Chapter 1
The Relevance and Challenges of Studying Microbial Evolution

Pabulo Henrique Rampelotto

1 Introduction

The pioneering work of Charles Darwin, unveiling key insights into how the evolutionary process works to generate different forms of life, has provided a cornerstone for understanding evolutionary relationships among different organisms. Nevertheless, Darwin's work primarily dealt with the macroscopic forms of life covering the most recent 1.0 billion years. The evolution of microbes, on the other hand, had been underway for about 3 billion years, covering much of the earlier evolutionary history of life. Thus, an understanding of the evolutionary relationships among microbes is of central importance for deciphering the origin and diversification of different forms of life on Earth.

Even now, most of the biodiversity of life on Earth is microbial. Many of the genes, molecular machines, regulatory, metabolic, and synthetic pathways found in all living organisms today evolved first in microorganisms. The great diversity of microbes allows them to synthesize or break down a vast range of chemical substrates and govern biogeochemical cycles that make Earth a habitable planet. As such, microbes are essential to Earth's functioning at every scale, and understanding them is imperative for a complete understanding of life.

Our own body is also home to a diverse assemblage of microbial cells. Bacteria that colonize our gastrointestinal tract help us maintain our health by extracting energy from undigested carbohydrates, synthesizing vitamins, and metabolizing xenobiotics. On a very practical level, understanding the mechanisms of microbial evolution will improve our ability to develop more effective antibiotics and vaccines,

P. H. Rampelotto (✉)
Center of Biotechnology and PPGBCM, Federal University of Rio Grande do Sul, Porto Alegre, RS, Brazil
e-mail: p.rampelotto@mail.ufsm.br

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predict disease outbreaks and changes in virulence, and harness microorganisms' potential for rapid evolutionary change to create new products and processes. In this regards, basic research on microbial evolution has the potential to contribute across sectors and address applied problems in many fields, thereby leading to new approaches to treating disease, raising agricultural productivity, monitoring and addressing climate change, and producing clean energy.

Based on such tremendous potential, it is possible to realize that a better understanding of microbial evolution may give us more than just the ability to understand microbial diversity; it will help understand the world around us. The Darwinian revolution in the nineteenth century went far beyond the scientific domain and had the broadest philosophical and cultural implications. At the beginning of the twenty-first century, we are clearly moving toward similar direction in the microbial world.

As a brief introduction to this book, herein I highlight some of the reasons why understanding how microbes evolve is important to science and society and how challenging is to study microbial evolution.

2 Why Understanding Microbial Evolution Is Important

2.1 Major Events in Life's History Was, and Continuous to Be, Influenced by Microbes

Throughout the history of Earth, microorganisms have radically reshaped life on the planet, from creating the very air we breathe to wiping out almost all life on Earth.

2.1.1 How the Earth's Atmosphere Got Oxygen

For the first half of our planet's history, there was no oxygen in the atmosphere. This gas only started to appear about 2.4 billion years ago, in an episode known as the Great Oxidation Event (GOE), one of the most important events to ever happen on this planet. Such colossal event was triggered by cyanobacteria producing oxygen, which developed into multicellular forms as early as 2.3 billion years ago (approximately 200 million years before the GOE) (Schirrmeister et al. 2013). Interestingly, cyanobacteria are inferred to be ancestrally nonphototrophic and acquired the ability for photosynthesis by lateral gene transfer from another, unknown species, which further evolved within the group (Soo et al. 2017).

Before the GOE, any free oxygen produced by cyanobacteria was chemically captured by dissolved iron or organic matter. The GOE started when these oxygen sinks became saturated, at which point oxygen produced by cyanobacteria was free to escape into the atmosphere (Hamilton et al. 2016). The increased production of oxygen set Earth's original atmosphere off balance. Because oxygen was poisonous for large numbers of anaerobic organisms, most anaerobic types of bacteria were eliminated, opening up ecological "niches" for aerobic organisms to develop (Schirrmeister et al. 2015). Cyanobacteria were therefore responsible for one of the most significant mass extinctions in Earth's history. At the same time, these photosynthetic microbes were also responsible for a major turning point in the evolution of life on our planet.

2.1.2 Microbes May Have Caused Earth's Biggest Mass Extinction

About 252 million years ago, Earth suffered the biggest mass extinction event in its history, known as the Great Dying. The atmosphere filled with carbon, the planet baked in a warmer climate, and the oceans acidified. When it was over, approximately 95% of marine species and 70% of terrestrial species are becoming extinct (Sahney and Benton 2008). Scientists have long blamed volcanoes for triggering this catastrophe by pumping the atmosphere full of greenhouse gases. However, a recent study attributed the surge of carbon to the rapid evolution of a new microbe which developed a mechanism for the conversion of organic matter to methane.

