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The history of life is a history of transitions between different units of selection.

—Leo W. Buss (1987, 171)

The hierarchy of life is the central landscape of collectivity in the living world—eusocial societies composed of multicellular organisms, multicellular organisms composed of single (eukaryotic or prokaryotic) cells, single (eukaryotic) cells composed of (prokaryotic) cells, cells composed of gene networks, and gene networks composed of replicating genes. The theory of evolutionary transitions addresses how cooperative collectives evolve into new units of evolution, that is, new kinds of evolutionary individuals. The transition between units of evolution was first discussed by Buss (1987) and Maynard Smith (1988; 1991), and then in a comprehensive and systematic way by Maynard Smith and Szathmáry (1995). In this chapter, we briefly review the major transitions in evolution (MTE) framework as originally formulated (Maynard Smith 1988; 1991; Maynard Smith and Szathmáry 1995), recent revisions to this framework (Szathmáry 2015), and the fitness-focused framework, evolutionary transitions in individuality (ETI) (Michod 1999). We also discuss criticisms of these frameworks and how they relate to other major evolutionary events that have occurred during the history of life.

## Transitions in Evolution

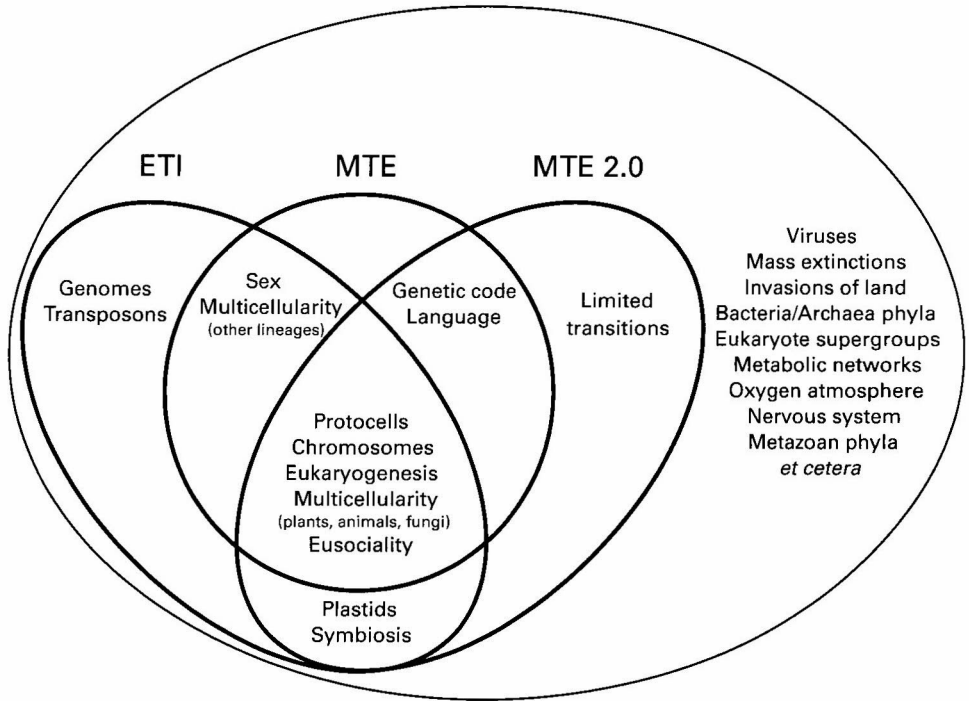
### MTE

Maynard Smith and Szathmáry argued that increases in complexity result from MTEs (Maynard Smith and Szathmáry 1995; Szathmáry and Maynard Smith 1995). These major transitions include the evolution of compartmentalized populations of self-replicating molecules, chromosomes from independent replicators, the genetic code, eukaryotes from prokaryotes, sexual populations from asexual populations, multicellular organisms from

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## Major Evolutionary Events



**Figure 20.1**

Diagram of evolutionary events according to the major transitions in evolution (MTE), MTE 2.0, and evolutionary transitions in individuality (ETI) frameworks. We have placed the transitions as originally listed.

unicellular ancestors, eusocial societies from solitary organisms, and the evolution of human language (see figure 20.1; Maynard Smith and Szathmary 1995).

