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# Editorial: Social evolution and the what, when, why and how of the major evolutionary transitions in the history of life

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## Editorial on the Research Topic

[Social evolution and the what, when, why and how of the major evolutionary transitions in the history of life](#)

In their foundational book, [Maynard Smith and Szathmáry \(1995\)](#) proposed eight rare events in the history of life on Earth that were transformative and seemingly needed to overcome significant selective barriers to their evolution and spread. These were called Major Evolutionary Transitions, or METs. Although subsequently this list of METs has been amended, edited, narrowed, and expanded by a variety of authors (e.g., [Bourke, 2011](#); [Calcott and Sterelny, 2011](#); [Szathmáry, 2015](#); [West et al., 2015](#); [Herron, 2021](#)), we still lack consensus regarding the defining qualities of METs in terms of their evolutionary and ecological consequences. In this Research Topic, we revisit these issues to synthesize new research and novel ideas that may illuminate the ecological and evolutionary conditions that give rise to and result from the METs. Some authors broadly consider what constitutes a MET ([Robin et al.](#); [Okasha](#)). Others provide novel insights into particular METs such as multicellularity, eusociality, mutualisms in the microbiome, and even identify previously overlooked transitions among insect endosymbionts that seem to track the same evolutionary path that gave rise to mitochondria ([Rose and Hammerschmidt](#); [Bernadou et al.](#); [da Silva](#); [Zachar and Boza](#); [Rafiqi et al.](#)). Finally, several propose fresh considerations of the evolutionary processes that facilitate METs ([Thies and Watson](#); [Lamm and Kolodny](#); [Watson et al.](#)).

Despite decades of debate, there is no clear consensus about what is or produces a MET. For example, ecological effects often are excluded in defining METs (e.g., [Szathmáry, 2015](#)). Nevertheless, an apparent large ecological impact correlated with a MET seems to be at least an implicit criterion. Would, for example, the origin of eukaryotes rank as a “major” event if eukaryotes had remained minor components in a

prokaryotic world, as they were for the first billion years of their existence? Therefore, Robin et al. examine how METs do or do not factor into Major System Transitions (MSTs) of entire ecosystems. Viewed in this way, a MST can result from METs that produce gains in information availability and storage capacity for organisms (i.e., through diploid genomes, learning recorded in neurons, or symbolic language etched into abiotic media), combining with METs in which previously independent entities fuse to become a single, integrated individual. Lamm and Kolodny further consider how populations can create novel and usable information as a distributed adaptation that is essential for individual success. Such adaptations do not exist within any individual and are only evident when observing the features of groups or populations. These papers follow Maynard Smith and Szathmáry (1995) original proposal that METs can reflect both changes in information and individuality. Alternatively, Okasha argues that unifying the concept of a MET is better served by excluding informational changes, and thus narrowing the definition to changes in individuality. What remains is a philosophical issue that requires differentiating across conceptual and ontological questions. The former includes the types of explanations and modeling approaches applied to METs, while the latter includes the nature and hierarchical organization of biological entities. In both categories, Okasha identifies areas where empirical science and philosophical analyses fruitfully overlap.

One such ontological question concerns the mechanisms underlying the origins of complex insect societies as a possible MET. This is addressed by da Silva showing that there may exist differing precursors to eusociality: semisociality (cooperating females of the same generation) and subsociality (cooperating mothers and daughters) for wasps and bees, respectively. Staying with insect societies, Bernadou et al. posit that worker sterility is key to allowing reproductives to simultaneously increase in fecundity and lifespan. Breaking this trade-off is what produces a “superorganism”, which they propose restricts the potential for a MET to only those insect societies with obligately sterile workers. Rafiqi et al. expand the general consideration of how a cooperative entity can evolve by using endosymbiotic evolution within insects as a model system for the role of development in integration of separate species into a single entity with aligned fitness outcomes. Finally, Rose and Hammerschmidt emphasize the importance of differentiating levels of multicellularity. They propose that the pathway to a MET follows three stages: individuals forming groups; groups acting as individuals; and entities subsuming their individuality into a singular organism. Different questions and processes are relevant across these stages.

The Research Topic also adds to the conceptual consideration of general theories for the evolution of METs (Okasha). Zachar and Boza raise the paradox of why there have been relatively few (or no) surviving

symbioses among prokaryotes comparable to the one that produced mitochondria. They examine why mutualisms do not lead to multilevel selection more often in microbial communities, resulting in community-wide inheritance and heritable multispecies phenotypes. While there is no theoretical objection for a multispecies community evolving to a superorganism, the lack of such events indicates that there may be only one way for microbes to make a major transition in individuality: endosymbiosis.

Changes in levels of selection are considered a critical MET characteristic. However, formal approaches to quantifying group selection (contextual analysis and the Price approach), can give contradictory answers. Distinguishing among causes of this discrepancy requires comparison of contrasting treatments/experimental interventions, which no statistical analysis of a single treatment can provide (Thies and Watson). Watson et al. then ask how functional relationships need to be organized to create fitness differences that properly belong to a collective and not its parts. Connectionist models of learning and cognition may identify formally non-decomposable collective phenotypes, providing this critical feature of METs.

In summary, the Research Topic examines and provides new insights into a range of what, when, why and how questions about METs. It opens new avenues for thinking about when in the history of life major events became possible, which events have profoundly altered the world, what those events required, and how and why they could arise through selective and evolutionary processes.

## Author contributions

All authors contributed to the writing and editing of the manuscript and approved the submitted version.

## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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