According to the study, a group of microbes called *Methanosarcina* acquired two genes from an unrelated bacterium via gene transfer about 250 million years ago (Rothman et al. 2014). The new metabolic pathway allowed these microbes to rapidly consume large deposits of organic carbon in marine sediments while releasing vast amounts of methane, a greenhouse gas that warmed the atmosphere and acidified the oceans. Volcanoes could have still played in a role in spewing out nickel, which is necessary for the chemical reaction that allows microbes to make methane gas.

Although such implications remain speculative, the findings suggest that microbial evolution has important consequences for the evolution of the environment as a whole and indicates how a particular microbe may have played a crucial role in the evolution of life on Earth.

2.1.3 Microbes Control Critical Biogeochemical Processes

Through the evolution of oxygenic photosynthesis and continuous cycling of carbon, nitrogen, and other elements, microbes created and continue to sustain the conditions for life on Earth. This is true at all scales and in all environments, on land, in the ocean, and under the Earth's surface. Microbes directly modulate the amount of bioavailable nitrogen, carbon, phosphorous, sulfur, and many important metals (Long et al. 2016). The ability to transform nitrogen gas from the atmosphere into a form that organisms use to make critical biomolecules, like DNA and proteins (the process of nitrogen fixation), evolved in microbes very early in the history of life, and microbial nitrogen fixation continues to serve as a fundamental link in the nitrogen cycle.

While various microorganisms involved in carrying out biogeochemical processes have been identified, biogeochemical process rates are only rarely measured together with microbial growth, and one of the biggest challenges for advancing our understanding of biogeochemical processes is to systematically link biogeochemistry to the rate of specific metabolic processes (Rousk and Bååth 2011; Rousk and Bengtson 2014). We also need to identify the factors governing these activities and if it results in feedback mechanisms that alter the growth, activity, and interaction between primary producers and microorganisms (Treseder et al. 2012). By determining how different groups of microorganisms respond to individual environmental conditions by allocating, e.g., carbon to production of biomass, CO_2, and other products, a mechanistic and quantitative understanding of formation and decomposition of organic matter, and the production and consumption of greenhouse gases, can be achieved.

Human activities are changing the environment in which microbes evolve, creating innumerable new evolutionary pressures. How microbes will react to this new set of variables is critically important but difficult to study. Over the long term, there is no doubt that if microbial ecosystems are disturbed, their "evolutionary trajectories" will be affected in ways that we cannot still predict.

2.1.4 Climate Change and Microbial Evolution

Microbial chemical cycling also plays a critical role in the current status of the planet's greenhouse effect (Tian et al. 2016). Microbes can both absorb or release carbon, depending on their diets, so the direction of their influence is not so clear. However, altogether, they are huge players in the carbon cycle (Bardgett et al. 2008). Just the microbes that decompose dead plants in the soil, for example, release 55 billion tons of carbon dioxide a year, which is eight times what humans contribute through fossil fuels and deforestation (EPA 2018).

In addition, climate change is changing how these microbes function. In Arctic permafrost, for instance, where nearly half of the organic carbon stored in soil around the world is contained, there is normally not much microbial activity. In recent years, however, the permafrost is releasing more carbon dioxide than it absorbs, which scientists believe is due to rising temperatures allowing more microbes to feed in the tundra and release carbon dioxide (Schuur et al. 2015; Ward et al. 2017). Consequently, this feedback can accelerate climate change.

Moreover, denitrifiers and nitrifiers can generate nitric oxide and nitrous oxide, which are powerful greenhouse gases that have 280–320 times more potential for warming than carbon dioxide (Szukics et al. 2010). Also, phytoplankton produce dimethyl sulfide and dimethylsulfoniopropionate, and the cycling of these compounds produces sulfur gases that impact cloud formation and, hence, the water cycle and the global albedo (reflectivity). Archaeal methane production is the dominant natural source of methane, a gas that is over 20 times more powerful a greenhouse gas than carbon dioxide (Nazaries et al. 2013).

In essence, microbes have been changing the climate and have been changed by the climate, throughout Earth's history (Singh et al. 2010; Ladau et al. 2018). Although scientists have been studying microbial ecosystems for many years, there remains much more to learn and understood about complex microbial functions and their interactions with climate change.