MTEs are characterized by changes in the unit of evolution and reproduction (Maynard Smith 1988; 1991). Reproduction changes in such a way that “entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it” (Maynard Smith and Szathmary 1995, 6). As a result of these evolutionary transitions, cooperative collectives evolve into new kinds of evolutionary individuals, which may form collectives of their own and in this way create the hierarchy of life. The way in which genetic information is stored and transferred between generations is reorganized during MTEs. For example, during the evolution of sex from an asexual ancestor, information that used to be directly transmitted from a single parent to offspring must now be combined with the genetic information of another parent in order for reproduction to occur (Szathmary and Maynard Smith 1995; Maynard Smith and Szathmary 1995).

## MTE 2.0

Szathmáry subsequently updated the MTE framework (Szathmáry 2015), altering which transitions are included (figure 20.1) and discussing and incorporating the concept of individuality. Szathmáry discusses the common features that unite the major transitions, emphasizing two main dimensions: (1) changes in individuality and the level of selection and (2) changes in information storage and transmission. MTE 2.0 highlights the transition from lower-level evolutionary units to higher-level evolutionary units, as well as the importance of division of labor in facilitating cooperation within higher-level units. Incorporating the concept of individuality returns the MTE framework to its focus on units of evolution as discussed by Maynard Smith (1988) and Buss (1987). This renewed emphasis also reflects the influence of the multilevel selection perspective, with Multilevel Selection 2 being most relevant for major transitions (see Okasha 2006 for a review). Finally, the updated MTE 2.0 framework requires that all major transitions be significant evolutionary events (i.e., they lead to large adaptive radiations).

Szathmáry (2015) identifies seven major transitions, adapted and revised from the original list: the origin of protocells, the genetic code and translation (prokaryotic cells), eukaryotic cells, plastids, multicellularity (in plants, animals, and fungi only), eusocial animal societies, and societies with natural language (see figure 20.1). This list primarily differs from that of the original MTE framework in the promotion of primary and secondary plastids and the elimination of eukaryotic sex (see figure 20.1). The evolution of sex was eliminated because it does not lead to additional changes in hierarchy and because lineages of mated pairs do not arise from mated pairs (Michod 2011). Moreover, MTE 2.0 introduces “limited transitions”: transitions that involve changes in the level of individuality and information storage and transmission but do not lead to adaptive radiations. The inclusion of limited transitions, which include the evolution of multicellularity in lineages other than plants, animals, and fungi (i.e., red, green, and brown algae), reflects the fact that transitions in individuality, changes in information storage, and subsequent adaptive radiations are all necessary for an evolutionary event to be considered a major evolutionary transition under the MTE 2.0 framework.

## ETI

Michod and colleagues used evolutionary and ecological models (both experimental and mathematical) to explain how units of evolution (i.e., evolutionary individuals) can change from one level to the next (Michod 1996; 1997a, 1997b, 1999, 2006, 2007; Michod and Roze 1999; Michod and Nedelcu 2003; Michod, Nedelcu, and Roze 2003; Michod et al. 2006; Hanschen, Shelton, and Michod 2015). The central question addressed by this theory is how can groups of individuals evolve into new kinds of individuals? The ETI framework is focused on common processes and outcomes. The common processes,

summarized below, result in the reorganization of fitness at the individual and group levels. The common outcome is groups of individuals becoming new kinds of individuals.

