

# Crystal Ball

## The coevolutionary history of the microbial planet

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In recent decades, there has been growing appreciation for the importance of symbiosis in structuring biodiversity on the planet, and there is now an abundance of compelling symbiotic systems under investigation. Personally, my favourite will always be the leaf-cutter ant symbiosis, which I was lucky enough to study as a graduate student at the University of Wisconsin-Madison. These charismatic creatures form the largest insect-built structures on the planet, often containing millions of individuals, and they owe their success to the fungal cultivar with which they have co-evolved for the past ~55 million years (Currie, 2003) (Fig. 1). Remarkably, these farming ants and their cultivar form the crux of a multi-partite symbiosis that involves several other fungi and bacteria, and new members continue to be discovered (Poulsen and Currie, 2006). Interactions in the leaf-cutter ant symbiosis vary in their strength and the degree to which members have co-evolved; some are cases of clear co-evolution in that they exhibit reciprocal adaptation, while other interactions are more transient or may lack specificity (Pinto-Tomás *et al.*, 2009; Aylward *et al.*, 2014; Barcoto *et al.*, 2020). What I find most remarkable about this symbiosis is how the evolutionary trajectories of all of the partners are intertwined to varying degrees, forming a complex co-evolutionary web in which each member uniquely shapes the ecology and selective pressures on the others.

Of course, this is just one example. To what extent is the complex multi-partite symbiosis of leaf-cutter ants characteristic of biotic interactions more broadly? We may be inclined to dismiss these ants as a curious but unique example, not particularly applicable to anything else. But as our knowledge of symbiosis has grown, so has our appreciation of how myriad microbial interactions – some tightly knit and co-evolved, others more transient – underpin ecosystems around the globe. Indeed, leaf-cutter ants themselves were

studied since the 19th Century as a two-member symbiosis until advances in recent decades revealed the extent of ecological complexity in this system. Likewise, work in other systems has come to reveal that microbial interactions are ubiquitous and can have enormous ramifications; examples of metabolic cross-feeding and emergent metabolic networks are becoming more common, and the implications of these phenomena for ecosystem-level processes are growing in importance (Klitgord and Segrè, 2011; D'Souza *et al.*, 2018; Smith *et al.*, 2019). If we turn to the marine environment, there has been fascinating work on metabolic co-dependencies between the globally abundant marine plankton *Prochlorococcus* and *Pelagibacter*; modelling has suggested that the long-term consequences of this interaction have had biome-scale impacts that drastically shaped the evolutionary trajectories of countless other marine lineages, and even global biogeochemical cycles (Braakman *et al.*, 2017). Other studies have provided a framework for understanding how metabolic co-dependencies influence genome evolution, further emphasizing the important role of these associations in shaping ecological-evolutionary networks (Morris *et al.* 2012; D'Souza *et al.* 2014).

This complex web of interactions has been a driving force in the diversification of life on the planet, although reconstructing the details can be tantalizingly difficult. Nevertheless, comparative genomic and molecular dating studies have begun to provide an evolutionary roadmap in which the biogeochemical impacts of some lineages can be linked to the diversification of others. Watershed events such as the evolution of oxygenic photosynthesis or the eukaryotic cell are dramatic examples that fundamentally shaped the subsequent evolution of life on Earth, but other important events are also coming into focus. For example, one study linked the diversification of heterotrophic marine *Roseobacter* with the emergence of the large eukaryotic phytoplankton with which they are often associated (Luo *et al.*, 2013), while other studies have reconstructed the evolution of saprotrophic fungi in the context of plant diversification (Floudas *et al.*, 2012; Krah *et al.*, 2018; Ayuso-Fernández *et al.*, 2019). Further studies have begun to disentangle the omnipresent coevolution between cellular life and viruses, such as recent work that has shed light on the origins and genomic diversity of eukaryotic giant viruses (Guglielmini *et al.*, 2019; Moniruzzaman *et al.*, 2020;

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**Fig. 1.** *Atta cephalotes* leaf-cutter ants tending their fungus garden. Photo by Don Parsons.

Schulz *et al.*, 2020). Lastly, microbiome studies have begun to examine how microbes influenced the emergence and diversification of multicellular eukaryotes (McFall-Ngai *et al.*, 2013; Alegado and King, 2014), which in turn created new ecological niches for microbial evolution (Foster *et al.*, 2017; Koskella and Bergelson, 2020). Although the details of these evolutionary scenarios are not always clear, these studies have begun to provide a compelling picture of how evolutionary innovations in some lineages resonate throughout the biosphere and inexorably drive the evolution of others.

As our knowledge of microbial community interactions grows, so will our knowledge of how they shape biodiversity and long-term evolutionary patterns. To be sure, the complex nature of microbial communities, the difficulty in determining the precise nature of many interactions, and the often unpredictable outcomes of ecological dynamics will make this task difficult. Nevertheless, my crystal ball shows a future in which we are better able to understand how a spectrum of interactions ranging from tight coevolution to more diffuse co-dependencies gave rise to the extant biodiversity on Earth. May leaf-cutter ants continue to provide a shining example for us all.

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