1. Introduction

# General introduction

What causes species diversity to vary among different places? Answers for this question can help sustain biodiversity and its stability, which has been a significant challenge under aggravating threat of species loss. In response, ecologists have devised a long list of theories to explain the maintenance of species diversity (Vellend, 2016). Community ecologists have expanded from the classic focus of species competition (e.g., Gause, 1934) to consider the effects of non-competitive interactions and multiple trophic levels (e.g., Chesson and Kuang, 2008, McCann, 2011, Bascompte and Jordano, 2013), thus better reflecting the complexity of natural systems. However, as multiple mechanisms operate simultaneously to shape species diversity (Amarasekare, 2007), developing a general predictive framework would be challenging if theories continue to be developed with little crosstalk.

Plants and their soil microbial communities represent one association where the players are engaged in complex interactions with consequences that are not fully explored. Plants interact with a wide variety of soil microbes, ranging from pathogenic to mutualistic microbes with various degrees of host specificity (Bever et al., 2010, van der Putten et al., 2013). Plants can also indirectly influence the performance of nearby competitors by modi- fying soil microbial communities, a phenomenon commonly studied under the framework of plant–soil feedback (Bever et al., 1997, Bever, 2003). Moreover, these plant–soil mi- crobe interactions are inherently age-dependent as it takes time for plants to condition the soil (Kardol et al., 2013a). Explicit consideration of the temporal dynamics of these interactions can have critical implications in both natural and agricultural systems, guiding plant restoration and agricultural practices (Kulmatiski et al., 2006, Mariotte et al., 2018). However, this aspect of plant–soil microbe interactions remains rarely studied.

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In this dissertation, I explore the complementarity of different frameworks for un- derstanding species coexistence and, with plant–soil microbe association as an example, highlight the multi-trophic and age-dependent nature of ecological communities.

# Overview

I start by exploring the theoretical and empirical relationships among contemporary niche theory and modern coexistence theory, which are two powerful frameworks for under- standing the niche’s role in species coexistence (Chesson, 2000b, Chase and Leibold, 2003). Contemporary niche theory provides a mechanistic understanding of how the resource supply ratio and trade-offs in the impact and requirement niches of competing species affect their coexistence; modern coexistence theory formularize coexistence as the balance between equalizing (i.e., lower fitness differences) and stabilizing (i.e., greater niche differ- ences) processes. In Chapter 2, I ask how the criteria for coexistence under contemporary niche theory translate into the stabilizing and equalizing processes of modern coexistence theory. I show that varying resource supply ratios reflect an equalizing process; varying impact niche overlap reflects a stabilizing process; varying requirement niche overlap may be both stabilizing and equalizing, but has no qualitative effect on coexistence. In Chapter 3, I extend the approach developed in Chapter 2 to discuss how priority effects, the phe- nomenon that species arrival order affects competitive outcomes (Fukami, 2015), fit within the stabilizing and equalizing concepts of modern coexistence theory. I argue that the only compatible priority effects are those characterized by positive frequency dependence, irrespective of whether they emerge in equilibrium or non-equilibrium systems. By explor- ing the connections among different frameworks of species coexistence, the two chapters together lay a foundation for further conceptual advances to incorporate more complicated interactions.

In Chapter 4, I ask how the interactions between plants and soil microbes influence plant coexistence. It is known that systems vary in the impacts microbes have on plants and in the ways plants compete with each other, rendering a general predictive theory difficult (Lekberg et al., 2018). Building on the previous two chapters, I argue that the concepts of niche and fitness difference from modern coexistence theory should be used to contextualize how soil microbes contribute to plant coexistence (Ke and Miki, 2015). With a general plant–soil microbe interaction model, I show that, depending on host-specificity, both pathogens and mutualists can affect the niche difference between competing plants. Moreover, soil microbes can affect plant fitness differences and modify the importance of plant–plant competition for determining plant coexistence, a role that is often overlooked by the literature. I then propose experimental designs that can efficiently measure both plant– soil microbe and plant–plant interactions. With an empirical case study, I demonstrate how the proposed predictive framework can provide a better way to identify the actual processes through which soil microbes affect plant coexistence.