The theory of ETIs is based on processes in population biology: the evolution of cooperation and conflict, conflict mediation, multilevel selection, division of labor, and life-history trade-offs. These processes are the basis for how fitness becomes reorganized during an ETI. The emphasis on fitness and the use of mathematical models to understand its reorganization is one way in which the ETI framework differs from the MTE and MTE 2.0 frameworks, although this emphasis stemmed from the work of Buss (1987) on individuality and Maynard Smith (1988; 1991) on units of evolution. The basic steps of an ETI include (1) the formation of groups leading to multilevel selection, (2) increase of cooperation among the lower-level units, (3) cheating leading to conflict among lower level units, (4) mediation of this conflict, which further increases levels of cooperation, (5) evolution of division of labor, and (6) decoupling of group fitness from lower-level fitness (Hanschen, Shelton, and Michod 2015).

Group living provides the opportunity for costly forms of cooperation such as altruism to evolve. As altruism evolves, the costs of altruism reduce fitness at the lower level while the benefits of cooperation increase the fitness of the group. Thus, altruism has the effect of transferring fitness from the lower level to the level of the collective. The evolution of cooperation sets the stage for cheating and conflict among group members to arise. Under certain conditions this can lead to the evolution of conflict mediators, which are developmental traits that reduce the opportunity for conflict while enhancing cooperation among group members. Multiple organismal traits act as conflict mediators; these traits include germ–soma division of labor, programmed cell death, and genetic control of group size (Michod 2003). Such conflict mediators alter development to produce groups with greater cooperation, fitness, and group-level heritability of fitness, resulting in greater individuality of the group.

In order for natural selection to operate on new kinds of individuals, heritable variation in fitness is required. Thus, fitness must be reorganized during an ETI, increasing at the group level and decreasing at the lower level. Taking a life-history perspective (Roff 2002), the fitness of any evolutionary unit has two basic components, fecundity (or reproduction) and viability (or survival); in the simplest models, overall fitness is defined as the product of these two components. Resources are invested in one fitness component at the expense of the other, leading to trade-offs among fitness components. As a result of these trade-offs, lower-level units can evolve to specialize on a single component of group fitness (Michod 2006; 2007; Michod et al. 2006). For example, during the unicellular to multicellular ETI, germ cells specialize in group-level reproduction but contribute little to the survival of the group. Similarly, nonreproductive somatic cells specialize in group-level survival but contribute little to the reproduction of the group. As a result of this specialization, overall cell fitness would decline if a specialized cell were to leave the group. For this reason, cellular specialization results in the decoupling of group fitness

from cell fitness, ultimately resulting in individuality arising at the group level, the level of the new multicellular organism.

The decoupling of group fitness from lower-level cell fitness has been studied in both “weak” and “strong” forms. “Weak” fitness decoupling occurs with the evolution of cooperation (steps 2–4), resulting in cells that are poorly adapted outside of the group context. This “weak” form of fitness decoupling can select for the reinforcement of group living, which in turn can lead to further group-level adaptation (Maliot, Shelton, and Michod 2015). The “strong” form of fitness decoupling occurs when cells specialize on the fitness components of the group (step 5). Cells specialized in one fitness component are therefore lacking in another necessary component and would have low fitness were they to leave the group. So group fitness can be quite high while cell fitness is quite low.

### Empirical Studies of the ETI Framework

The focus of the ETI framework on fitness encourages empirical investigations into evolutionary transitions, with the volvocine green algae being used as an experimental model system. The volvocine algae are a clade of motile, photosynthetic eukaryotes that contains unicellular species, undifferentiated colonial species, and differentiated multicellular species, with a range of body sizes, organismal complexity, and aspects of individuality. Larger species display traits relevant to the evolution of individuality that are absent in smaller species, including cellular differentiation and extracellular matrix (ECM) production. This diversity of species exhibiting differences in traits related to the evolution of individuality make the volvocine green algae an excellent model system for studying ETIs, particularly the evolution of multicellularity and the evolution of sex.