2.2 Models to Understand General Principles of Evolution

Just as microbes have served as highly flexible model systems for molecular biology experimentation, microbes and microbial consortia can also be used for experiments on evolution (Adams and Rosenzweig 2014; O'Malley 2018). Microbes in experimental systems and in real-world situations like infectious disease offer the opportunity to test and observe microbial evolution in action (Koonin and Wolf 2012).

With larger organisms, until the advent of molecular biology, biologists were often forced to make inferences about evolution from observation. Genetic study has vastly enriched our understanding of the mechanisms of evolution, but the ability to carry out evolutionary experiments is still limited in long-lived organisms with large and complex genomes. By contrast, experimental evolution with microbes offers a rich alternative by providing a testable system based on hypothesis, experiment, and outcome (Elena and Lenski 2003). Control over selective pressures represents another advantage. Moreover, in microbiology it is possible to save and see the "mistakes" or evolutionary dead ends in an experiment; we don't necessarily "lose the losers" in an evolutionary microbiology experiment.

In practical terms, microbes are ideal models for understanding the effects of climate change on the diversity and evolution of biological systems. Because they have generation times as short as a few hours, they will do so at higher rates than most other organisms. Scientists can study the effects of climate change on microbes to both understand and hopefully predict the future effects of these environmental changes on all forms of life.

In a new frontier of science, the genomic and post-genomic studies of microorganisms living in extreme conditions on Earth are providing new insights about what it takes to life evolve in environments that were once thought uninhabitable, including potential habitable environments elsewhere in the universe (Rampelotto 2013; Bakermans 2015). Such fascinating studies are paving the way for the stablishment of astrobiology as a strong and vibrant field of research. Indeed, our increasing knowledge about the evolution of microbes in extreme habitats has led numerous scientists to raise the possibility of finding life in various planetary bodies within the Solar System (Rampelotto 2010).

2.3 Animal Origins and Evolution

Animal evolution traditionally has been viewed as the result of interactions between animals or with the physical environment. However, this understanding of evolution overlooks a huge missing piece of the puzzle: microbes. To put it bluntly, complex life-forms probably would never have evolved on planet Earth if it were not for microbes.

Bacteria have exerted critical influences on the evolution of eukaryotes and, ultimately, the origin and evolution of animals (Alegado and King 2014). Bacteria and archaea contributed to the cellular and genetic building blocks for the first eukaryotic cells, and bacteria formed stable associations with early eukaryotes in the form of mitochondria and plastids (McFall-Ngai et al. 2013). Moreover, bacteria were likely an important source of food for the progenitors of animals, as well as the first animals themselves (Rosenberg and Zilber-Rosenberg 2016).

After helping get animals started, bacteria also played an important role in helping them along their evolutionary path. While animal development is traditionally thought to be directed primarily by the animal's own genome in response to environmental factors, recent research has shown that animal development may be better thought of as an orchestration among the animal, the environment, and the coevolution of numerous microbial species (Bosch and Miller 2016).

Not only do animals share evolutionary history with microbes, but they also continue to interact with them on a daily basis—often in very profound ways. Bacteria living inside of animals can provide them with metabolic capabilities that the animal itself does not possess. Cows could not eat grass if it were not for the resident microbes that ferment it in the cow's rumen. Certainly, the evolution of the cow was heavily influenced by—if not largely dependent on—its microbial allies.

2.4 Microbes and Humans

Just like other animals, humans also share an interesting and deep evolutionary history with microbes (McFall-Ngai et al. 2013). Of the roughly 23,000 genes in the human genome, for instance, 37% are similar to genes in *Bacteria* and archaea. Another 28% are similar to genes in unicellular eukaryotes. Thus, a full 65% of human genes show similarity to microbes. Only 6% are found uniquely in primates.

Our bodies are made up of many more microbial cells than human cells. Thousands of species of bacteria, fungi, viruses, and other microbes live almost everywhere in and on our bodies, including the digestive system, nose, and skin, to name just a few (Gilbert et al. 2018). Some of the earliest research showed that the microbes living in our digestive systems help us digest food, make some of the vitamins we need, and balance the immune system (Arora and Bäckhed 2016; Foster et al. 2016). Since then, we've learned that these microbes, collectively called the microbiome, can affect body weight, susceptibility to cancer, and even behavior (Paun et al. 2017; Vuong et al. 2017; Goodman and Gardner 2018). The gut microbiome interacts with its host using signaling networks that employ the immune system, hormones, and the nervous system.

In short, microbes have a profound effect on our overall health and may become a key component of precision medicine (Kashyap et al. 2017; Petrosino 2018). As such, a better understanding on how microbes have adapted and evolved to colonize and influence our body will certainly revolutionize the way we view our health.