In Chapter 5 and 6, I focus on the temporal development of plant–soil microbe interactions at Bodega Bay, a coastal foredune community dominated by four perennial species: the introduced grass *Ammophila arenaria* (Poaceae), the introduced succulent dwarf- shrub *Carpobrotus edulis* (Aizoaceae), and the native shrubs *Baccharis pilularis* (Asteraceae) and *Lupinus arboreus* (Fabaceae). I use a series of high-resolution aerial photos, which were taken annually from 1992 to 2016, to estimate the age of individual plants (Danin et al., 1998). From the age estimations, I reconstruct a chronosequence of soil conditioning length, ranging between 1 to 11 years for *L. arboreus* and between 2 to 25 years for the other three species. In Chapter 5, I examine the successional dynamics of soil fungal communities associated with *C. edulis* and *L. arboreus*. By collecting soil from plant individuals along the chronosequence, and re-sampling a subset of individuals for three consecutive years, I test the hypothesis that a deterministic force is structuring fungal communities and drives

their convergence (Connell and Slatyer, 1977, Dini-Andreote et al., 2015, Li et al., 2016). I show that the beta diversity among fungal communities decreased and our ability to predict the fungal community composition increased as plants aged. I argue that the combination of chronosequence and longitudinal data strengthened the inference of an underlying deterministic process shaping soil fungal communities.

Despite our growing knowledge on the successional dynamics of soil microbes, how their effects on plants vary with conditioning time remains rarely studied (Kardol et al., 2013a, Lepinay et al., 2018). This is presumably because preparing soils with different con- ditioning lengths is often not feasible in the greenhouse (Kardol et al., 2013a, Kulmatiski, 2018), and the length of soil conditioning in the field can only be quantified with coarse res- olution (e.g., Day et al., 2015, Speek et al., 2015). Taking advantage of the chronosequence, in Chapter 6, I study the turnover of soil microbial communities associated with all four dominant plants at Bodega Bay. I then design a greenhouse experiment that preserved age- specific microbial communities to study how their turnover affected plant performance. I show that compositional turnovers of soil microbes translated into temporally varying plant–soil microbe interactions, and different plant–soil combinations showed different temporal development patterns. Using a general individual-based model (Fukami and Nakajima, 2013), I further show that the temporal development patterns of microbial ef- fects alters the transient dynamics of plant community assembly. With the combination of high-throughput sequencing, greenhouse experiment, and simulation models, Chapter 5 and 6 together develop a dynamic perspective of plant–soil feedback to understand their long-term consequences on plant community dynamics.

# Overall conclusion and future perspectives

Two common themes emerge from this dissertation. First, mechanisms that maintain species diversity often operate simultaneously and are tightly coupled (Amarasekare, 2007, Letten et al., 2018). For example, plants are engaged in plant–plant and plant–soil microbe interactions at the same time, and the strength of one process affects the relative importance of the other (Chapter 4). To study how multiple mechanisms interactively determine species coexistence, I contextualize the effects of different mechanisms with higher-level processes proposed in general coexistence theories (see also Vellend, 2016). In particular, I show how differences in resource consumption traits (Chapter 2 and 3) and microbial traits (Chapter

4) translate to niche and fitness differences of modern coexistence theory, and how the two components can be used as a common currency for understanding coexistence. As the list of theories explaining the maintenance of species diversity continues to increase, this approach provides a route to synthesize the overall effects of different trophic levels and interaction types (Bartomeus and Godoy, 2018, Lanuza et al., 2018).