The basic steps of an ETI discussed above are exemplified by studies of the volvocine green algae: (1) formation of groups, (2) evolution of cooperation, (3) cheating, (4) conflict mediation, (5) evolution of division of labor, and (6) decoupling of group fitness from cell fitness. Empirical studies have focused on the genetic, developmental, and phenotypic changes associated with each of these steps. Control of the cell cycle at the group level (Hanschen et al. 2016) plays a critical role in step 1, the formation of groups, along with modifications to the cell wall that result in post-cell-division adhesion of daughter cells (Nozaki 1990). The evolution of group-level control of the cell cycle occurred early in the volvocine lineage (Herron et al. 2009) and plays a critical role in determining group size (Rashidi, Shelton, and Michod 2015; Shelton and Michod 2014) and changing life-history characteristics that allow for reproduction to emerge at the group level (Maliot, Shelton, and Michod 2015). Indeed, structural modifications to a cell cycle regulator, *RB*, cause the formation of cell groups in the volvocine algae (Hanschen et al. 2016). Cycles of increasing (2) cooperation, (3) conflict among lower-level units, and (4) conflict mediation leading to further cooperation have been examined by comparing extant species and reconstructing likely ancestral character states (Herron and Michod 2008). The costly

production of ECM by cells can set the stage for conflict between cells and cheating; this conflict may have been resolved by genetic control of cell number and group size (Michod 2003; Herron and Michod 2008). Another cycle of cooperation and conflict may involve the evolution of somatic cells and cheating via mutations resulting in the reproduction of somatic cells (Herron and Michod 2008; Hanschen, Ferris, and Michod 2014; Grochau-Wright et al. 2017).

The evolution of cell types specialized in reproduction and survival exemplifies step 5, the evolution of division of labor. As lower-level units specialize on the basic components of fitness, fundamental constraints and trade-offs at the cell level are avoided. In the volvocine algae, cellular machinery such as basal bodies is used for both motility via flagellation and reproduction via cell division. This forms the “flagellation constraint” (Koufopanou 1994), in which reproduction interferes with a colony’s ability to swim toward light and areas of nutrient availability (Sommer and Maciej Gliwicz 1986; Solari, Kessler, and Michod 2006). Cellular specialization allows for division of labor, with flagellated somatic cells specializing in motility (group survival) while nonflagellated reproductive cells specialize in group reproduction. In this way, a colony can simultaneously reproduce and remain motile, something a single cell cannot do.

The flagellation constraint illustrates a general point about the origin of altruism during step 2, how altruistic behaviors can emerge in a group context from lower-level life-history behaviors which trade-off in their effects on fitness. A unicellular organism will optimally balance the trade-off between flagellation and mitosis. However, in a group setting, cells that begin specializing on flagellation are altruistic, as they are giving up reproduction while benefiting the group (assuming flagellation similarly benefits the survival of cell groups as it does single cells). The origin of somatic altruism through the specialization on mitosis may be understood in a similar way.

Lastly, step 6, the decoupling of group fitness from lower-level cell fitness, has been studied in both “weak” and “strong” forms. In the volvocine green algae, an example of weak fitness decoupling is seen in the evolution of costly ECM production, which may benefit the group through increased cohesion and integration and possibly nutrient storage (Bell 1985; Koufopanou and Bell 1993). The “strong” form of fitness decoupling occurs during the evolution of cellular specialization, which enables colonies to overcome the flagellation constraint. While both cell types would have low fitness were they to leave the multicellular group, the fitness of the multicellular organism remains high.

### **Relationship of ETI and MTE Frameworks**

The ETI framework makes no mention of “major” evolutionary transitions. Whether ETIs result in “major” macroevolutionary consequences is certainly interesting, but it is not a defining feature of an ETI. While many events are shared among the MTE and ETI frameworks, the ETI framework’s focus on fitness and fitness reorganization leads

to several transitions being considered ETIs that are not included as MTEs or MTE 2.0s. For example, the evolution of sex is considered an ETI and an MTE but is excluded from MTE 2.0. In addition, during the origin of the genome, it has been hypothesized that self-replicating genes formed a cooperative hypercycle (Michod 1983; 1999; Eigen and Schuster 1979). In this situation, genes perform different functions (i.e., division of labor), and any replicative advantage a single gene develops (cheating) must be policed to ensure stability and replication of the group, the genome (Michod 1983; 1999). A similar situation occurs when transposons within a host genome experience a fitness trade-off between proliferation (reproduction) and persistence (viability) (Durand and Michod 2010; Agren 2014). These two previously independently replicating entities (the transposons and the host genome) may transition into a single replicating individual, the genome with its domesticated transposon (see figure 20.1). Transposable elements that contain multiple regulatory sequences (Smit 1996) may be the product of ETIs themselves, analogous to the origin of chromosomes.

