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## Soil bacterial community assembly during succession

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# Summary

Understanding how distinct factors drive microbial community assembly and dynamics is an important, yet poorly understood, topic in microbial ecology. Community assembly is mediated by an interplay of ecological processes shaping the structure of communities in different spatiotemporal scales, namely selection, dispersal, ecological drift and diversification. Evaluating patterns of microbial succession can inform on how distinct processes and mechanisms operate at various scales. Also, this can enable a link between community assembly and key aspects of ecosystem functioning. In natural forming ecosystems, microbes play major roles in colonizing newly formed habitats/niches, and then form successional sequences with the arrival and replacement of species over time. This occurs in a similar fashion, albeit at faster pace, as observed in successional trajectories of macro-organisms. Using a salt marsh chronosequence spanning over 100 years of primary succession as a model ecosystem (Schiermonnikoog, the Netherlands), I systematically examined the extent to which distinct community assembly processes operate and change in relative contributions overtime structuring soil bacterial communities. I set a particular focus on partitioning species abundances between the common and rare biospheres and provide novel conceptual and empirical knowledge on how distinct processes operate on governing their dynamics.

This thesis starts with an overview of relevant topics in **Chapter 1**. Here, I introduce novel developments on the understanding of environmental microbial communities, syntheses and theories on ecological processes controlling species coexistence and dynamics, as well as provide an overview of the microbial rare biosphere. Last, I outline the aim of this thesis and the research questions explored in details in each chapter.

**Chapter 2** provides a review of the general patterns of microbial community turnover during primary and secondary succession. It also provides an overview of how recent molecular technologies have been facilitating advances in this field of science. In brief, here I present a general introduction to the topic by arguing that microbial communities often develop from simplified to more complex structures with an increase of total biomass during primary succession. While there is less consistency during secondary succession, as historical contingency might determine the community responses to disturbance. Further, this chapter provides a review of previous studies at the island of Schiermonnikoog, which addressed how both micro- and macro-organism communities through a course of over 100 years primary succession change in terms of species composition, ecological traits and interactions of functional groups.

Microbial succession is mediated by shifts in community assembly processes. However, the quantification of the relative influence of these processes might be biased depending on whether DNA- or RNA-based sequencing approaches are used. To test this, in **Chapter 3**, bacterial communities were profiled by sequencing the 16S rRNA amplicons from environmental DNA and RNA transcripts extracted from soil

collected along five successional stages of ecosystem development at the island of Schiermonnikoog, using four sampling time points during the growth season (bimonthly sampling). Here I show that, in comparison with the DNA-based approach, the RNA-based approach revealed a higher temporal turnover of bacterial communities in both short-term (bimonthly) and long-term (over 100 years succession) community turnover. The community assembly based on RNA-inferred communities was more closely associated with variable selection driven by environmental heterogeneity, while results obtained from the DNA-inferred communities revealed a greater influence of homogeneous selection driven by the consistent environmental conditions. The discrepancy between these two approaches likely relates to different stabilities of extracellular RNA and DNA, and therefore their distinct time retained in the environment (e.g. extracellular relic DNA), and thus detected in our sequencing analyses. Overall, these results illustrate the need for benchmarking approaches to properly elucidate how community assembly processes structure microbial communities. It also highlights that caution is warranted in interpreting and comparing results using distinct sequencing strategies.

Similar to macro-organisms but perhaps with a steepest shape, species abundance curves of microbial communities present a skewed abundance distribution. This is characterized by the existence of a few abundant taxa and a long tail of less abundant taxa that often termed as ‘the rare biosphere’. Particularly in microbial ecology, little is known about the mechanisms mediating the assembly and persistence of the rare biosphere. In **Chapter 4**, I develop a synthesis that partitions the distinct types of rarity, i.e. permanently, conditionally and transiently rare taxa, and link their types with the distinct interplay of community assembly processes. In particular, I conceptually aligned our knowledge on community assembly (*sensu* Vellend, 2016), and the relative contribution of distinct eco-evolutionary processes — selection, dispersal, drift and diversification — with the structure and type of microbial rarity. In doing so, I provide a framework to empirically test this synthesis using null model analysis coupled with phylogenetic information.

In **Chapter 5**, I empirically evaluated the set of hypotheses developed in Chapter 4. I did this by using sequencing data on bacterial 16S rRNA transcripts presented in Chapter 3. The combination of empirical data with a mechanistic framework enabled examining the dynamics of the rare biosphere across both short (bimonthly) and long (succession over 100 years) temporal scales. Meanwhile, the five successional stages also serve as an environmental gradient across space, as the space-for-time replacement is used to represent the successional stages during the primary succession. In brief, I showed the rare biosphere assembly to be mostly driven by homogeneous selection, while the common biosphere — that consists of abundant species — is driven by a broader array of processes, in which variable selection plays a major role. I also showed that homogeneous selection explains the prevalence of permanently rare taxa, whereas variable selection explains the dynamic of conditionally rare taxa. Together, this chapter contributes empirical data to increase our understanding of how ecological processes structure the rare biosphere, and how rare microbes fluctuate over spatiotemporal scales and then form different types of rarity.

Dispersal is one of the simplest and most important processes influencing the assembly of soil bacterial communities in salt marshes. This occurs because early successional stages are daily subjected to the influence of the tides. In **Chapter 6**, I used a microcosm experiment to investigate the extent to which soil bacterial communities from different successional stages respond in terms of community difference to changes in inundation frequency. Here, artificial application of natural sea water was used to simulate four levels of inundation frequency, i.e. 2× per day, 1× per day, 1× per 3 days, and 1× per 7 days. Soils collected from early (0-year) and intermediate/late (70-year) successional stages were used. In addition, sterile sea water was used as a control to enable distinguishing between the influence of biotic (dispersal of microbial cells) and abiotic (chemical changes) factors in community responses. Soil bacterial communities were profiled by sequencing 16S rRNA genes at 6 time points in an experiment run for 20 days. In brief, I found no significant effect of the overall influence of inundation across the four levels of frequency tested at soils from both successional stages. In this study, sampling time is the most important factor driving the variation of bacterial communities. Both  $\alpha$ - and  $\beta$ -diversity of bacterial communities change systematically with time in the early stage soil, but are relatively stable in the late stages soil, which might link to the higher diversity, selection pressure and historical contingency in this stage. The higher temporal turnover of bacterial communities in the soil at the early stages is mostly governed by changes in members of the rare biosphere. This suggests rare microbes in the early successional stage of salt marsh are sensitive to inundation and can be vulnerable to accelerated sea-level rise. Furthermore, the difference between natural and sterile sea water treatments, even though not significant, suggesting the impact of inundation to soil bacterial communities mainly through changes of soil physicochemical conditions, but to a lesser extent through dispersal.

Last, In **Chapter 7**, I provide a synthesis of this thesis. Here, I discuss the outlook of this thesis with emphases on the general conclusions, current challenges and potential future directions in this field of research. I propose that future study designs can profit from the conceptual and empirical work provided here, in particular with respect to the dynamic processes structuring the soil rare biosphere. Advancing this field of science can also profit from testing this framework across distinct microbial community types, beyond the soil spectrum. This is important to provide data that corroborate, contradicts and expands the work I present here.