Another common theme among the chapters is that the strength of species interac- tions are not constant: they vary depending on the arrival order of species (Chapter 3 and 4; Fukami, 2015, Duhamel et al., 2019), the timing of the interaction, and the age-/stage- structure within the species’ population (Chapter 5 and 6; Kardol et al., 2013b, Peay, 2018). Using plant–soil microbe interactions as an example, I show that the microbial community structure (Chapter 5) and their effects on plant performance (Chapter 6) vary with the dura- tion of soil conditioning, and the temporal development patterns of these interactions have a strong effect on community dynamics. The fact that interaction strengths are time- and age-dependent is not unique to plant–soil interactions but a general phenomenon that ap- plies to almost all multi-cellular organisms (Miller and Rudolf, 2011, de Roos and Persson,

2013, Nakazawa, 2015). In some cases, not only the strength but also the type of species in- teractions change as individuals mature (Yang and Rudolf, 2010, Ke and Nakazawa, 2018). Overall, my results highlight the temporal complexity of ecological communities and call for more understanding on how species’ interactions are coordinated in time.

My future work continues to explore the temporal dimensions of species interactions. Moving forward, I aim to study how ecological processes with different dynamical rates interactively affect community stability. When studying the effects of multi-trophic inter- actions on species coexistence, theories often assume that non-focal trophic levels change with rates much faster than the focal community (e.g., Chesson, 2008; see also Chapter 4). However, species turnover and ecological processes can vary significantly in their dynami- cal rates (Rinaldi and Scheffer, 2000, Menge et al., 2012, Li and Chesson, 2016). Consider the belowground interactions among plants as an example, soil microbial succession can occur at various timescales, sometimes even persisting long after their host plant dies. Moreover, while plant–plant competition for nutrient uptake may be a fast process, nutrient release from plant litter can be extremely slow (Menge et al., 2008). By combining empirical and theoretical approaches, like that done in this dissertation, I hope to open new avenues to develop a temporally-explicit perspective of community ecology.

# Author Contributions

Throughout my dissertation, I worked closely with many collaborators whose contributions are detailed below. These collaborators are listed as co-authors on the peer-reviewed manuscripts (or manuscripts in preparation) corresponding to each of my dissertation chapters.

## Chapter 2 – Linking modern coexistence theory and contemporary niche theory

Andrew Letten and Tadashi Fukami worked with me to develop the ideas for the research. I designed the simulation and performed the mathematical analysis. All authors contributed to the writing and revision of the manuscript. Funding supporting this work came from the Center for Computational, Evolutionary, and Human Genomics (CEHG), the Department of Biology and the Terman Fellowship of Stanford University, and the National Science Foundation (NSF). The research has been published as a peer-reviewed manuscript in *Ecological Monographs*.

**Chapter 3 – Coexistence theory and the frequency-dependence of priority effects** Andrew Letten worked with me to design the research, assisted in numerical analyses, and contributed to manuscript writing and revision. Funding supporting this work came from the Center for Computational, Evolutionary, and Human Genomics (CEHG), the Department of Biology of Stanford University, and the Studying Abroad Scholarship from the Ministry of Education, Taiwan. The research has been published as a peer-reviewed manuscript in *Nature Ecology & Evolution*.

## Chapter 4 – Effects of soil microbes on plant competition: a perspective from modern coexistence theory

Joe Wan worked with me to develop the research and formulate the analysis. He also worked with me on manuscript preparation and revision. Funding supporting this work came from the Department of Biology of Stanford University and the Studying Abroad Scholarship from the Ministry of Education, Taiwan. The research is under peer-review at *Ecological Monographs*.

## Chapter 5 – Testing chronosequence predictions with longitudinal data reveals microbial community convergence

Tadashi Fukami worked with me to design the research. Tadashi Fukami and J. Nick

Hendershot assisted in data analysis and manuscript preparation. Funding supporting this work came from the Department of Biology and the Terman Fellowship of Stanford University, the National Science Foundation (NSF), and the Studying Abroad Scholarship from the Ministry of Education, Taiwan.

## Chapter 6 – Dynamic plant–soil microbe interactions: the neglected effect of soil condi- tioning time

Tadashi Fukami worked with me to design the research and assisted in the analyzing the empirical data. Peter Zee helped me develop the individual-based model and performed numerical simulations. Tadashi Fukami and Peter Zee contributed to manuscript prepara- tion and revision. Funding supporting this work came from the Department of Biology and the Terman Fellowship of Stanford University, and the National Science Foundation (NSF), and the Studying Abroad Scholarship from the Ministry of Education, Taiwan.