assume that the explanations of ETIs will be replication-driven explanations: many major shifts in the organization of life were not brought about by ETIs or even tokens of natural kind-like transitions, and many major ETIs were metabolically 'motivated' and established. Finally, a metabolic perspective gives macroevolutionary pride of place to the wondrous microbial inventions that make our—and indeed any—complex biological world possible and actual.

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