The focus on fitness and changes in the units of evolution present in the ETI framework also excludes several transitions that are considered MTEs (see figure 20.1). The evolution of human language represents an unprecedented change in how information is transmitted and is considered an MTE. However, from the point of view of ETIs, while language certainly helps to integrate groups, Darwinian fitness has not been reorganized to become a property of the group with human individuals specializing in components of fitness of the group. Similar issues were acknowledged early in the original formulation of major transitions (Maynard Smith 1988). Similarly, the evolution of the genetic code (the reassignment of nucleotide codons to encode for different amino acids) drastically changed how information is transmitted from one generation to the next (Maynard Smith and Szathmary 1995; Szathmary 2015), yet no new hierarchical level evolves.

The evolution of multicellularity in the volvocine algae discussed above constitutes an ETI, but does it also represent an MTE or an MTE 2.0? The evolution of multicellularity in the volvocine algae can be regarded as an MTE because lower-level units (i.e., cells) that once reproduced and evolved independently now only do so as part of the larger whole (i.e., multicellular organism). However, this event would be considered a “limited transition” under the MTE 2.0 framework because, unlike the evolution of plants, animals, and fungi, this transition to multicellularity has not led to a major evolutionary event such as vast phylogenetic radiation with global consequences (like animals and plants).

## Discussion of Critiques

### Fitness during ETIs

The ETI framework has been criticized for claiming that the lower-level fitness of specialized cells (in the case of the evolution of multicellularity) living in groups is zero

(Godfrey-Smith 2011; Bourrat 2015). However, cell-level fitness is zero only if completely specialized cells were to leave the group. In the context of the group, their cell fitness (inclusive fitness in case of soma) can be quite high. Cells specialized in reproduction or survival can achieve high fitness because their low investment of effort in one fitness component is compensated for by other cells in the group that specialize in the other component.

The evolution of altruism serves to reorganize fitness because the costs of altruism decrease the fitness of lower-level units within the group while the benefits of altruism increase the fitness of the group. The costs and benefits must satisfy a condition known as Hamilton's rule in order for altruism to evolve (Hamilton 1963; Hamilton 1964; Michod 1982). The ETI framework describes the evolution of altruism as resulting in the transfer of fitness from the lower level to the group level. Referring to the "transfer" of fitness does not mean that fitness is a conserved quantity, nor is it intended to be metaphorical (Godfrey-Smith 2011), as fitness is reorganized during an ETI.

### **Major Transitions as a Natural Kind**

McShea and Simpson (2011) argued that MTEs are not explainable as part of a larger narrative and instead are independent events that have occurred over the course of history. In this view, the evolution of life's hierarchical structure is simply a series of events, "one damn thing after another" (McShea and Simpson 2011, 23). However, this criticism ignores the very basis of the MTE and ETI frameworks: the restructuring of genetic information and how it is transmitted, and how changes in levels of selection give rise to the hierarchical organization of life. ETIs, and MTEs as first considered (Maynard Smith 1988; Maynard Smith 1991), constitute a natural kind, events sharing similar processes and having common outcomes of collectives of individuals evolving into individuals. Although the MTE 2.0 framework accounts for the phylogenetic impact of events when defining them as "major" or "limited," its collection of transitions are also all defined by information restructuring and changes in individuality.