2.5 Pathogen Evolution

During evolution, humans developed many ways to protect themselves against bacterial pathogens. On the other hand, bacteria have developed strategies to evade, subvert, or circumvent these defenses. These microbial pathogens have a remarkable capacity for rapid evolution because they have large population sizes, short generation times, and high mutation rates. This capacity, combined with large dense human populations and rapid air travel, are leading to greatly increased risk of the evolution of novel pathogens.

As such, bacterial pathogens continue to cause problems for humans with the continuous evolution of known pathogens and the emergence of new ones (Martínez 2013). The immense social and economic impact of bacterial pathogens, from drug-resistant infections in hospitals to the devastation of agricultural resources, has resulted in major investment to understand the causes and consequences of pathogen evolution. Recent genome sequencing projects have provided insight into the evolution of bacterial genome structures, revealing the impact of mobile DNA on genome restructuring and pathogenicity (Jackson et al. 2012; Nuccio and Bäumler 2015; Tibayrenc 2017). Sequencing of multiple genomes of related strains has enabled the delineation of pathogen evolution and facilitated the tracking of bacterial pathogens globally (Bentley and Parkhill 2015). Other recent theoretical and empirical studies have shown that pathogen evolution is significantly influenced by ecological factors, such as the distribution of hosts within the environment and the effects of coinfection (Britton et al. 2015; Lloyd-Smith et al. 2015).

With a better knowledge on the molecular mechanisms of pathogen evolution, researchers can attempt to predict where disease outbreaks are likely to occur. Strategies can also be developed to control disease, for example, by promoting a lifestyle that maintains populations of beneficial microbes in our bodies and prevents the evolution or ingress of pathogens. In addition, researchers might be able to prevent the evolution of virulence by removing conditions that promote pathogen evolution and perhaps could even reverse adaptive changes.

2.6 Microbial Evolution Can Be Used to Solve Global Problems

Microorganisms can be used to solve some of the global problems through the generation of fuels, production of bio-based materials, improvement of crop productivity, remediation of pollution, and recyclement of wastes. These approaches show great promise for contributing to a transition to a sustainable human society. To improve microbial performance toward these aims, metabolic engineering is generally used. However, the remarkable complexity of dynamic interactions in cellular systems often prevents practical applications of metabolic engineering due to the requirement of extensive genetic and metabolic information on the organism of interest (Alkım et al. 2014). In contrast, evolutionary engineering follows the natural principles of evolution (i.e., variation and selection). The lack of need for prior genetic knowledge underlying the phenotypes of interest makes this a powerful approach for strain development for even species with minimal genotypic information (Cakar et al. 2012; Winkler and Kao 2014). Therefore, it is a complementary strategy that offers compelling scientific and applied advantages for strain development and process optimization.

With a more detailed and systematic understanding of microbial evolution, the manipulation of microbial communities can be applied to more complex problems. Whether the goal is to use microbial communities to produce desired materials, remedy environmental damage, or mitigate climate change, a comprehensive and predictive understanding of how microbial communities respond to change and stress in time is critical.

3 Challenges in the Study of Microbial Evolution

Despite their great relevance for the habitability of the planet and maintenance of our health, our understanding of the diversity, functioning, and evolution of microbial life is far from being complete.

This is partially due to our inability to bring microbial life into the lab for comprehensive and detailed investigations. In most cases, it is very challenging to successfully isolate individual microbes from their dynamic and complex environments and keep them functionally alive in a controlled setting. Even when isolation is possible, understanding how well the isolated members of microbial populations represent their environmental population is not necessarily always clear. Thankfully, in parallel to conventional approaches, we can use modern molecular and computational techniques to recover the genomic content of naturally occurring microbes directly from the environment and investigate some of the most fundamental aspects of their life and evolution.

Although tremendous progress has been achieved with the use of such advanced molecular techniques, the own complex nature of microbial systems imposes additional challenges for the study of microbial evolution. Microorganisms have several ways to generate far more dramatic and rapid genetic variation than plant and animals. They employ an impressive array of mechanisms to generate genetic variation, and this makes the study of their evolution a difficult task.

To tackle such challenging matter and discuss new insights on the molecular mechanisms of microbial evolution, some of the most distinguished team leaders in the field were invited to bring their interesting or provocative perspectives on topics of primary relevance for the theme. The outcome was a collection of 14 enlightening chapters that will drive you through the most interesting groundbreaking discoveries and emerging concepts on how microbes evolved and continue to evolve. The underlying goal of this volume was to span a range of topics and viewpoints to produce a timely and timeless work, one that would not become obsolete by the next generation of molecular data.

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