The MTE framework was a starting point to better understand the vast increases in complexity that have occurred during the history of life. It provides two narratives to unify the major transitions, the evolution of a higher level of organization and subsequent reproduction as part of a group, and changes in the transfer of genetic information. The ETI framework provides a narrative explaining how groups become new kinds of individuals through fitness reorganization. Given that the MTE 2.0 framework now explicitly involves changes in individuality (Szathmáry 2015), the theoretically unified and mathematically rigorous ETI framework provides a narrative that underpins major transitions in units of evolution.



## Major Evolutionary Events

Over the approximately 4 billion year history of life on Earth many different events have had major impacts on life and further evolution. Maynard Smith and Szathmáry (1995) specifically did not include a variety of such formative evolutionary events, including the invasion of the land, the evolution of flight, and the evolution of endothermy, as they do not constitute changes in the method of information transmission. The ETI framework makes no mention of these major events.

O'Malley and Powell (2016) proposed that the evolution of oxygenic photosynthesis and the resulting oxygenation of the Earth should be included as a major transition in evolution. While this event clearly had profound consequences for the trajectory of evolution, it does not constitute an MTE or an ETI and does not result directly in changes to collective organization. O'Malley and Powell (2016, 167) even acknowledge as much when they observe that, although "this novel photosystem did not generate a new level of individuality, it transformed the entire biological world." They recognize that oxygenic photosynthesis falls outside of the MTE and ETI frameworks. We agree that the oxygenation of the atmosphere had an irreversible and transformative effect on the evolution of life on Earth, but remarkable alteration of evolution's trajectory is not necessary for an evolutionary event to be considered an MTE (under the original MTE formulation) or an ETI, nor is it considered sufficient under the MTE 2.0 framework.

Koonin (2007) proposed a new framework for identifying major transitions in biological evolution, identifying six biological big bang events. This framework defines major transitions as those that involve the rapid origination and diversification of new forms and includes the emergence of complex RNA molecules and structural elements, the evolution of viruses, the emergence of archaea and bacteria cell types, the emergence of archaea and bacterial major lineages, the evolution of the eukaryotic cell and eukaryotic supergroups, and the origin of major lineages within eukaryotic supergroups as being major transitions. While some of these transitions, such as the origin of cellular differentiation, involve changes in collective behavior, including individuality and information storage and transmission (and are included in the MTE, MTE 2.0, and ETI frameworks; see figure 20.1), they are included in Koonin's framework because of their macroevolutionary properties and significance (Koonin 2007), not necessarily because they involve shared processes. This framework is useful for understanding and categorizing major evolutionary events in which new forms rapidly originated and diversified, but loses the focus of a common set of processes and outcomes underpinning the hierarchy of life and transitions in individuality.

While we think the MTE 2.0 framework improves upon the original formulation by including a more explicit focus on multilevel selection and the evolution of individuality, the creation of the category of limited transitions in MTE 2.0 is problematic, as it moves away from the theoretical basis and first principles approach used in defining MTEs. As a result, Szathmáry (2015) considered the evolution of multicellularity in animals, plants,

and fungi to be major transitions, disregarding dozens of other origins of multicellularity (Grosberg and Strathmann 2007). Moreover, the evolution of societies with natural language does not appear to be leading to an adaptive radiation, so its inclusion as a major transition appears inconsistent with the framework as a whole.

## Conclusions

The MTE and ETI frameworks have contributed significantly to our understanding of the evolution of collective organization. The MTE framework first provided a way of understanding how events that appear different and occurred at vastly different stages in the history of life are in fact underpinned by similar mechanisms and have a common outcome. The MTE 2.0 framework makes headway by incorporating plastids and building on the theoretical strengths and empirical studies of the ETI and multilevel selection frameworks. However, the MTE 2.0 framework loses its theoretical footing by including macroevolutionary diversification as a defining property. ETI theory, with its focus on groups becoming evolutionary individuals through fitness reorganization, is an empirically testable research program. Changes in units of evolution and individuality do not necessarily result in major shifts in diversity, yet they constitute a natural kind. Recent criticisms of the MTE and ETI frameworks have failed to recognize this natural grouping of evolutionary transitions.

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